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Transactions of the
SYMPOSIUM ON THE BIOLOGICAL RESOURCES
OF THE CHIHUAHUAN DESERT REGION
United States and Mexico

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**Transactions of the
SYMPOSIUM ON THE BIOLOGICAL RESOURCES
OF THE CHIHUAHUAN DESERT REGION
United States and Mexico**

Sul Ross State University
Alpine, Texas
17-18 October 1974

Edited by
Roland H. Wauer
David H. Riskind

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering the wisest use of our land and water resources, protecting our fish and wildlife, preserving the environmental and cultural values of our national parks and historical places, and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to assure that their development is in the best interests of all our people. The Department also has a major responsibility for American Indian reservation communities and for people who live in Island Territories under U.S. administration.

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Foreword

The Chihuahuan Desert region, including the numerous isolated mountain ranges, has an incredibly diverse physiography. It is also the least-known desert region of North America. With the exception of a few major population centers, such as Chihuahua City, El Paso, Albuquerque, Juarez, Durango, Torreon, Monclova, and Saltillo, the region is sparsely populated; yet little of the desert is uninhabited. In the past, the sparse population of this vast region has been a blessing in preserving the desert's biological and aesthetic resources. More recently, population expansion and resultant demands upon the resources have initiated changes that threaten every part of the Chihuahuan Desert region.

After the Mexican Revolution, the Mexican Government embarked upon a widespread land reform policy. In the Chihuahuan Desert this has meant, especially in recent years, a redistribution of population from the densely populated Central Valley of Mexico into the sparsely populated arid lands of northern Mexico. The resultant government-subsidized communal settlements, or *ejidos*, have markedly affected the delicate and easily disturbed desert ecosystem. While on the one hand the Mexican government must be commended for attempting to ameliorate the plight of the *campesinos*, concern must be voiced for the resource base which will sustain the *ejidos* now and in the future. Although the immediate concern is the short-term solution of human problems, we, as biologists, educators, and politicians must realize that the long-term biological integrity of the resource base, the physical, chemical, and biological resources, is the prime issue.

Mexico is not alone with its problems of human coexistence with the biological resource base. For both Mexico and the United States, arid lands constitute new frontiers for exploitation. While exploitation of these arid lands progresses relentlessly every day, the biological resources have been only cursorily surveyed and are as yet minimally understood. Conversely, the resources which may have immediate bearing upon the economy of the area have been and are being studied in detail. Such resources as water, pasturage, fiber plants, oil, gas, uranium, lignite, barite, fluor spar, timber, and game animals have been surveyed and currently are being assessed. But what of the other economically significant, though less well known resources? What of unique habitats, communities, or ecosystems? That, in essence, is the basis for this Symposium. Such resources must be assessed and evaluated before it is too late. Sadly it is very nearly too late in some instances!

Several salient examples should serve to add substance to our contention. As early as 1935, biologists, government officials, businessmen, and politicians realized the outstanding resources of the Sierra del Carmens of Coahuila, Mexico, located opposite what was to become Big Bend National Park in Texas. The concept of a joint U.S.-Mexican park was a burning issue. Ernest G. Marsh, Jr., was commissioned by the United States National Park Service to survey the del Carmen and Santa Rosa mountains in Mexico in order to assess and evaluate the region's resources. As was expected, the resources were outstanding. Talk of an International or Companion Park persisted; new and significant biological disclosures continued to be made and reported. Today, four decades later, Mexican officials are still considering some type of preserve for that area. In the meantime, the heavily forested slopes in the Maderas del Carmen were cut during the late 1940s and into the 1950s, and the area's faunal resources suffered severely. What had been a virgin, extensive mixed-conifer forest in the 1930s is today but a remnant of its former state. Biological losses, to say nothing of the aesthetic tragedy, are perhaps incalculable.

The Cuatro Ciénegas Basin was discovered, in a biological sense, by Ernest Marsh in 1939. Since that time the Cuatro Ciénegas Basin has been the site of extensive study, with the result that the Basin now is described as one of the outstanding natural resources of the Western Hemisphere. In spite of extensive biological reconnaissance and research, the Basin is incompletely known. Recent cultural developments have significantly affected the natural resources of the area. Irrigation canals have changed the aquatic and subaquatic environments to the extent that it is difficult even to reconstruct natural drainage patterns. Human impact in the Basin has been extensive, yet scientists have only begun to understand the remarkable and unique biological resources of the area. Possibilities for biological research on natural ecosystems in the Cuatro Ciénegas Basin become dimmer with the passing of each day.

Sadly, such biologically destructive events as those previously mentioned continue to occur in kind if not in degree. Human population in the Chihuahuan Desert continues to increase and the natural resources continue to be assaulted.

Roads which once were unimproved now are paved. Resources once hardly accessible now are reached and exploited easily. Unique and beautiful parts of the Chihuahuan Desert region are being abused. Mineral exploitation into new, previously inaccessible regions has opened vast areas to hunting and grazing pressures. Increased population pressure continues to have profound impact on the remnant grasslands and the aquatic and relict forest ecosystems.

In the past, the plight of Mexico's natural resources has been eloquently stated by a number of eminent biologists—Zinser, Beltran, Villa, Leopold—to mention but a few. It would appear that a conservation ethic has, to a degree, taken hold in Mexico. More important, academic institutions and government agencies recently have taken active conservation roles. However, much of the concern for conservation apparently has been focused on the tropical ecosystems in southern Mexico. Of course, this reflects the global concern, or perhaps preoccupation,

with tropical resources but it also reflects pragmatism—population centers of Mexico are located in close proximity to the tropical zone.

Now is not the time to be petty and possessive about this or that resource. Regardless of geography or politics, a deep-rooted understanding of biological systems is one key which may assist us in the wise and prudent utilization of an area's resources. What is needed is a balanced, objective appraisal of natural resources. We must strive to assess our natural heritage, in this case a biological resource which transcends an international or political boundary, and act responsibly and with great conviction. The organization of this Symposium on the Biological Resources of the Chihuahuan Desert Region, United States and Mexico, is the embodiment of a growing concern and at the same time a vehicle deemed appropriate to focus attention on the vast and little known resources of the Chihuahuan Desert region.

We have focused attention on those desert resources which lie in Mexico. To us the reason is obvious, but perhaps should be explained for increased clarity. The most important reason is that the majority of the Chihuahuan Desert is in Mexico. Additionally, we must take note that the United States has included representative portions of the Chihuahuan Desert in a number of Federal and State preserves. (Mexico has as yet designated very few preserves in her portion of the Chihuahuan Desert.) Most persons would agree that significant portions of the desert region are unprotected. While it is true that much of the desert in the United States still is threatened, Mexico has the most to lose. We therefore feel our emphasis on Mexico is in keeping with contemporary circumstances.

Sul Ross State University in Alpine, Texas, was chosen as the site for this Symposium. Alpine is logistically more suitable than most of the appropriate localities in Mexico, and is the gateway to the most significant biological preserve in the Chihuahuan Desert—Big Bend National Park and the adjacent Texas Parks and Wildlife Department's Black Gap Wildlife Management Area.

The subject matter of the Symposium was designed to provide a broad factual background for persons interested in the biological resources of the Chihuahuan Desert region. At the same time it was our intention to provide a forum wherein investigators from the various biological disciplines could acquaint themselves with the diversity of research underway in the region. The general nature of most of the presentations reflects the status of our knowledge today. However, we feel that the contents of this symposium are sufficient in depth and in scope to enable policymakers in the United States as well as in Mexico to make more intelligent decisions with regard to the conservation and exploitation of natural resources within the Chihuahuan Desert region.

Throughout the papers runs a recurring theme—that man constitutes an immediate threat to the poorly understood Chihuahuan Desert resources. It is man who changes the productive grasslands to desert scrub, who changes the forests to chaparral, or worse, who severely assaults the fragile desert water resources. At the same time, most would agree that if the region's resources are to be conserved, man is the salvation. It is our hope that perhaps this Symposium is

the beginning of that resource salvation; but unless strong, well directed measures are implemented at once on both sides of the border there will be little to conserve. Even the most remote mountain ranges do not escape the ever-present grazing and browsing stock of the *campesino* or rancher. Industry-related development and, to a lesser extent, land development extends into every corner of the region. Vast distances and isolation alone offer no guarantee of resource conservation in the Chihuahuan Desert.

It is unfortunate that most of the inhabitants of the Chihuahuan Desert region will never know the substance of this Symposium. Most of what has been said herein has little, if any, immediate relevance to most who dwell in the desert. Yet nothing could be more important to the desert's inhabitants and the welfare of the land than long-term, sustained productivity. For the most part, politicians must ultimately conserve the desert. We, as scientists and educators, can assist only with our understanding and knowledge of the land and its finite resources.

Finally, we would like to extend our sincere appreciation and thanks to our respective sponsoring agencies, the Southwest Region of the National Park Service and the Texas Parks and Wildlife Department, who have made this Symposium possible, and to Sul Ross State University and the city of Alpine for graciously hosting the conference. Naturally, there are many individuals whose efforts have materially contributed to the success of this Symposium and we extend our collective, grateful appreciation.

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Introduction

RO WAUER

David Riskind and I are very proud that this symposium is a reality. We hope that what we do here during the next 3 days will result in the initiation of more positive goals and actions to preserve resources within the Chihuahuan Desert system for our children and our children's children.

Every meeting of this kind must have a mentor or a host. The Symposium on the Biological Resources of the Chihuahuan Desert Region is no exception. Sul Ross State University has accepted that role, and I believe that its people have done an admirable job preparing for this meeting. No other institution can claim the privilege of a location such as can Sul Ross—the heart of the northern Chihuahuan Desert. The leader of the Sul Ross team is its President, Dr. Hugh Meredith. This new and enthusiastic President is a Southwesterner. A native of Muskogee, Oklahoma, Dr. Meredith received his academic training within the Southwest: at Texas Christian University, Oklahoma Baptist University, Southwest Baptist Theological Seminary, and the University of Texas at Austin.

Dr. Meredith only minored in biology, but already has begun to see the importance of a significant biology program at Sul Ross. This symposium will deepen his enthusiasm and create new horizons, not only for Sul Ross but for the advancement of knowledge of the Chihuahuan Desert. I introduce to you a man who has the personality, the drive and a wide range of experience ranging from academic circles to the Peace Corps to fulfill that promise. Our host for the next 3 days, President of this institution, Dr. Hugh Meredith.

Welcome

HUGH MEREDITH, President, Sul Ross State University

It is my pleasure, on behalf of the faculty, the students, and the Administration of Sul Ross, to welcome you to our campus. In particular, it is a delight to me to welcome especially our guests from Mexico, who will be participating in the Symposium program. Also, a number of ex-students from this University are here whom we welcome. One or two will be on the program. It is a distinct honor for Sul Ross and the community of Alpine that the Symposium is being presented here. We are grateful to the National Park Service and the Texas Parks and Wildlife Commission for focusing attention through this Chihuahuan Desert Symposium on the uniqueness of this area. The Symposium itself is a manifestation that scientists all over North America do recognize and appreciate what we observe daily here in our own front yard, this Chihuahuan Desert. We hope that you who visit here will find it intellectually stimulating, physically invigorating, and socially satisfying.

We hope that you enjoy yourself. If you rise early—breathe the clean, fresh, unsaturated, smogless air through which you can see without squinting. Welcome to the north rim of the Chihuahuan Desert.

This area of the southwest United States and Northern Mexico is perhaps one of the richest areas in the Western Hemisphere in natural scientific resources. Botanists, paleoenvironmentalists, mammalogists, ichthyologists, herpetologists, ornithologists, geologists, zoologists, paleoecologists, geoscientists, statisticians, ecologists, geneticists, simple local florists and even, along with my wife, bird watchers, all find themselves requiring a thesaurus of unlimited proportions to describe this land which by many neophytes and by the myopic is sometimes called a wasteland. With the scholar, the poet, the artist, the scientist, the musician, one must say, as Goethe did when he took his knife and carved in one of the great door beams “Wen Gott lieb hat, erlaubt er herzukommen.” (He was on an outing with Carl August of Weimar in his hunting lodge in Bavaria and realized he was in one of the most beautiful and glorious mountain regions of Southern Europe.)

“Those whom God loves, he permits to come here.”

So we hope that your experiences here as a scientist and ecologist and humanitarian will do the same for you. The person who comes to this region for his first visit must face it as a college freshman, initially encountering Shake-

speare's *Hamlet*, *Richard II*, or *As You Like It*. You must remember that it is not the renowned Shakespeare who is on trial, but the freshman himself. He must find the genius therein. So here it is—only he who sees clearly, distinctly, and intensely will find the treasures that can go inadvertently unnoticed.

Dr. Barton H. Warnock, Director of the Division of Science, Chairman of the Biology Department, has spent 28 years on the faculty of Sul Ross State University. He came here directly on completing his doctorate in botany at the University of Texas in 1946. He is well known as a botanist, specializing in plants of west Texas and particularly in plants of the Big Bend region, with several significant publications on this area including the exceptionally well-done *Wildflowers of the Big Bend Country* that was issued in 1970.

Last Saturday he took me and five other faculty members from Sul Ross (a geologist, a social scientist, two chemists, and the Director of Physical Plant Operations) to the Big Bend country. For some 8 hours we received a grand botanical tour of the Big Bend Park. As we drove along or stopped or hiked, he pointed out the lechuguilla, sotol, ocotillo, Spanish dagger, giant dagger, creosotebush, tar bush, ephedra, and century plant in bloom; the candelilla, golden eye, sage, huisache, windmill wheel, yellow trumpet, alligator juniper, Apache plume, madrone, and on and on.

However, Dr. Warnock has become engrossed in this Chihuahuan Desert and he would not let us get away from it. As we entered the Lodge Restaurant in the park, we were following a group of young ladies clad in very short skirts. As the door of the restaurant opened, a strong gust of wind played havoc with those skirts. Dr. Warnock was heard to whisper a very excited exclamation, "Chihuahua."

Impressions of the Chihuahuan Desert Plant Life

BARTON H. WARNOCK

Recently, it was my pleasure to take a group from Sul Ross State University to the Big Bend National Park and give them my impressions of the plant life in the Chihuahuan Desert. Dr. Hugh Meredith, President of Sul Ross, was one of the members and as you can tell was most interested in the desert. He learned quite a few of the common members of our desert.

This is a homecoming for me to see so many of my former students and colleagues, and it is my 40th anniversary in the Chihuahuan Desert. That is longer than most of you have lived. The years I have spent working in the Chihuahuan Desert while teaching full time at Sul Ross have been difficult but always interesting. Difficult because of the conditions under which I have had to work in the desert, interesting because I find the plant life such a challenge. My work has been limited to the U.S. side of the Rio Grande, and I left the largest part which lies in Mexico for those with more time and money available.

The Chihuahuan Desert in Texas and southern New Mexico is some seven or eight times smaller than it is in Mexico. The desert enters Texas primarily along two routes. The largest area includes the Rio Grande drainage system from the vicinity of Del Rio and continues to approximately Albuquerque, New Mexico. The alternate route is from the mouth of the Pecos River to approximately Roswell, New Mexico. The plants of this desert occur primarily on soils of calcareous origin. I like to think of the Chihuahuan Desert in Texas as a young desert because of the abundance of grassland that is still present after the invasion of the key indicator plants of the desert, namely creosotebush, *Larrea tridentata*; tarbush, *Flourensia cernua*; and mesquite, *Prosopis glandulosa*.

A large portion of the Trans-Pecos is not usually considered Chihuahuan Desert. This area is most of the land above 4000-4500 ft elevation, including much of the following mountain ranges: Guadalupe, Davis, Chisos, Chinati, Eagle, Franklin, Sierra Diablo, Quitman, Van Horn, Baylor, Beech, Delaware, and Apache. Much of the intermountain valleys of these ranges support some of

the best grama grasses in Texas, especially above 4000 ft elevation. The members of these short grass communities extend from Canada to Mexico on the eastern slopes of the Rocky Mountains and the Sierra Madre in Mexico. In addition to the grassland we have a woodland that is well represented in the three highest ranges (Guadalupe, Davis, and Chisos mountains) by several species of oak, *Quercus* spp.; juniper, *Juniperus* spp. (commonly known as cedars over much of Texas); and the pinyon pines, *Pinus* spp. Most of the woodland lies above 5000 ft elevation. The Guadalupe, Davis, and Chisos mountains support remnants of an early forest including *Pinus ponderosa*; big tooth maple, *Acer grandidentatum*; and quaking aspen, *Populus tremuloides*. Douglas fir, *Pseudotsuga Menziesii*, occurs in the Guadalupe and Chisos Mountains but not in the Davis Mountains, while timber pine, *Pinus strobiformis*, occurs in the Guadalupe and Davis mountains but not in the Chisos Mountains. Arizona cypress, *Cupressus arizonica*, occurs only in the Chisos Mountains of the Big Bend National Park.

The area in the Trans-Pecos where the Chihuahuan Desert appears to reach its greatest development is in the Big Bend National Park surrounding the Chisos Mountains, and in the Toyah Basin, surrounded by Fort Stockton, Grandfalls, Pecos and Balmorhea.

The principal dominant plants of the Chihuahuan Desert in Texas consist of creosotebush, *Larrea tridentata*; tar bush (or black brush as it is called locally by ranchers in the Fort Stockton area), *Flourensia cernua*; and several forms of mesquite *Prosopis glandulosa*. Associated with these shrubs are several kinds of desert grass. These desert grasses consist primarily of tobosa grass, *Hilaria mutica*; burro grass, *Scleropogon brevifolius*; Bigelow desert-grass, *Blepharidachne Bigelowii* which occurs primarily on caliche soils of Brewster, Culberson, El Paso, and Pecos counties; ear muhly, *Muhlenbergia arenaceca*; bush muhly, *Muhlenbergia Porteri*; and several species of *Tridens* including *Erioneuron*. It appears to me that these desert short grasses occupied thousands of acres in the Trans-Pecos for many years and probably were kept in control by frequent fire burns that were caused by natural factors and by Indians. An excellent place to observe the invasion of the Chihuahuan Desert into this grassland is in the vicinity of Roswell, New Mexico. With the increase of livestock in New Mexico and Texas all grasses were utilized too heavily and the result was more and more brush. In the Big Bend country of Texas, one of the increasers associated with the loss of grass of any kind is the ocotillo-blind prickly pear, *Fouquieria splendens*—*Opuntia rufida* association now observed on the gravelly outwash soils so abundant in Panther Junction and Boquillas of the Big Bend National Park. Another very important association in the Big Bend National Park is chino grama-lechuguilla, *Bouteloua ramosa*—*Agave lecheguilla*, which covers many of the gravelly rolling hills surrounding the Chisos Mountains but is observed more easily on the low hills of the north and eastern portion of the park. Another unique association is the false agave—lechuguilla—candelilla, *Hechtia scariosa*—*Agave lecheguilla*—*Euphorbia antisiphilitica*, located on the hills near the tunnel in the Big Bend National Park. There are too many plant

associations in the park and elsewhere in the Trans-Pecos to enumerate at this time, but many of the papers in this Symposium will go into more detail about those that are recognized by competent researchers. Many of the associations exist primarily because of such factors as gradient, temperature, precipitation, and soil.

At elevations where the Chihuahuan Desert associations have not invaded our grassland, and this is primarily above 4000 ft, we have represented 11 species of grama grass, *Bouteloua* spp., many species of muhly grasses, *Muhlenbergia* spp., and three-awns, *Aristida* spp. The best areas to observe this great grassland are in the vicinity of Alpine, Fort Davis, and Marfa of the Davis Mountains. I recommend to you the beautiful Davis Mountains scenic drive where you will see our woodland formation well represented with alligator juniper, *Juniperus deppeana*. A unique member of the woodland formation in the Chisos Mountains is represented by the drooping juniper, *Juniperus flaccida*. This handsome tree is known in the United States only from the Chisos Mountains. I certainly hope that those of you who have not been to the Big Bend National Park will make that trip on Saturday. The sculptured, eroded Tornillo Flats are presently covered with a low annual herb known as dogweed, *Dyssodia aurea* var. *polychaeta*. Creosotebush, candelilla, members of the four o'clock family, spurges by the millions, and an occasional *Yucca Torreyi* are in flower now. This late flowering period was the result of the 11 inches or more of rain that we had a few weeks ago.

If you had the time to climb the Chisos, Davis, or Guadalupe peaks, you would still find that it is almost like spring at these high elevations, especially in the Chisos Mountains where we have not had as much cool weather. About 15 September is usually the most beautiful time to see wildflowers on these high peaks.

My good friends Drs. Billie Turner and Michael Powell will tell you about our most interesting gypsum soil plants. Just recently I visited the north side of the Guadalupe Mountains National Park with my friend Tony Burgess and Mr. Green. We saw one of the tallest outcrops of gypsum I have seen in the Trans-Pecos. Several hills were composed almost entirely of gyp soil. In places where sand had drifted into pockets on these hills we found several large Indian camp sites with bits of painted pottery that caused us to stop and reflect upon the past. Yeso grama or gyp grama, *Bouteloua breviseta*, is abundant on these hills, and I imagine it would be called climax. Our characteristic indicator plant, *Coldenia hispidissima*, is abundant as usual on these gypsum hills.

We are so happy that you are here, and I know that we are going to have many interesting reports concerning the biological resources of the Chihuahuan Desert region of the United States and Mexico; and we are especially happy to have our Mexican friends from across the Rio Grande.

Contents

| | |
|---|------|
| <i>Foreword</i> | iii |
| <i>Participants</i> | vii |
| <i>Introduction</i> —ROLAND H. WAUER | xi |
| <i>Welcome</i> —HUGH MEREDITH | xiii |
| <i>Introduction: Impressions of the Chihuahuan Desert Plant Life</i> — BARTON H. WARNOCK | xv |

SESSION I: QUATERNARY ENVIRONMENT

| | |
|---|-----|
| LATE QUATERNARY POLLEN RECORDS FROM THE EAST-CENTRAL PERIPHERY OF THE CHIHUAHUAN DESERT Vaughn M. Bryant, Jr. | 3 |
| WISCONSIN AGE ENVIRONMENTS IN THE NORTHERN CHIHUAHUAN DESERT: EVIDENCE FROM THE HIGHER VERTEBRATES <i>Arthur H. Harris</i> | 23 |
| SOME QUATERNARY MOLLUSCAN FAUNAS FROM THE NORTHERN CHIHUAHUAN DESERT AND THEIR PALEOECOLOGICAL IMPLICATIONS <i>Artie L. Metcalf</i> | 53 |
| POST-GLACIAL ORIGIN OF THE PRESENT CHIHUAHUAN DESERT LESS THAN 11,500 YEARS AGO <i>Philip V. Wells</i> | 67 |
| THE HERPETOFAUNA OF HOWELL'S RIDGE CAVE AND THE PALEOECOLOGY OF THE NORTHWESTERN CHIHUAHUAN DESERT <i>Thomas R. Van Devender and Richard D. Worthington</i> | 85 |
| LATE PLEISTOCENE BIOTIC COMMUNITIES FROM THE GUADALUPE MOUNTAINS, CULBERSON COUNTY, TEXAS <i>Thomas R. Van Devender, Paul S. Martin, Arthur M. Phillips III, and W. Geoffrey Spaulding</i> | 107 |
| A RECONNAISSANCE SURVEY OF POLLEN RAIN IN BIG BEND NATIONAL PARK, TEXAS: MODERN CONTROL FOR A PALEOENVIRONMENTAL STUDY <i>Edward R. Meyer</i> | 115 |

SESSION II: MAMMALOGY

| | |
|---|-----|
| THE STATUS OF MAMMALS IN THE NORTHERN REGION OF THE CHIHUAHUAN DESERT <i>James S. Findley and William Caire</i> | 127 |
| MAMMALS OF THE SOUTHERN CHIHUAHUAN DESERT: AN INVENTORY <i>Robert L. Packard</i> | 141 |
| MAJOR GAME MAMMALS AND THEIR HABITATS IN THE CHIHUAHUAN DESERT REGION <i>Bernardo Villa Ramirez</i> | 155 |
| FACTORS GOVERNING THE DISTRIBUTION OF MAMMALS IN THE CHIHUAHUAN DESERT REGION <i>David J. Schmidly</i> | 163 |
| REPRODUCTIVE STRATEGIES IN DESERT RODENTS <i>Walt Conley, James D. Nichols, and Alan R. Tipton</i> | 193 |
| PAST, PRESENT AND FUTURE STATUS OF THE DESERT BIGHORN IN THE CHIHUAHUAN DESERT REGION <i>Tommy L. Hailey</i> | 217 |
| MAMMALS OF THE CHIHUAHUAN DESERT REGION—FUTURE PROSPECTS <i>Rollin H. Baker</i> | 221 |

SESSION III: BOTANY

| | |
|---|-----|
| DESERT VEGETATION IN THE GUADALUPE MOUNTAINS REGION <i>Tony L. Burgess and David K. Northington</i> | 229 |
| THE NATURAL PRODUCTS CHEMISTRY OF <i>LARREA TRIDENTATA</i> CAV. IN THE CHIHUAHUAN DESERT <i>Tom J. Mabry, Masayuki Sakakibara, Charles Bohnstedt and Dan DiFeo, Jr.</i> | 243 |
| A PHYSIOGNOMIC ANALYSIS OF THE TYPES OF TRANSITIONAL VEGETATION ON THE EASTERN PARTS OF THE CHIHUAHUAN DESERT IN COAHUILA, MEXICO <i>Jorge S. Marroquín</i> | 249 |
| ASPECTS OF REPRODUCTION IN CHIHUAHUAN DESERT NYCTAGINACEAE <i>Richard Spellenberg and Rebecca K. Delson</i> | 273 |
| SALINE HABITATS AND HALOPHYTIC VEGETATION OF THE CHIHUAHUAN DESERT REGION <i>James Henrickson</i> | 289 |
| ASPECTS OF THE PLANT BIOLOGY OF THE GYPSUM OUTCROPS OF THE CHIHUAHUAN DESERT <i>A. Michael Powell and B. L. Turner</i> | 315 |

| | |
|---|-----|
| VEGETATION AND FLORA OF THE CUATRO CIENEGAS BASIN, COAHUILA, MEXICO | |
| <i>Donald J. Pinkava</i> | 327 |
| BRIEF RESUME OF BOTANICAL, INCLUDING VEGETATIONAL, FEATURES OF THE CHIHUAHUAN DESERT REGION WITH SPECIAL EMPHASIS ON THEIR UNIQUENESS | |
| <i>Marshall C. Johnston</i> | 335 |

SESSION IV: ICHTHYOFAUNA

| | |
|--|-----|
| INTRODUCTION | |
| <i>Clark Hubbs</i> | 363 |
| COMPOSITION AND DERIVATION OF THE NATIVE FISH FAUNA OF THE CHIHUAHUAN DESERT REGION | |
| <i>Robert Rush Miller</i> | 365 |
| ENDEMIC FISHES OF THE CUATRO CIÉNEGAS BASIN, NORTHERN COAHUILA, MEXICO | |
| <i>W. L. Minckley</i> | 383 |
| SPECIATION ASPECTS AND MAN-MADE COMMUNITY COMPOSITION CHANGES IN CHIHUAHUAN DESERT FISHES | |
| <i>Salvador Contreras-Balderas</i> | 405 |
| SUMMARY AND CONCLUSION | |
| <i>Clark Hubbs</i> | 433 |

SESSION V: HERPETOFAUNA

| | |
|--|-----|
| IS THERE A CHIHUAHUAN DESERT? A QUANTITATIVE EVALU- ATION THROUGH A HERPETOFAUNAL PERSPECTIVE | |
| <i>David J. Morafka</i> | 437 |
| SEMI-AQUATIC REPTILES AND AMPHIBIANS OF THE CHIHUAHUAN DESERT AND THEIR RELATIONSHIPS TO DRAINAGE PATTERNS OF THE REGION | |
| <i>Roger Conant</i> | 455 |
| ANCIENT PLAYAS AND THEIR INFLUENCE ON THE RECENT HERPETOFAUNA OF THE NORTHERN CHIHUAHUAN DESERT | |
| <i>Ralph W. Axtell</i> | 493 |
| SOME RECENT CHANGES IN THE HERPETOFAUNA OF THE NORTHERN CHIHUAHUAN DESERT | |
| <i>James F. Scudday</i> | 513 |
| THE BLACK GAP WHIPTAIL LIZARDS AFTER TWENTY YEARS | |
| <i>William W. Milstead</i> | 523 |
| A CHANGING ENVIRONMENT: DOCUMENTATION OF LIZARDS AND PLANTS OVER A DECADE | |
| <i>William G. Degenhardt</i> | 533 |

SESSION VI: AVIFAUNA

| | |
|---|-----|
| THE AVIFAUNA OF THE SOUTHERN PART OF THE CHIHUAHUAN DESERT | 559 |
| <i>J. Dan Webster</i> | |
| DISTRIBUTIONAL RELATIONS OF BREEDING AVIFAUNA OF FOUR SOUTHWESTERN MOUNTAIN RANGES | 567 |
| <i>Roland H. Wauer and J. David Ligon</i> | |
| TEMPORAL CHANGES IN NORTHERN CHIHUAHUAN DESERT BIRD COMMUNITIES | 579 |
| <i>Ralph J. Raitt and Stuart L. Pimm</i> | |
| EFFECTS OF HABITAT ATTRITION ON VIREO DISTRIBUTION AND POPULATION DENSITY IN THE NORTHERN CHIHUAHUAN DESERT | 591 |
| <i>Jon C. Barlow</i> | |
| CHANGES IN THE BREEDING AVIFAUNA WITHIN THE CHISOS MOUNTAINS SYSTEM | 597 |
| <i>Roland H. Wauer</i> | |
| THE SIGNIFICANCE OF WILDERNESS ECOSYSTEMS IN WESTERN TEXAS AND ADJACENT REGIONS IN THE ECOLOGY OF THE PEREGRINE | 609 |
| <i>W. Grainger Hunt</i> | |
| SUMMARY OF AVIAN RESOURCES OF THE CHIHUAHUAN DESERT REGION | 617 |
| <i>Allan R. Phillips</i> | |
| PANEL DISCUSSION | |
| Moderator: <i>Myron Sutton</i> | |
| Participants: <i>Horacio Gallegos, Robert M. Linn, W. Frank Blair, Robert McIntosh, John Henneberger</i> | 623 |
| <i>First Keynote Address—BERNARDO VILLA RAMÍREZ</i> | 649 |
| <i>Second Keynote Address—BOB BURLESON</i> | 651 |

Session I
Quaternary Environment

Late Quaternary Pollen Records from the East-Central Periphery of the Chihuahuan Desert

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SITE LOCATIONS AND PHYTOGEOGRAPHY

The Amistad Reservoir (Fig. 1), a recent impoundment of the Rio Grande above Del Rio, is located along the east-central periphery of the Chihuahuan Desert in west Texas. The region has long been known to both archeologists (Martin 1933; Pearce and Jackson 1933; Davenport 1938) and relic collectors because it contains hundreds of archeological sites, many of which have lengthy cultural records extending from the Paleo-Indian era up through the end of the Late Archaic.

The present vegetation in the Amistad region, as characterized by Flyr (1966), is quite different from the juniper-oak-mesquite parklands and savannas of the central and eastern portions of the nearby Edwards Plateau. As one travels southwest toward the Amistad region from Edwards and Kinney counties, the thick juniper-oak parkland vegetation gradually changes first to a juniper-oak savanna and finally into a desert scrub savanna. This vegetational change is correlated with decreases in the amount of annual precipitation coupled with a drop in elevation from 701 m (2300 ft) above sea level at Rocksprings in Edwards County to 305 m (1000 ft) at Del Rio in Val Verde County. Mixed among the juniper (*Juniperus*) and oak (*Quercus*) trees at the higher elevations just south of Rocksprings are populations of pinyons (*Pinus cembroides* var. *remota*), Little 1966). However, below 549 m (1800 ft) elevation pinyons are absent from the juniper-oak parkland vegetation. Between 518 m (1700 ft) and 396 m (1300 ft) elevation, the junipers and oaks become increasingly more scarce in the oak-juniper savanna and are replaced by scrubby species of acacia (*Acacia*) and mesquite (*Prosopis*). Below 396 m (1300 ft), the vegetation becomes a desert scrub savanna, with oaks and junipers entirely absent and only an occasional mesquite or

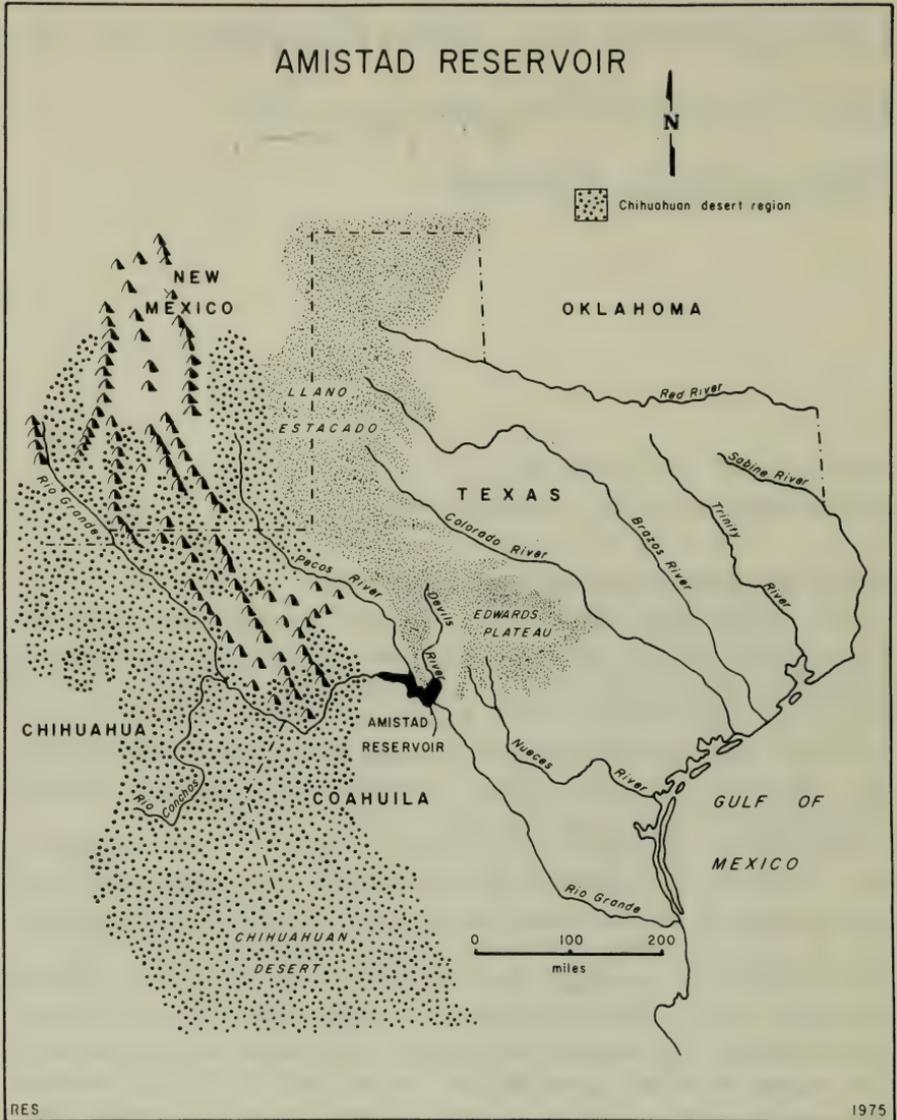


Fig. 1. Map showing the study area located on the east-central periphery of the Chihuahuan Desert.

acacia dotting the otherwise barren landscape. The mesophytic grasses and herbs found in the understory in the higher elevations of the western region of the Edwards Plateau are similar to the understory vegetation in the eastern regions of the plateau. However, at lower elevations below 396 m (1300 ft), the vegetation is confined primarily to more xerophytic species of threeawn (*Aristida*) and muhly (*Muhlenbergia*) such as

scratchgrass (*Muhlenbergia asperifolia*) and plants such as ocotillo (*Fouquieria splendens*), lechuguilla (*Agave lecheguilla*), resinbush (*Viguiera stenoloba*), Buckley yucca (*Yucca constricta*), sacahuista (*Nolina texana*), Texas sotol (*Dasyilirion texanum*), pencil cactus (*Opuntia leptocaulis*), Texas pricklypear (*Opuntia lindheimeri*), tarbush (*Flourensia cernua*), and creosotebush (*Larrea tridentata*).

From Del Rio west across the upland regions of the Amistad Reservoir area, the thin layer of topsoil is often completely removed exposing the limestone below and giving the landscape a rough and barren appearance. In these areas the vegetation becomes almost desert-like in composition. However, in the myriad small canyons which dissect the edges of the plateau, one finds a slightly more mesophytic vegetation since rainwater is often trapped in the cracks and potholes of the canyon floors and in the talus slopes along the edges of the canyons. Plants found in these canyons such as Mexican buckeye (*Ungnadia speciosa*), sugar hackberry (*Celtis laevigata*), netleaf hackberry (*Celtis reticulata*), little walnut (*Juglans microcarpa*), Vasey shin oak (*Quercus pungens*), wafer ash (*Ptelea trifoliata*), longleaf willow (*Salix interior*), Texas persimmon (*Diospyros texana*), Texas mountain laurel (*Sophora secundiflora*), western soapberry (*Sapindus saponaria* var. *drummondii*), and coyotillo (*Karwinskia humboldtiana*) are confined to this special ecological habitat and generally do not occur in the more xeric environments of the upland region.

The terraces along the three major rivers that dissect the Amistad region support an even more luxuriant flora than do the canyons. Along the terrace edges grow scattered, but dense, thickets of giantreed (*Arundo donax*) and common reed (*Phragmites communis*) mixed with saltcedar (*Tamarix gallica*) and heavy growths of bermudagrass (*Cynodon dactylon*). Higher on the banks of the terraces above the cane thickets one can find a variety of trees including willow (*Salix*), sycamore (*Platanus*), pecan (*Carya*), and mulberry (*Morus*). Still higher on the terrace the trees are replaced by bushes of guajillo (*Acacia berlandieri*), huisache (*Acacia smallii*), devils claw (*Acacia greggii*), blackbush (*Acacia rigidula*), and honey mesquite (*Prosopis glandulosa*). Other plants characteristically found along the upper portions of terraces in the Amistad region include tree tobacco (*Nicotiana glauca*), castorbean (*Ricinus communis*), waterwillow (*Baccharis glutinosa*), narrowleaf globemallow (*Sphaeralcea angustifolia*), buffalo gourd (*Cucurbita foetidissima*), and spiny aster (*Aster spinosus*).

The vegetation east of Marathon, in the lower elevations of the trans-Pecos region, is almost indistinguishable from the near-desert vegetation in the upland regions of the Amistad area to the east. The vegetation, as characterized by Gould (1962), is sparse, yet some of the more dominant plants include creosotebush (*Larrea tridentata*), purple sage

(*Leucophyllum frutescens*), lechuguilla (*Agave lecheguilla*), scabra agave (*Agave scabra*), banana yucca (*Yucca baccata*), Spanish dagger (*Yucca torreyi*), palmilla (*Yucca elata*), Thompson yucca (*Yucca thompsoniana*), Texas pricklypear (*Opuntia lindheimeri*), fishhook cactus (*Echinocactus uncinatus*), pencil cactus (*Opuntia leptocaulis*), Heyder cactus (*Mammillaria gummifera* var. *Applanata*), fishhook cactus (*Mammillaria microcarpa*), smooth sotol (*Dasyllirion leiophyllum*), Texas sotol (*Dasyllirion texanum*), and scattered bunches of grass such as bush muhly (*Muhlenbergia porteri*).

At Marathon in Brewster County, the vegetation becomes slightly more luxuriant due primarily to a rise in elevation from 427 m (1400 ft) at Langtry in the Amistad region to 1158 m (3800 ft) above sea level at Marathon. The vegetation around Marathon is still dominated by creosotebush (*Larrea tridentata*), but for the first time, west of Pandale, a few isolated scrub junipers (*Juniperus*), mesquites (*Prosopis*), and sumac (*Rhus*) begin to dot the landscape composed of a slightly denser growth of grass including Griseback bristlegrass (*Setaria grisebachii*), green foxtail grass (*Setaria viridis*), burrograss (*Scleropogon brevifolius*), curlymesquite (*Hilaria belangeri*), squirrel-tail grass (*Hordeum jubatum*), tobosagrass (*Hilaria mutica*), and desert muhly (*Muhlenbergia glauca*).

Between Marathon and the higher elevations of the Davis Mountains, the vegetation alternates back and forth between a desert shrub savanna and a high elevation grassland, depending on elevation changes, edaphic factors, and available moisture. However, in the foothills of the Davis Mountains north of Alpine, the vegetation shifts to a juniper-oak parkland mixed with a rich understory of mid grasses.

As elevation increases, the numerous small creeks and streams become lined with cottonwood (*Populus hinckleyana*), quaking aspen (*Populus tremuloides*), narrowleaf cottonwood (*Populus angustifolia*), southwestern black willow (*Salix gooddingii*), and American sycamore (*Platanus occidentalis*), while the adjacent rounded hillsides become covered with oaks and junipers. At the higher elevations between 1676 m (5500 ft) and 2134 m (7000 ft), the juniper-oak woodland is replaced by mixed pinyon-juniper woodlands. Ponderosa pine (*Pinus ponderosa*) forms localized forests in favorable high altitude sites.

Between the Davis Mountains and the foothills of the Guadalupe Mountains near the Texas-New Mexico border, the vegetation can be characterized as a desert scrub savanna and is similar in composition to the region between Marathon and the foothills of the Davis Mountains. Mesquites and acacias dominate the overstory. Scattered small scrub junipers and thick growths of saltbush (*Atriplex*), goosefoot (*Chenopodium*), grasses such as alkali sacaton (*Sporobolus airoides*), curlyleaf muhly (*Muhlenbergia setifolia*), slim tridens (*Tridens mu-*

ticus), and woollyfoot grama (*Bouteloua eriopoda*) dominate the understory.

In the lower elevations of the Guadalupe Mountains, between 1219 m (4000 ft) and 1676 m (5500 ft), the vegetation becomes more mesophytic. Dominant overstory plants include fragrant sumac (*Rhus aromatica*), alligator juniper (*Juniperus deppeana*), one-seeded juniper (*Juniperus monosperma*), gray oak (*Quercus grisea*), pink mimosa (*Mimosa borealis*), and resinbush (*Viguiera stenoloba*) while the understory contains brownsapine pricklypear (*Opuntia phaeacantha*), Engelmann pricklypear (*Opuntia engelmannii*), lechuguilla (*Agave lecheguilla*), smallseed nolina (*Nolina microcarpa*), smooth sotol (*Dasyliirion leiophyllum*), creosotebush (*Larrea tridentata*), and a mixture of grasses including threeawn (*Aristida*), sideoats grama (*Bouteloua curtipendula*), and curlyleaf muhly (*Muhlenbergia setifolia*). The higher elevations above 1676 m (5500 ft) are dominated by either oneseeded or alligator juniper and pinyon pine (*Pinus edulis*). However, Douglas fir (*Pseudotsuga menziesii*), southwestern white pine (*Pinus strokiformis*), and western yellow pine (*Pinus ponderosa*) are found only in restricted locales above 1676 m and dominate some areas above 2377 m (7800 ft) (Gehlbach 1967).

MATERIALS AND METHODS

Bonfire Shelter was originally sampled by the author and R. H. Hevly for palynological purposes in June 1965. A trial study was conducted and, on the basis of that survey and the knowledge that Bonfire Shelter contained an extremely important archeological record, the site was chosen for more detailed pollen studies. In August 1967, I returned to Bonfire Shelter and excavated a 0.46 m² (5 ft²) test pit 1.5 m (5-ft) deep into the spall zone below the limit of previous excavations (Dibble and Lorrain 1968). A new series of soil samples was then collected at one-half foot intervals from the cleaned vertical wall of the northernmost excavation pit at coordinates N108/W50 beginning with the bottommost level of the test pit. The provenience of each of the 30 soil samples collected at Bonfire Shelter is shown in Fig. 2.

I collected surface samples of the modern pollen rain from a variety of west Texas locales in order to better understand and to interpret the fossil pollen data. These are shown in Fig. 3.

Each surface sample was collected using the pinch technique outlined by Hevly and Martin (1961), since it has been shown to be more effective than collecting samples from enclosed cattle tanks or from only a single small area less than 30 cm in diameter (Potter and Rowley 1960; Hevly 1964; Potter 1967).

Extraction techniques vary with the type of archeological sediment being analyzed, yet four chemical treatments are common to almost

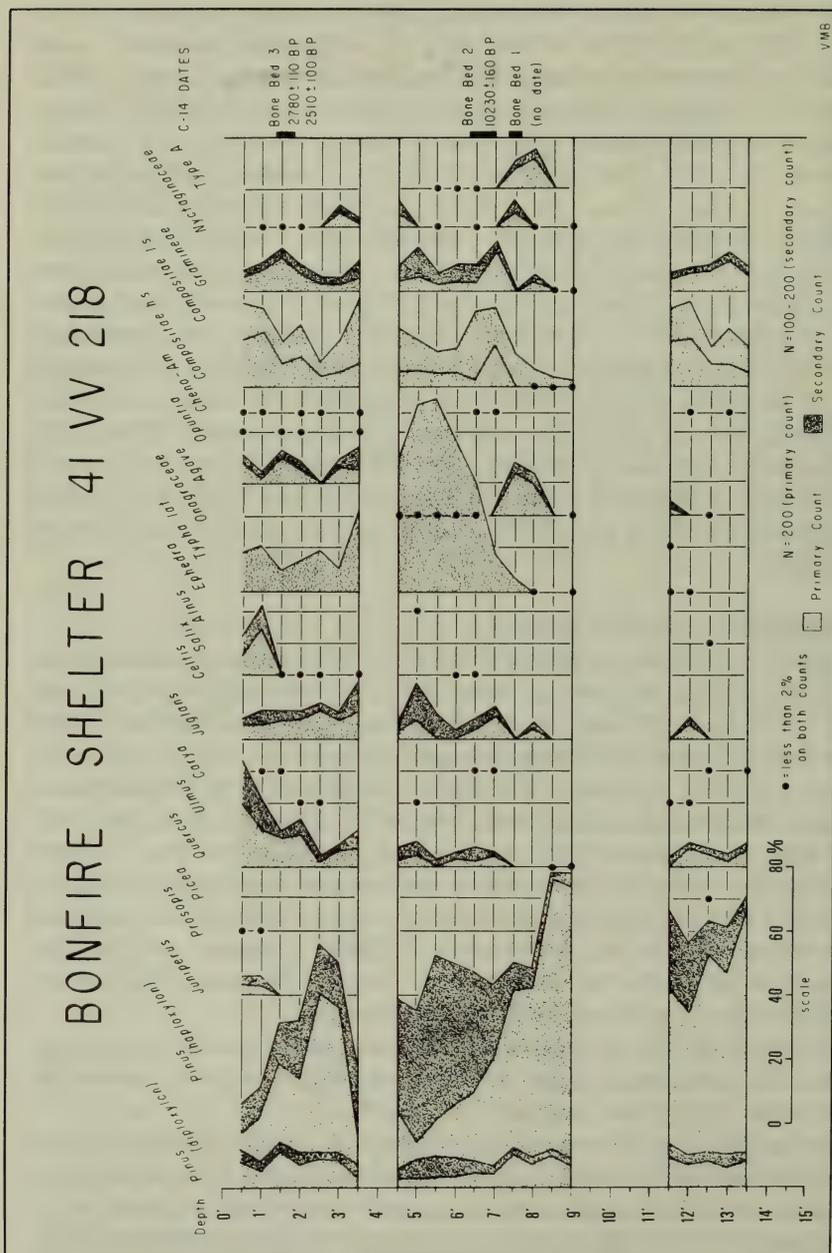


Fig. 2. Pollen diagram of Bonfire Shelter.

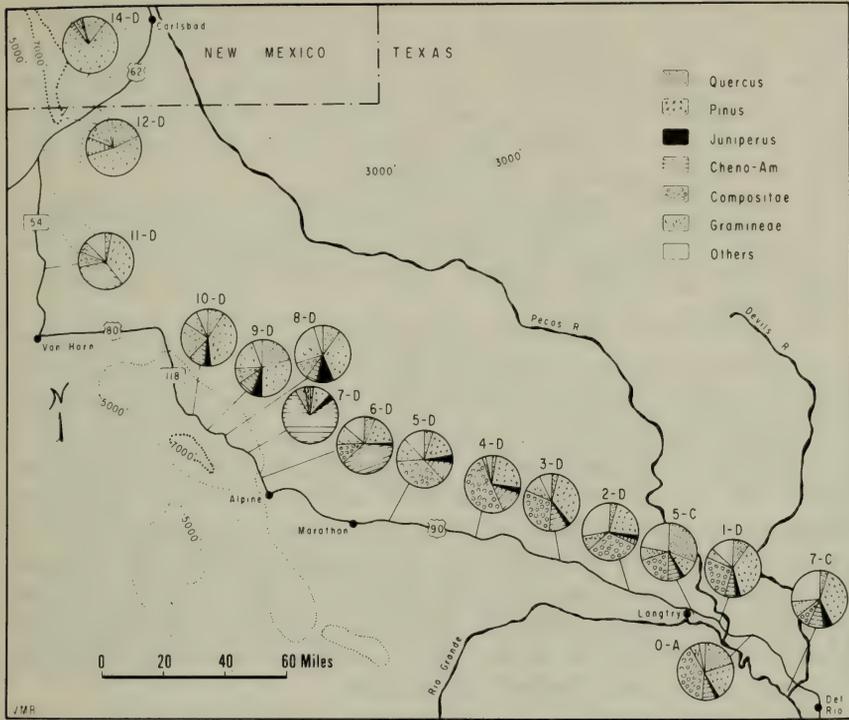


Fig. 3. Pollen diagram of modern pollen transect in west Texas.

every pollen analytical extraction procedure: (1) removal of carbonates by hydrochloric acid; (2) removal of silicates by hydrous hydrofluoric acid; (3) removal of organic materials by acetylation; and (4) removal of humic acids with a 10% solution of potassium hydroxide.

Identifications of pollen types in this report were based upon morphological comparisons with pollen samples in The Texas A&M Modern Pollen Reference Collection which is permanently stored in the Palynology Laboratory located on the Texas A&M University campus.

A standard 200-grain pollen count was attempted for all fossil and modern samples as suggested by Barkley (1934). Each identifiable whole pollen grain was recorded on tabular sheets. Fragments of known pollen types were included in the standard count. Broken pine grains, for example, were counted as one-third of a grain for each bladder and one-third for the body of the grain. Badly crushed and deteriorated grains beyond identification and cryptogamic spores were excluded from the pollen counts. However, well-preserved pollen which could not be identified were included in the counts as "unknowns."

At Bonfire Shelter, I considered it necessary to conduct a primary and

a secondary pollen count because of an abundance and over-representation of one or more pollen types. The primary count, or first count, consisted of a standard 200-grain count which included all pollen types. The secondary count, of 150 grains, omitted the over-represented pollen type (e.g., Compositae and *Ephedra* pollen in Bonfire Shelter deposits), but included all other pollen taxa.

In this report all references to "primary or first" count refer to the initial 200-grain counts, while references to "secondary or second" count refer to the subsequent 150-grain count excluding the over-represented pollen types.

The pollen of fir (*Abies*), spruce (*Picea*), and pine (*Pinus*) are easily distinguished from one another on the generic level but are more difficult to separate into individual species using only a light microscope (Whitehead 1964). Fir pollen has a total grain breadth of over 90 μ (Wodehouse 1935) and is easily recognized by its thick, coarsely granulated body cap. Spruce grains (ca. 68-91 μ) are only slightly larger than pollen of some pine species, yet they have a finer body texture than the grains of pine. However, the most distinguishable difference between the grains of spruce and pine is the absence in spruce pollen of a constriction in the region where the bladders connect onto the body of the grain. Both pine and fir pollen have a definite constriction where the bladders connect onto the body of the grain.

Pine pollen, although not easily identified to the species level, can be separated into its two subgenera (*Diploxylon* and *Haploxylon*) based upon pollen morphological characteristics (Uneo 1958). Pollen grains of the subgenus *Diploxylon* (e.g., *Pinus ponderosa*) do not have distal body verrucae along the germinal furrow, but those of the subgenus *Haploxylon* (e.g., *Pinus cembroides*) do. This distinction works well in areas such as west Texas where only two known species of pine native to that region belong to the subgenus *Haploxylon* (*Pinus cembroides* and *Pinus edulis*) and, therefore, their pollen can be recognized in both the modern and fossil record from pollen grains of the subgenus *Diploxylon*.

The grains of joint-fir (*Ephedra*) can be divided into two groups (*E. nevadensis* and *E. torreyana*) based upon their pollen morphology (Steeves and Barghoorn 1959). The *E. torreyana* group is distinguished by its large number of unbranched straight furrows and undulating ridges with numerous conspicuous hyaline strands intersecting the furrows at various points along the grain. However, since no more than 1% of the total joint-fir pollen in the deposits of any locale sampled during this study came from species assigned to the *E. nevadensis* group, it was deemed unnecessary to distinguish between these types on the pollen diagrams.

The composite pollen in this report was divided into three categories based upon morphological differences: (1) Ambrosieae or low-spine;

(2) high-spine; and (3) *Artemisia*. The two categories, low-spine and high-spine, are arbitrary divisions of the subfamily Tubiflorae. The low-spine group includes those composite types which have anemophilous pollen grains with spines less than 2μ in length. The high-spine group, on the other hand, consists of composites with zoophilous pollen that have echinate grains with spines longer than 2μ (Martin 1963). Sagewort (*Artemisia*) pollen grains are easily distinguished from the other composite types because of their highly raised mesicopial regions. In this study sagewort pollen was assigned percentages on pollen diagrams only when it occurred in percentages greater than 2%. When the percentages of sagewort pollen were less than 2%, they were incorporated into the category "low spine."

Pollen grains belonging to the Liguliflorae group of the composites have a fenestrate morphology, but in this report were included in the high-spine group on the pollen diagrams since no more than two Liguliflorae pollen grains were encountered in any of the individual pollen samples.

I have followed Martin's (1963) proposed term "Cheno-Am" for pollen of the family Chenopodiaceae and the genus *Amaranthus*. Their pollen grains are so similar morphologically that it is nearly impossible to distinguish conveniently one type from another under the light microscope.

DISCUSSION

The pollen-analytical evidence recovered from playa lakes in west Texas (Hafsten 1961) extends back to the mid-Wisconsin (ca. 35,000 B.P.) and was interpreted to indicate that slightly prior to the maximum spread of the advancing Wisconsin glaciation, the vegetation in west Texas could be characterized as a cool-moist grassland with trees either absent or very rare. Hafsten states that the fossil-pollen data indicate conditions were fairly stabilized during this period (ca. 33,500 to 22,500 B.P.) and remained virtually unchanged until the beginning of the full-glacial around 22,000 years ago. With the onset of the full-glacial, conifers probably invaded the former grassland region since the pollen records of this period from Rich Lake and Arch Lake on the Llano Estacado show a steady and rapid rise in the percentages of both spruce (*Picea*) and pine (*Pinus*) pollen (Hafsten 1961). By ca. 15,000 years B.P., conifer pollen in deposits of Rich Lake, Crane Lake, and Tahoka Lake (all located on the Llano Estacado of west Texas) completely dominated the fossil record and reached peaks in excess of 98%. According to Hafsten, the full-glacial vegetation in west Texas was probably composed of an open woodland of mixed spruce and pines. He points out that the few fir (*Abies*) pollen grains found in the fossil record of full-glacial deposits on the Llano Estacado did not, in his estimation,

suggest that fir was a component of the regional vegetation. He does admit that fir probably extended its range significantly eastward out of the Rocky Mountains during the full-glacial but suggests that the eastward migration probably did not reach west Texas. This assumption is strengthened by the absence of fir macrofossils in late Pleistocene age, pack-rat middens from the Guadalupe Mountains in west Texas (see Van Devender et al. this volume). Had fir trees been present it is probable that some of their plant remains would have been present in the pack-rat middens along with the recovered plant, macrofossils of spruce, limber pine, Douglas fir, and pinyon pine.

Bonfire Shelter, located along the east-central periphery of the Chihuahuan Desert (Fig. 1) in the Amistad region, is believed to contain a record of late full-glacial sediments and provides tentative support for Hafsten's original vegetational interpretations for this period. The earliest pollen data from Bonfire Shelter are derived from deposits 2 m (7 ft) deeper than the strata from which the earliest radiocarbon data of $10,230 \pm 160$ B.P. was obtained (Dibble and Lorrain 1968). These lowermost pollen bearing strata (levels 3 m [8.5 ft] to 4 m [13.5 ft]) have been assigned tentatively to the late full-glacial period, based upon geologic aspects of the spall zone and the fossil-pollen record. Deposits below a depth of 3 m (8.5 ft) in Bonfire Shelter are composed entirely of thick spalls which were probably loosened from the roof and walls of the shelter by severe ice wedging during the cold winters of the late full-glacial. Very high percentages of pine pollen, over 60% in the primary pollen count and over 80% in the secondary count, recovered from these same spall zones below 3 m (8.5 ft) suggest that during the late full-glacial the Amistad region may have been covered by a woodland (defined in this report as an open canopy forest), with pinyon pines forming the major arboreal component. The high ratio (over seven to one) of *Haploxylon* to *Diploxylon* pine pollen and the occurrence of only one spruce grain from these deposits indicate that the pinyon pollen was probably of local origin, while the sources of *Diploxylon* pine (i.e., *Pinus ponderosa*) and spruce pollen were probably located outside the Amistad region. How far distant these nonpinyon, conifer sources were located is difficult to determine from an analysis of the pollen record, yet the late full-glacial fossil record from Crane Lake contains over 90% pine pollen and between 1-4% spruce pollen. Crane Lake is 770 m (2525 ft) above sea level or 343 m (1125 ft) higher in elevation than Bonfire Shelter, 185 km (115 miles) to the southwest. Hafsten (1961) did not make a distinction between pinyon and nonpinyon pine grains on his pollen diagram of Crane Lake, but he does state that in his opinion the majority of the full-glacial pine pollen at that locale did not come from pinyon (*Pinus edulis* or *P. cembroides*).

Studies by Wells (1966) of plant macrofossils from pack-rat middens

in the Chisos Mountains of west Texas also contain data relevant to Hafsten's assumptions concerning the absence of pinyon pines from the regional vegetation at Crane Lake during the full-glacial period. Wells found that during the full-glacial period in the Chisos Mountains the more mesophytic conifers such as western yellow pine (*Pinus ponderosa*) probably descended less than 396 m (1300 ft) in elevation, while the less mesophytic conifers such as pinyon and juniper (*Juniperus*) probably descended at least 792 m (2600 ft) in elevation.

One of the primary unanswered questions concerning the west Texas full-glacial vegetation is whether or not spruce and fir were present. As stated earlier, Hafsten felt that the percentages of spruce pollen were sufficiently high in full-glacial playa lake deposits to assume spruce was present at that time in west Texas. This assumption is strengthened by the fact that spruce needles recently have been recovered from ancient pack-rat middens in the Guadalupe Mountains (van Devender et al. this volume). These middens, dated ca. 13,000 B.P., show that spruce trees in that region survived into the late glacial period (ca. 14,000-10,000 B.P.). How abundant they may have been is difficult to theorize. If we take the highest percentage of spruce pollen found in late full-glacial deposits of that region (10% from Rich Lake), we find that it is probably too high to have resulted solely from long distance transport of individual pollen grains. When the 90% pine pollen from these same deposits is divided by four, as Faegri and Iversen (1968) suggest doing in order to obtain a more nearly accurate representation for pine, then the reconstructed forest would contain only twice as many pines as spruce. It is not suggested that the late full-glacial vegetation in west Texas contained two-thirds pine and one-third spruce, but it is suggested that, based upon pollen representation rates, it is suspected that spruce occurred in much greater percentages than the pollen record indicates.

The presumed presence of spruce in areas of west Texas during the late full-glacial period raises questions about the inferred climate of that period. Based on the present distribution of spruce, one might conclude that portions of west Texas as far south as Crane Lake (31° north latitude) had a late full-glacial July mean temperature of 21°C (70°F) or less. This assumption is based upon a study of the distribution of present species of spruce. Leopold (1957) reports that the present limits for both black spruce (*Picea mariana*) and white spruce (*Picea glauca*) in North America coincide with the 21°C (70°F) mean July temperature isotherm which, according to Kendrew (1961), presently extends as far south as Fargo, North Dakota; Saginaw, Michigan; Montreal, Canada; and in isolated regions of higher elevations along the Cascade and Rocky Mountain ranges.

Present mean July temperatures in west Texas are in excess of 27°C (80°F) and portions of the Amistad region near Bonfire Shelter have

mean July temperatures in excess of 32°C (90°F) (Kendrew 1961). Based upon the present thermal maximums for present populations of spruce, a mean July temperature decrease of at least 5.5°C (10°F) would be needed in order for known populations of spruce to presently survive in regions of west Texas as far south as Crane Lake.

Hydrological studies of sediments on the Llano Estacado (Reeves 1966) have been interpreted to indicate that an average midsummer temperature decrease of at least 5°C (9°F) would have to be accompanied by a maximum precipitation rate of approximately 84-86 cm (33-34 inches) and an evaporation rate of not more than 112 cm (44 inches) in order to restore the west Texas pluvial lake basins to their full-glacial levels. At present, this region receives from 30-51 cm (12-20 inches) of annual precipitation and has an annual evaporation rate of 152 cm (60 inches), which reflects lower effective moisture levels than the requirements stated by Reeves.

Based upon the pollen and hydrological studies, I tentatively suggest that during the late full-glacial period the Amistad region may have had an average midsummer temperature as much as 5.5°C (10°F) lower than the present. Even if this tentatively reconstructed model is correct, the summer temperatures in the Amistad region would have been higher than those to the north and would have caused greater evaporation than that occurring on the Llano Estacado. This would have resulted in less effective annual moisture in the Amistad region than in the cooler regions of west Texas which may, in part, explain the apparent absence of spruce in the Amistad region during the late full-glacial period.

During the late-glacial (ca. 14,000-10,000 years B.P.) a change in vegetation and climate occurred throughout Texas and in other regions of North America. West (1961) reported that pollen analyses of late-glacial deposits in Wisconsin indicate an invasion of spruce forests into the region vacated by the retreating glacier. Pollen records from deposits in Kirchner Marsh in southeastern Minnesota (Wright et al. 1963) do not date older than late-glacial and are characterized by increasing percentages of deciduous tree pollen such as ash and oak and gradual loss of spruce pollen suggesting a temperate climate.

Mehring (1967) found that the pollen record from Tule Springs, Nevada, showed a sharp decline in juniper and a corresponding rise in Cheno-Am pollen about 12,000 B.P., which suggests a warming of the Las Vegas Valley climate during the late-glacial interval. At the Lehner Mammoth Site, Mehring and Haynes (1965) reported that pollen evidence suggests a major climatic and vegetational change occurred prior to 11,000 B.P. in southeastern Arizona. Martin and Mehring (1965) reported that the collapse of the proposed full-glacial pine parklands of the present desert grassland and the woodlands of the Mohave Desert were completed by 11,000 B.P.

Hafsten (1961) reported that playa lake sediments in northwest Texas, dating from the late-glacial, yielded a pollen record representative of a mesophytic grassland containing some elements of mixed spruce and pine woodlands. However, the overall decrease in conifer pollen during this period, when compared to the full-glacial deposits of these same playa lakes, led Hafsten to suspect that elevated summer temperatures during the late-glacial may have caused denudation of most woodlands in northwest Texas.

Based upon the pollen record, I have tentatively assigned deposits below Bone Bed 2 and above 2.4 m (8 ft) in Bonfire Shelter to the late-glacial period. In these deposits the decrease in the percentage of pinyon-pine pollen slightly prior to the deposition of Bone Bed 1 may reflect a partial loss of these trees in the regional vegetation of the Amistad area. I believe that such a reduction may have resulted in a shift of regional vegetation from the proposed late full-glacial pinyon pine woodland to a late-glacial parkland (defined in this report as a grassland interrupted by isolated trees and clumps of trees). This proposed shift in vegetational composition during the late-glacial may have resulted from a variety of factors including a suspected reduction in effective moisture and elevated summer temperatures.

Between ca. 10,000 B.P. and approximately 7000 B.P., the pollen records from Bonfire Shelter and Eagle Cave (McAndrews and Larson 1966), located near Langtry, and the Devil's Mouth Site (Bryant and Larson 1968), located near Del Rio, suggest that the regional parkland vegetation in the Amistad area remained fairly stable during this 3000-year period. A close correlation between the pollen records from the Amistad region and the modern pollen rain in juniper-pinyon parklands of the Davis Mountains, Texas, was noted (Fig. 3). However, I suspect that it is possible that the absence of juniper pollen in Amistad deposits prior to 7000 B.P. may, as Potter (1967) has suggested for similar deposits in New Mexico, reflect oxidation of these grains in the alkaline soils of the American Southwest. If this were true, then junipers may have been a component of the proposed Amistad parkland vegetation of that period but their fragile grains were not preserved in the fossil record.

As seen in the pollen diagram of Bonfire Shelter (Fig. 2), joint-fir (*Ephedra*) was one of the major contributors to the fossil record between 10,000-7000 B.P. The assumption that joint-fir can be classified as an economically important plant used by prehistoric man in the American Southwest is not unreasonable since Coville (1892), Stevenson (1915), and Saunders (1920) note that some groups of Indians in the American Southwest used boiled joint-fir stems to make beverages, and used ground joint-fir seeds to make flour. Bohrer (1968) noted that the recovery of 44.5% pollen of joint-fir from an archeological pit-house

floor in eastern Arizona suggests a culturally caused pollen distortion. However, there is no evidence from coprolitic studies (Riskind 1971; Bryant 1974) or plant-fragment analyses of archeological midden debris in the Amistad region that this plant was ever used or eaten by man in that area. Furthermore, the highest percentages of pollen from joint-fir are recovered in Bonfire Shelter only from strata which contain no cultural evidence of man (Dibble and Lorrain 1968).

Based upon this information, I assume that the high percentages of joint-fir pollen in Bonfire Shelter deposits may reflect either a natural pollen rain, or may represent the introduction of this pollen by rodents such as the pack rat (*Neotoma*).

The Altithermal period of the post-glacial (ca. 7000-4500 B.P.) in the Amistad region, like many areas of the arid American Southwest (Haynes 1968), is characterized in the alluvial sediments by erosional contacts. At the Devil's Mouth Site located at the confluence of the Rio Grande and Devils River, horizontal alluvial deposits are truncated by dipping strata containing Shumla and Pandale projectile points and charcoal which has been radiocarbon dated as 4080 ± 380 years B.P. (Dibble 1967). The similarity between the alluvial stratigraphy of the Devil's Mouth Site and Arenosa Shelter and the presence at both sites of Shumla and Pandale projectile points in sediments resting upon the erosional contact imply that both sedimentary sequences may represent the same geologic events.

The causes of the widespread erosion in the Amistad region slightly prior to 4000 B.P. are not fully understood, yet based upon the pollen records of the Devil's Mouth Site, it is suspected that the causes were not major climatic changes. The fossil pollen record of undated strata immediately below the erosional contact contains high levels of grass, pine, and herb pollen similar to the modern pollen rain in savanna regions (defined in this report as a grassland containing scattered trees and shrubs but where the continuity of the grassland is not interrupted) of west Texas (Fig. 3). Above the erosional contact, the fossil record contains slightly reduced percentages of pine and grass pollen, moderate increases in pollen from joint-fir, and the first occurrence of pollen from mesquite, acacia, and agave. I interpret these data as suggesting that the composition of post-erosional regional vegetation in the Amistad region remained basically similar to the pre-erosional composition even though some local variations may have occurred.

One possible explanation of the widespread erosion in the Amistad region is that minor elevations in summer temperatures or a short drought could have led to partial denudation of the upland vegetation, thereby allowing increased rainfall runoff and rises in river discharge. Another possible explanation could be increased precipitation during the latter portion of the Altithermal Period as Haynes (1968) has suggested.

Neither of these explanations is entirely adequate, yet at present none of the Amistad pollen records definitely can be assigned to the time span of the Altithermal. At Bonfire Shelter the absence of radiocarbon dates from strata of probable altithermal-age and the inability to recover preserved pollen from some strata tentatively assigned to this interval prevent any accurate statement concerning the nature of altithermal climates. The presence of an erosional contact in the stratigraphy of the Devil's Mouth Site requires that the pollen record from pre-contact strata be interpreted with caution. Until more is known concerning the length of the erosional period and the degree to which the terraces in the Amistad region were eroded, no definitive statement can be made concerning the climatic conditions in southwest Texas during the Altithermal. However, the widespread alluvial erosion, which in the Amistad region is dated as immediately prior to 4000 B.P. and the absence of preserved pollen in rockshelter deposits such as Bonfire Shelter suggest a possible Altithermal climatic sequence similar to the one Haynes (1968) has outlined for the American Southwest beginning with a hot and dry period between ca. 7500-6000 B.P. and a slightly more mesic interval between ca. 6000-3500 B.P.

The last 4000 years of the post-glacial pollen record in the Amistad region reveals the presence of a widespread but brief mesic interval around 2500 B.P. The fossil record from Bonfire Shelter indicates that between the 1.22-m (4-ft) level and the height of the brief mesic interval (represented by strata deposited slightly prior to and during Bone Bed 3) the vegetation may have been slightly more xerophytic than prior to the deposition of strata below the 1.22-m (4-ft) level. Decreased percentages of pine pollen coupled with increases in herb and deciduous tree pollen in the 1.06-m (3.5 ft) level suggest that slightly elevated temperatures and/or reduced effective moisture may have favored the growth of herbs, oak, and walnut trees in protected canyons but also may have caused a reduction of pinyons in the upland regions.

The occurrence of a short-lived late post-glacial mesic period in the Amistad region approximately 2500 B.P. may not have been restricted to the Bonfire Shelter locale. Instead, I suggest that it was widespread and that it provides both the archeologist and palynologist with a convenient "marker zone" for stratigraphic correlation between sites containing radiocarbon dates and sites without such dates. At both Bonfire Shelter and the Devil's Mouth Site, the brief mesic interval is characterized in the fossil record by rises in pine pollen and slight decreases in herbaceous pollen, suggesting that a brief reinvasion of pinyons into the Amistad region may have occurred during this period.

One of the most intriguing events in the Amistad region connected with the late post-glacial mesic period was the discovery of an estimated

800 bison (*Bison bison*) (Dibble and Lorrain 1968) in Bone Bed 3 of Bonfire Shelter. Two radiocarbon dates from charcoal in Bone Bed 3 yielded dates of 2780 ± 110 and 2510 ± 100 and thus confirm the contemporaneousness of those deposits with the short-lived mesic period seen in the pollen record of the Devil's Mouth Site.

No archeological site thus far excavated in the Amistad region, except Bonfire Shelter, contains more than a trace of bison bones in deposits assigned to the late post-glacial (ca. 4000 B.P. to present) period. These data combined with an apparent absence of bison from local pictographs (Newcomb 1967) imply that bison may have been unavailable in the Amistad region throughout most of the post-Altithermal interval.

Pollen evidence from Bonfire Shelter and the Devil's Mouth Site (Bryant and Larson 1968) suggests that widespread savanna conditions probably accompanied by a slightly cooler climate existed in the Amistad region for one brief period (ca. 2500 B.P.) during the last 4000 years. The association of massive bison-bone deposits resulting from a bison jump in deposits dating from this short-lived mesic interval leads to the speculation that bison herds may have been available for exploitation in the Amistad region over a very limited span of time and that they were probably exploited by knowledgeable bands of bison hunters following the herds into southwest Texas (Dibble and Lorrain 1968). The assumption that indigenous "Amistad Man" did not exploit the bison is evident by the almost total absence of bison bones in other archeological sites of the region. This suggests that the local inhabitants may have been unable to devise effective methods of exploitation because the bison were not present in the Amistad region long enough for an economic reorientation to occur.

The Amistad pollen records of the last 2500 years reflect a general trend toward increased aridity. At Bonfire Shelter, the fossil record shows a decrease in the percentage of pinyon pollen suggesting that in the uplands the frequency of these trees was reduced. Rises in the percentages of oak and hackberry pollen in deposits of Bonfire Shelter above Bone Bed 3 suggest that these plants were able to increase in numbers during this period, but that they were probably confined to the slightly more mesic environments of the canyons since neither the Devil's Mouth Site nor Arenosa Shelter pollen records (Bryant 1969) reveals similar rises in these pollen types during comparable time periods. This assumption is strengthened by contemporary vegetational studies in the Amistad region which show that the present distribution of these two taxa is almost entirely restricted to talus slopes in mesic canyons.

The trend (as seen in the pollen records of Bonfire Shelter, the Devil's Mouth Site, and Arenosa Shelter) toward increased aridity following the end of the Late-Glacial was not confined to the Amistad re-

gion. Similar trends are seen in the fossil records of playa lakes in west Texas (Hafsten 1961).

Based upon the pollen record, Hafsten (1961) divided the last 10,000 year depositional record (post-glacial) into four subzones: A₄, A₃, A₂, and A₁. None of these subzones is assigned specific dates by Hafsten but he states that they may correspond to the European post-glacial periods. Each of Hafsten's subzones is differentiated from the others on the basis of a dominance of one or more pollen types (e.g., A₄, the oldest of the subzones, is identified by high percentage of composite pollen; A₃ is identified by high percentage of Cheno-Am pollen; A₂ is represented by increases in pine and composite pollen; and A₁ is characterized by high percentages of Cheno-Am pollen) yet when considered as a single unit, they show a definite trend toward increased aridity after 10,000 B.P.

One of Hafsten's subzones, A₂, is of considerable importance since it is characterized primarily by marked increases in pine pollen. At the Wolf Ranch Canyon sampling location a radiocarbon date of 2850 ± 100 was obtained from sediments marking the beginning of subzone A₂. The rapid increase in the percentage of pine pollen from Wolf Ranch Canyon sediments of subzone A₂ directly above the radiocarbon date corresponds with indications of a mesic period (ca. 2500 B.P.) in the pollen records of the Amistad region and suggests that the brief late post-glacial mesic period was not a local phenomenon, but was instead of regional importance.

SUMMARY

The pollen records from sites in the Amistad Reservoir area represent our only source of paleoenvironmental record along the east-central periphery of the Chihuahuan Desert. These pollen records are important since they reveal a long period of changing environments during the late Quaternary. The data suggest that during part of the full-glacial period in southwest Texas the vegetation of the Amistad region probably consisted of a pinyon pine woodland. Later, as climatic conditions began to change, these proposed woodlands were replaced by parklands slightly prior to 10,000 years ago. The postglacial period in the Amistad region is characterized by a general progression toward increased aridity.

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Wisconsin Age Environments in the Northern Chihuahuan Desert: Evidence from the Higher Vertebrates

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The aims of this study have been to bring together data in the literature on late Pleistocene vertebrate faunas from the Chihuahuan Desert and its periphery, to add unpublished data from studies at the Museum of Arid Land Biology, and to synthesize these data into a logical, useful picture of the area now occupied by the Chihuahuan Desert as it must have been in the late Pleistocene. Lack of data prevents fulfillment of these aims for much of the desert area, but sufficient information now is available for at least partial reconstruction of the northern desert area, and some data bear on conditions farther to the south.

There are more than 260 vertebrate taxa known from 27 Wisconsin age or sub-Recent cave sites within or near the Chihuahuan Desert (Table 1; Fig. 1). About 45 of these taxa are extinct and some 39 are extralimital (defined here as historically occurring no nearer than 32 km (20 miles) from a site—reasons for this definition are discussed later). These figures are approximate because some personal judgment has been exercised in determining which questionable identifications to accept and because of the scantiness of knowledge about modern vertebrate distribution in Mexico.

In terms of environmental reconstruction, the extralimital forms are most valuable in showing how Pleistocene conditions must have differed from those of today, for not only must conditions have been different to have allowed their presence, but their current distributions give clues as to the nature of those differences. At the same time, occurrences of forms still living in the area today place limits to the degree of change that could have occurred.

In Table 1, the sites have been split into four age intervals: >25,000 B.P., 25,000-12,500 B.P., 12,500-10,000 B.P., and <10,000 B.P. Place-

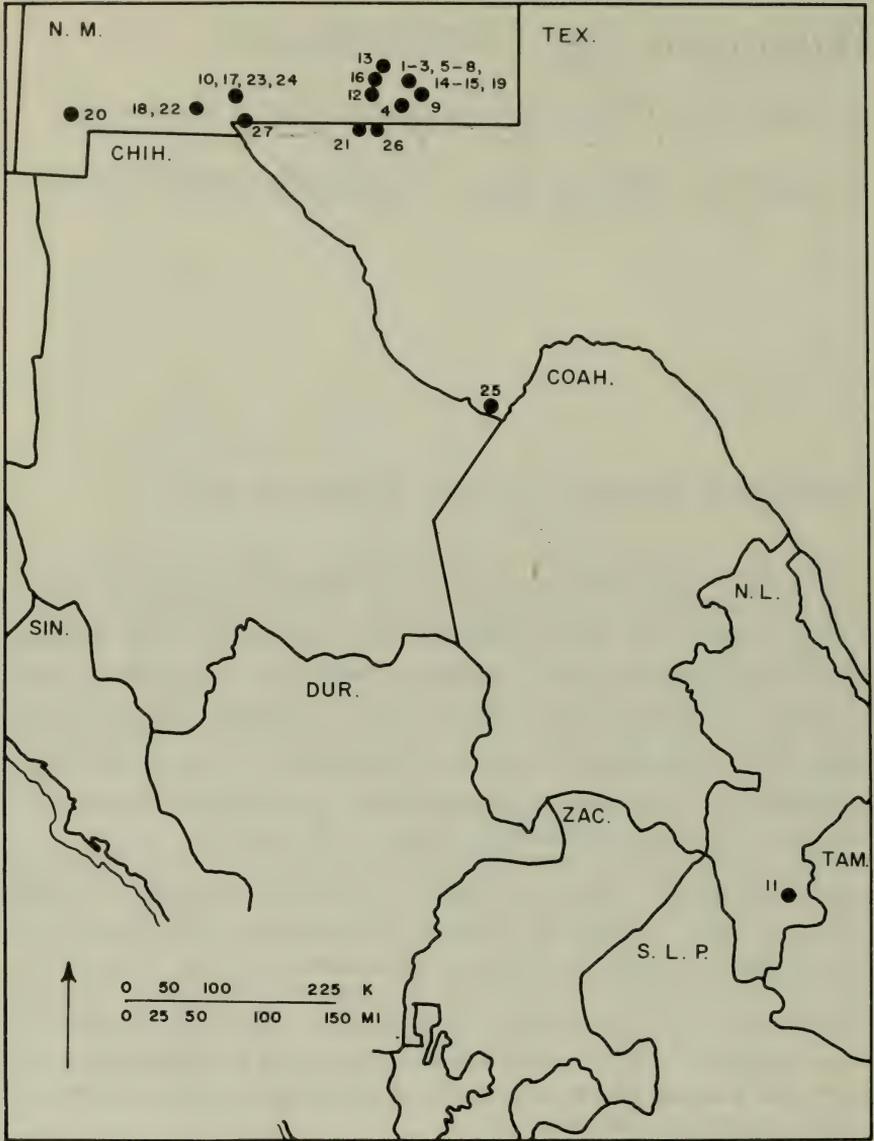


Fig. 1. Cave sites containing late Pleistocene vertebrate faunas and located in or near the Chihuahuan Desert. Numbers refer to sites recorded in Table 1.

ment of sites into these categories should not be taken too seriously, particularly where radiocarbon dates are lacking; placement of several sites, especially between the 12,500-10,000 and <10,000 categories has been on highly arguable data. Howells Ridge Cave, in particular, seems

to me to be partly within the pre-10,000 interval on a faunal basis, but I defer to the dating of Van Devender and Worthington (this volume) at present. In sites where stratigraphic information is unavailable, more than one time interval probably is represented. In several sites (including Shelter Cave and Rocky Arroyo Cave), deposition continued into "Basket Maker" time, but what portion, if any, of the fauna dates from this time is not always clear.

The three early sites (>25,000 B.P.) are in Dry Cave, about 24 km (15 miles) west of Carlsbad and the Pecos Valley, at the northern edge of the Chihuahuan Desert. Today, Dry Cave lies in the ecotone between Lower and Upper Sonoran life zones (Harris 1970b). Indicative of a relatively moderate climate is presence of land tortoises (*Gopherus* sp., *Geochelone* sp.), armadillo (*Dasypus* sp.), cotton rat (*Sigmodon* sp.), and gray fox (*Urocyon cinereoargenteus*). Armadillos probably do not occur natively in New Mexico at present (Humphries 1974). Presence at Dry Cave is based on a single carapace element: chances are high that it was carried to the cave from some distance by scavengers, since death of even a single individual provides hundreds of identifiable elements. Cotton rats are absent from all the stadial sites (excepting San Josecito Cave, far to the south and the farthest outside the desert region of all the sites considered here), as are gray foxes (a presumed Pleistocene record, not shown in Table 1, exists for Torreon, Coahuila [Freudenberg 1910, cited by Alvarez 1965]), but appear in Holocene deposits and are presently near or at most sites.

Presence of these taxa allows some estimates of climatic severity. Brattstrom (1961) noted that the desert tortoise (*Gopherus agassizi*) primarily is an animal of the desert, but "it does not occur in the low, hot Colorado desert, but rather in the high Mohave Desert of California and in the high deserts of Nevada, Arizona, and Utah. This area is classified . . . as dry subtropical." This species does not approach our area now, implying that present temperatures are too extreme, despite the protection of its burrowing habit. Mohlhenrich (1961) reported that neither *Sigmodon hispidus* nor *S. fulviventor* occur regularly in New Mexico where the mean annual temperature is less than 13°C (55°F) or the growing season is less than 180 days long. Humphries (1974) stated that distribution of the nine-banded armadillo (*Dasypus novemcinctus*) seems limited by "a lower limit of about 380 mm annual precipitation and an approximate upper limit of 9 freeze-days a year," a freeze-day being a day in which the air temperature does not climb above 0°C (32°F). Limiting factors on *Urocyon* are unknown at present.

Presence of the prairie vole (*Microtus ochrogaster*) throws light upon moisture relationships. At present, this rodent reaches only as far southwest as northeastern New Mexico (Rowlett 1972). Its habitat consists of grasslands, thicker and somewhat more mesic than found today

TABLE 1. Pleistocene and early Holocene vertebrates from cave sites in and near the Chihuahuan Desert. Presence of a taxon is indicated by a +. Numbers following the taxon refer to the list of sites and references at the end of the table. Extinct taxa are marked by †.

| OCCURRENCE | TAXON |
|---|---|
| ^ 25,000 25,000-12,500 12,500-10,000 <10,000 Historic | |
| + + + + + | Osteichthyes 3, 5, 22 |
| | Amphibia |
| | Caudata |
| | Ambystomatidae |
| o + + + + | <i>Ambystoma tigrinum</i> 6, 7, 19, 20 |
| | Anura |
| | Pelobatidae |
| o o + + + | <i>Scaphiopus couchi</i> 17 cf, 20 |
| o + o + + | <i>Scaphiopus bombifrons</i> 6, 7, 20 |
| o + o + + | <i>Scaphiopus hammondi</i> 7, 20 |
| | Bufonidae |
| o o o + + | <i>Bufo debilis</i> 20 |
| o + o + + | <i>Bufo punctatus</i> 7, 20 |
| o o o + + | <i>Bufo speciosus</i> , <i>B. cognatus</i> , and/or <i>B. woodhousei</i> 20 |
| o + o o + | <i>Bufo woodhousei</i> 6, 7 |
| o o o + + | <i>Bufo speciosus</i> 26 cf |
| | Hylidae |
| o + o o o | <i>Pseudacris triseriata</i> 6 |
| o o o + + | <i>Hyla arenicolor</i> 20 |
| | Ranidae |
| o + + + + | <i>Rana pipiens</i> 7, 17 cf, 20, 26 |
| | Reptilia |
| | Chelonia |
| | Testudinidae |
| + o o o o | † <i>Geochelone</i> 1 |
| o o + o o | <i>Terrapene carolina</i> 16 |
| + + + o o | <i>Gopherus</i> 2 |
| o + + o o | <i>Gopherus agassizi</i> 10 cf, 17 cf |
| | Squamata |
| | Lizard 27 |
| | Iguanidae |
| + + + + + | <i>Crotaphytus collaris</i> 2, 7, 17, 23, 26 |
| o + o o + | <i>Sceloporus undulatus</i> 6, 7, 26 |
| + + + + + | <i>Phrynosoma</i> 3, 19 |
| o + o + + | <i>Phrynosoma douglassi</i> 6, 7, 26 |
| o + + o + | <i>Phrynosoma cornutum</i> 7, 17 |
| o + o o + | <i>Phrynosoma obiculare</i> 11 |
| o + o o o | † <i>Phrynosoma josecitensis</i> 11 |
| | Scincidae |
| o o o + + | <i>Eumeces multivigatus</i> 26 |

TABLE 1. (Continued)

| OCCURRENCE | | | | TAXON |
|------------|---------------|---------------|----------|--|
| >25,000 | 25,000-12,500 | 12,500-10,000 | <10,000 | |
| | | | Historic | |
| ○ | ○ | + | + | <i>Eumeces obsoletus</i> 17, 23, 26 |
| | | | | Teiidae |
| ○ | ○ | ○ | + | <i>Cnemidophorus</i> 26 |
| | | | | Snake 16, 19, 27 |
| | | | | Colubridae |
| ○ | + | ○ | + | <i>Thamnophis</i> 26 |
| ○ | + | ○ | ○ | <i>Thamnophis (cyrtopsis, elegans, marcianus, radix group)</i> 7 |
| ○ | + | ○ | ○ | <i>Thamnophis proximus</i> 7 |
| ○ | ○ | ○ | + | <i>Masticophis</i> or <i>Coluber</i> 26 |
| ○ | + | + | ○ | <i>Coluber constrictor</i> 10, 17 |
| ○ | ○ | + | ○ | <i>Masticophis flagellum</i> 17 |
| ○ | + | ○ | ○ | <i>Salvadora</i> 6, 7 |
| ○ | ○ | ○ | + | <i>Arizona elegans</i> 26 |
| ○ | + | ○ | + | <i>Elaphe guttata</i> 7, 26 |
| ○ | + | + | + | <i>Elaphe subocularis</i> 10, 17, 23 |
| ○ | ○ | ○ | + | <i>Hypsiglena torquata</i> 26 |
| ○ | + | + | ○ | <i>Pituophis melanoleucus</i> 10, 17 |
| ○ | ○ | + | + | <i>Lampropeltis getulus</i> 17, 26 |
| ○ | ○ | ○ | + | <i>Rhinocheilus lecontei</i> 26 |
| ○ | ○ | ○ | + | <i>Tantilla</i> 26 |
| | | | | Crotalidae |
| ○ | + | + | + | <i>Crotalus</i> 6, 26 |
| ○ | + | + | + | <i>Crotalus atrox</i> 7, 10, 17, 24 |
| | | | | Aves |
| | | | | Podicipediformes |
| | | | | Podicipedidae |
| ○ | + | ○ | ○ | <i>Podiceps caspicus</i> 9 |
| ○ | ○ | + | ○ | <i>Aechmophorus occidentalis</i> 16 |
| | | | | Pelecaniformes |
| | | | | Phalacrocoracidae |
| ○ | + | ○ | ○ | <i>Phalacrocorax auritus</i> 9 |
| | | | | Ciconiiformes |
| | | | | Ardeidae |
| ○ | + | ○ | ○ | <i>Nycticorax nycticorax</i> 11 |
| | | | | Anseriformes |
| | | | | Anatidae |
| ○ | + | ○ | ○ | <i>Branta canadensis</i> 10 |
| ○ | ○ | + | ○ | <i>Anser albifrons</i> 17 ? |
| ○ | ○ | + | + | † <i>Anabernicula gracilentia</i> 17, 20 |
| ○ | + | ○ | ○ | † <i>Anabernicula oregonis</i> 9 cf |
| ○ | + | ○ | ○ | <i>Anas platyrhynchos</i> 9 |
| ○ | + | + | + | <i>Anas acuta</i> 9, 17, 20 tent. |

TABLE 1. (Continued)

| OCCURRENCE | TAXON |
|---------------|---|
| >25,000 | |
| 25,000-12,500 | |
| 12,500-10,000 | |
| <10,000 | |
| Historic | |
| o + + + + | <i>Anas carolinensis</i> 9 ?, 17, 20 tent. |
| o o o + + | <i>Mareca americana</i> 20 gen. & sp. tent. |
| o + o o + | <i>Aix sponsa</i> 9 |
| o + o o + | <i>Aythya valisineria</i> 9 |
| o o o + + | <i>Aythya collaris</i> or <i>A. affinis</i> 20 gen. & sp. tent. |
| o + o o o | <i>Histrionicus</i> 11 nr |
| o + o o + | <i>Mergus</i> 9 ? |
| | Falconiformes |
| | Cathartidae |
| + + + o + | <i>Cathartes aura</i> 1 gen. & sp. ?, 10, 13, 15 poss. Holocene, 16, 17, 20 |
| o o + o + | <i>Coragyps atratus</i> 13, 16 |
| + + + + o | † <i>Coragyps occidentalis</i> 1, 2, 3, 5, 8, 9, 10, 11, 15, 19, 20 |
| o + + o o | † <i>Breagyps clarki</i> 1, 3, 17 |
| o + + + o | <i>Gymnogyps californianus</i> 5 gen. & sp. ?, 9, 10, 11, 13, 16, 20, 25 |
| o + o o o | † <i>Teratornis merriami</i> 11 |
| | Accipitridae |
| o + o o o | <i>Elanus leucurus</i> 11 |
| o + + + + | <i>Buteo jamaicensis</i> 5, 6, 9, 17, 20 |
| o + + o + | <i>Buteo swainsoni</i> 5, 10, 13, 14, 16, 17 |
| o o + o + | <i>Buteo albonotatus</i> 17 ? |
| o + o o + | <i>Buteo lagopus</i> 9 |
| o + o o + | <i>Buteo nitidus</i> 9 |
| o + o o + | <i>Parabuteo unicinctus</i> 11 |
| o + + + + | <i>Aquila chrysaetos</i> 5, 9, 10, 11, 17, 20 |
| o + o o o | † <i>Spizaetus grinnelli</i> 11 |
| o o o + o | † <i>Spizaetus willetti</i> 20 |
| o + o o + | <i>Haliaeetus leucocephalus</i> 10 |
| o + + o o | † <i>Buteogallus fragilis</i> 5 gen. & sp. ?, 17 |
| o + o o o | † <i>Wetmoregyps daggetti</i> 11 |
| o + o o o | † <i>Neophrontops americanus</i> 9, 11 |
| o + o o o | † <i>Neogyps errans</i> 11 |
| o o + o + | <i>Accipiter striatus</i> 17 |
| o + + o + | <i>Accipiter cooperi</i> 5, 9, 13, 16 |
| o + o o + | <i>Circus hudsonius</i> 11 |
| | Falconidae |
| + + + + + | <i>Falco</i> 14 |
| o + o o o | † <i>Falco swarthi</i> 9 |
| o + + + + | <i>Falco mexicanus</i> 9, 10, 11, 13, 20 |
| + o + o + | <i>Falco peregrinus</i> 2, 17 |
| o + + o + | <i>Falco sparverius</i> 5, 9, 10, 11, 16, 17 |
| o + + o o | † <i>Caracara prelutosa</i> 5, 6, 8, 9, 10, 11, 14, 15, 17 |

TABLE 1. (Continued)

| OCCURRENCE | | | | TAXON | |
|------------|---------------|---------------|---------|----------|--|
| >25,000 | 25,000-12,500 | 12,500-10,000 | <10,000 | Historic | |
| ○ | ○ | ○ | + | + | <i>Caracara cheriway</i> 25 |
| + | + | + | + | + | Galliformes |
| | | | | | Tetraonidae |
| ○ | + | ○ | ○ | ? | Grouse 9 (2 spp. ?) |
| ○ | + | + | ○ | ? | <i>Tympanuchus pallidicinctus</i> 13, 16, 9 ? |
| ○ | + | + | + | ○ | <i>Centrocercus urophasianus</i> 10, 17, 20 |
| | | | | | Phasianidae |
| ○ | + | + | + | + | Quail 9 (2 spp. ?) |
| ○ | ○ | ○ | + | + | <i>Colinus virginianus</i> 25 |
| ○ | ○ | + | ○ | + | <i>Callipepla squamata</i> 17 |
| ○ | + | + | ○ | + | <i>Lophortyx</i> 10, 17 |
| ○ | ○ | + | + | ○ | <i>Oreortyx pictus</i> 13, 16, 17, 20 gen. & sp. tent. |
| ○ | + | ○ | ○ | + | <i>Cyrtonyx montezumae</i> 11 |
| ○ | + | ○ | ○ | ○ | <i>Dendrortyx</i> 11 ? |
| | | | | | Meleagrididae |
| ○ | + | ○ | ○ | ○ | † <i>Agriocharis crassipes</i> 11 |
| + | + | + | + | + | <i>Meleagris gallopavo</i> 1 cf., 9 ?, 10, 13, 16, 17, 20 gen. & sp. tent., 21 gen. & sp. cf |
| | | | | | Gruiformes |
| | | | | | Gruidae |
| ○ | ○ | + | ○ | + | <i>Grus canadensis</i> 16 |
| | | | | | Rallidae |
| ○ | + | ○ | ○ | ○ | † <i>Epirallus natator</i> 11 |
| ○ | ○ | + | ○ | + | <i>Porzana carolina</i> 17 |
| ○ | + | + | ○ | + | <i>Fulica americana</i> 11, 17 |
| | | | | | Charadriiformes |
| | | | | | Charadriidae |
| ○ | + | ○ | ○ | + | <i>Eupoda montana</i> 9 |
| ○ | + | ○ | + | + | <i>Numenius americanus</i> 5 gen. & sp. ?, 20 |
| ○ | + | ○ | ○ | ○ | † <i>Palnumenius victima</i> 11 |
| | | | | | Laridae |
| ○ | ○ | + | ○ | + | <i>Larus</i> 17 |
| | | | | | Burhinidae |
| ○ | + | ○ | ○ | ○ | <i>Burhinus</i> 11 |
| ○ | + | ○ | ○ | ○ | † <i>Burhinus</i> (small, extinct) 9 |
| ○ | + | ○ | ○ | ○ | <i>Burhinus</i> (larger) 9 |
| | | | | | Columbiformes |
| | | | | | Columbidae |
| ○ | + | ○ | ○ | + | <i>Columba fasciata</i> 11 |
| ○ | + | + | + | + | <i>Zenaidura macroura</i> 9, 11, 17, 20 |
| ○ | + | ○ | ○ | ○ | † <i>Ectopistes migratorius</i> 9 |

TABLE 1. (Continued)

| OCCURRENCE | TAXON |
|---------------|--|
| >25,000 | |
| 25,000-12,500 | |
| 12,500-10,000 | |
| <10,000 | |
| Historic | |
| | Psittaciformes |
| | Psittacidae |
| ○ + ○ ○ + | Parrot 9, 11 |
| ○ + ○ ○ + | <i>Rhynchopsitta pachyrhyncha</i> 11 |
| | Cuculiformes |
| | Cuculidae |
| ○ ○ + + + | <i>Geococcyx californianus</i> 17 (poss. all Holocene) |
| ○ + + + ○ | † <i>Geococcyx conklingi</i> 9, 10, 11, 17, 22 cf, 26 |
| | Strigiformes |
| | Tytonidae |
| ○ + + + + | <i>Tyto alba</i> 8, 9, 10, 11, 17, 20 |
| | Strigidae |
| + + + ○ + | <i>Otus</i> 2, 14 |
| ○ + + ○ + | <i>Otus asio</i> 11, 17 |
| ○ + ○ ○ + | <i>Otus trichopsis</i> 11 |
| ○ + ○ ○ + | <i>Otus flammeolus</i> 11 |
| ○ ○ ○ ○ ○ | <i>Bubo</i> (not <i>B. virginianus</i>) 11 |
| + + + + + | <i>Bubo virginianus</i> 2, 5, 6, 9, 11, 13, 16, 17, 20, 25 |
| ○ + ○ ○ ○ | <i>Ciccaba virgatus</i> 11 |
| ○ + ○ ○ + | <i>Glaucidium gnoma</i> 11 ? |
| ○ + + ○ + | <i>Speotyto cunicularia</i> 9, 10, 15, 17 |
| ○ + ○ ○ + | <i>Strix occidentalis</i> 11 |
| + ○ ○ ○ ○ | † <i>Strix brea</i> 2 cf |
| ○ + + + + | <i>Asio otus</i> 10 ?, 11, 14, 20 |
| ○ + + ○ + | <i>Asio flammeus</i> 5, 9 ?, 13, 16, 19 |
| ○ ○ + ○ ○ | <i>Aegolius funereus</i> 17 |
| ○ + + ○ + | <i>Aegolius acadicus</i> 11, 17 |
| | Caprimulgiformes |
| | Caprimulgidae |
| ○ + ○ ○ + | <i>Phalaenoptilus nuttalli</i> 9, 11 |
| | Apodiformes |
| | Apodidae |
| ○ ○ + ○ + | <i>Aeronautes saxatalis</i> 17 |
| | Piciformes |
| ○ + + ○ + | Picidae 5, 15 |
| ○ + + ○ + | <i>Colaptes</i> 13, 16 |
| ○ + + ○ + | <i>Colaptes cafer</i> 10, 17 |
| ○ + ○ ○ ○ | <i>Colaptes chrysoides</i> 11 |
| ○ ○ + ○ + | <i>Melanerpes formicivorus</i> 17 |
| | Passeriformes |
| | Tyrannidae |
| ○ ○ + ○ + | <i>Sayornis saya</i> 17 |

TABLE 1. (Continued)

| OCCURRENCE | TAXON |
|--|--|
| >25,000 25,000-12,500 12,500-10,000 <10,000 Historic | |
| | Alaudidae |
| ○ + + ○ + | <i>Eremophila alpestris</i> 10, 17 |
| | Corvidae |
| ○ ○ + ○ + | <i>Pica pica</i> 17 |
| + + + + + | <i>Corvus corax</i> 2 ?, 3, 5, 6, 8, 9, 10, 11, 14, 15, 17, 19, 20 |
| + ○ ○ ○ ○ | † <i>Corvus neomexicanus</i> 1, 2, 3 |
| ○ + + ○ + | <i>Gymnorhinus cyanocephalus</i> 10, 17 |
| | Troglodytidae |
| ○ ○ + ○ + | <i>Catherpes mexicanus</i> 17 |
| ○ ○ + ○ + | <i>Salpinctes obsoletus</i> 17 |
| | Mimidae |
| ○ ○ + ○ + | <i>Toxostoma</i> 17 |
| ○ ○ + ○ + | <i>Oreoscoptes montanus</i> 17 |
| | Turdidae |
| ○ + + ○ + | <i>Turdus migratorius</i> 10, 17 |
| ○ + + ○ + | <i>Sialia</i> 10, 17 |
| | Laniidae |
| ○ ○ + ○ + | <i>Lanius ludovicianus</i> 17 |
| | Icteridae |
| ○ ○ + ○ + | <i>Xanthocephalus xanthocephalus</i> 13, 16 |
| ○ + ○ ○ + | <i>Agelaius phoeniceus</i> 10 ? |
| ○ ○ + ○ + | <i>Molothrus ater</i> 17 |
| ○ ○ + ○ ○ | † <i>Pyelorhamphus molothroides</i> 17 |
| | Fringillidae |
| ○ + + ○ + | <i>Carpodacus mexicanus</i> 10, 17 |
| ○ ○ + ○ + | <i>Loxia curvirostra</i> 16 |
| ○ + + ○ + | <i>Pipilo erythrophthalmus</i> 10, 17 |
| ○ ○ + ○ + | <i>Pipilo fuscus</i> 17 |
| ○ ○ + ○ + | <i>Calamospiza melanocorys</i> 17 |
| | Mammalia |
| | Insectivora |
| | Soricidae |
| ○ + ○ ○ ○ | <i>Sorex cinereus</i> 11 |
| ○ + + ○ ○ | <i>Sorex vagrans</i> 5, 6, 12, 19 |
| ○ ○ + ○ ○ | <i>Sorex nanus</i> 12 |
| ○ + + ○ ○ | <i>Sorex merriami</i> 5, 6, 7, 15, 19, 27 |
| ○ + ○ ○ ○ | <i>Sorex sasseurii</i> 11 |
| ○ + + + ○ | <i>Cryptotis parva</i> 5, 19, 20 |
| ○ + ○ ○ ? | <i>Cryptotis mexicana</i> 11 |
| ○ + + + + | <i>Notiosorex crawfordi</i> 7, 12, 19, 20, 22, 27 |

TABLE 1. (Continued)

| OCCURRENCE | TAXON |
|---------------|--|
| >25,000 | |
| 25,000-12,500 | |
| 12,500-10,000 | |
| <10,000 | |
| Historic | |
| | Chiroptera |
| | Phyllostomatidae |
| ○ + ○ ○ + | <i>Leptoncyteris nivalis</i> (poss. <i>L. sanborni</i> of current classification) 11 |
| ○ + ○ ○ ○ | † <i>Desmodus stocki</i> 11 |
| | Vespertilionidae |
| ○ + + ○ + | <i>Myotis</i> 5, 6, 7, 19 |
| ○ + ○ ○ + | <i>Myotis velifer</i> 7 cf |
| ○ + ○ ○ ○ | † <i>Myotis magnamolaris</i> 7 cf |
| ○ + ○ ○ + | <i>Eptesicus fuscus</i> 6, 7, 11 |
| ○ + ○ ○ + | <i>Lasiurus cinereus</i> 6 cf, 11 |
| + + ○ ○ + | <i>Plecotus</i> 3 |
| ○ + ○ ○ + | <i>Plecotus townsendi</i> 6 cf |
| ○ + ○ ○ ○ | † <i>Plecotus tetralophodon</i> 11 |
| | Molossidae |
| ○ + ○ ○ ○ | † <i>Tadarida constantinei</i> 4 |
| + ○ ○ ○ + | <i>Tadarida brasiliensis</i> 3 |
| + ○ ○ ○ + | <i>Tadarida macrotis</i> 1, 3 cf |
| | Primates |
| | Hominidae |
| ○ + + ○ + | <i>Homo sapiens</i> 10, 16 |
| | Edentata |
| | Dasypodidae |
| + ○ ○ ○ ○ | <i>Dasypus</i> |
| + + ○ ○ ○ | † <i>Sloth</i> 2, 5 |
| | Megalonychidae |
| ○ + ○ ○ ○ | † <i>Megalonyx</i> 10 ? |
| | Megatheriidae |
| ○ + + + ○ | † <i>Nothrotherium</i> 10, 11, 17, 21 |
| ○ ○ + ○ ○ | † <i>Nothrotherium shastense</i> 18 |
| | Mylodontidae |
| ○ + ○ ○ ○ | † <i>Paramylodon</i> 10? |
| | Lagomorpha |
| | Leporidae |
| + + + + + | <i>Sylvilagus</i> 2, 3, 11, 15, 20, 27 |
| ○ + + ○ ○ | <i>Sylvilagus nuttalli</i> 5, 6, 7, 14, 19 cf |
| ○ ○ ○ ○ + | <i>Sylvilagus floridanus</i> 16 ref |
| + ○ ○ ○ ○ | <i>Sylvilagus auduboni</i> or <i>S. floridanus</i> 1 |
| ○ ○ + + + | <i>Sylvilagus auduboni</i> 16 ref, 21 |
| ○ + ○ ○ ○ | † <i>Sylvilagus leonensis</i> 11 |
| + + + + + | <i>Lepus</i> 2, 5, 7, 10, 15, 19, 20, 27 |
| ○ + + ○ ○ | <i>Lepus townsendi</i> 6, 16 |

TABLE 1. (Continued)

| OCCURRENCE | TAXON |
|---------------|--|
| >25,000 | |
| 25,000-12,500 | |
| 12,500-10,000 | |
| <10,000 | |
| Historic | |
| + ○ ○ + + | <i>Lepus californicus</i> 1, 3, 21 |
| ○ ○ + ○ ○ | <i>Lepus alleni</i> 16 ref |
| | Rodentia |
| | Sciuridae |
| ○ + + ○ ○ | <i>Marmota</i> 11, 12 |
| ○ + + ○ ○ | <i>Marmota flaviventris</i> 5 cf, 6 cf, 16 |
| + + + + + | <i>Spermophilus</i> 3, 10, 19, 20, 27 |
| ○ + ○ ○ ○ | <i>Spermophilus richardsoni</i> 6 ? |
| ○ + ○ ○ ○ | <i>Spermophilus tridecemlineatus</i> 5, 6, 7 |
| ○ + ○ ○ + | <i>Spermophilus spilosoma</i> 11 cf |
| ○ ○ ○ + + | <i>Spermophilus variegatus</i> 21 |
| + + + + + | <i>Cynomys</i> 3, 27 |
| ○ ○ + + + | <i>Cynomys luaovicianus</i> 16, 20 |
| ○ + ○ ○ ○ | <i>Cynomys (Leucocrossuromys)</i> 6 |
| ○ ○ ○ + ○ | <i>Cynomys gunnisoni</i> 21 ref |
| ○ + ○ ○ + | <i>Sciurus alleni</i> 11 ? |
| + + + + + | Geomyidae 3, 17 ? |
| + + + + + | <i>Thomomys</i> 2, 10, 19 |
| ○ ○ + ○ ○ | <i>Thomomys umbrinus</i> 16 |
| ○ + + + + | <i>Thomomys bottae</i> 5, 6, 7, 11, 16, 20 |
| ○ + ○ ○ ○ | <i>Thomomys talpoides</i> 5, 6, 7 |
| + + + + + | <i>Pappogeomys</i> 11, 16 ? |
| + + + + + | <i>Pappogeomys castanops</i> 1, 5 cf, 11, 15, 16, 21 |
| ○ + ○ ○ ○ | † <i>Heterogeomys onerosus</i> 11 |
| | Heteromyidae |
| ○ + ○ ○ + | <i>Liomys irroratus</i> 11 |
| + + ○ + + | <i>Perognathus</i> 3 |
| ○ ○ ○ + + | <i>Perognathus</i> (large) 20 |
| ○ + ○ + + | <i>Perognathus</i> (small) 7, 20 |
| ○ ○ ○ + + | <i>Perognathus intermedius</i> 21 ref |
| + ○ + + + | <i>Dipodomys</i> (small) 1, 20 |
| ○ ○ + ○ + | <i>Dipodomys ordi</i> 16 |
| + + + + + | <i>Dipodomys spectabilis</i> 3, 7, 19, 20 |
| | Cricetidae |
| ○ + ○ ○ + | <i>Reithrodontomys</i> 7 |
| ○ + ○ ○ + | <i>Reithrodontomys megalotis</i> 11 |
| + + + ○ + | <i>Peromyscus</i> 2, 3, 19, 26 |
| ○ + ○ ○ ○ | <i>Peromyscus crinitus</i> 6 ?, 7 ? |
| ○ + + ○ + | <i>Peromyscus maniculatus</i> 5 ?, 6 cf, 7 cf |
| ○ + ○ ○ + | <i>Peromyscus leucopus</i> 7 (poss. Holocene) |
| ○ + ○ ○ + | <i>Peromyscus boylii</i> 11, 7 ? |
| ○ + ○ ○ + | <i>Peromyscus difficilis</i> 6 cf |

TABLE 1. (Continued)

| OCCURRENCE | TAXON |
|--|--|
| >25,000 25,000-12,500 12,500-10,000 <10,000 Historic | |
| + + + o + | <i>Onychomys</i> 5 |
| + + + o + | <i>Onychomys leucogaster</i> 3, 6, 19 |
| + + o + + | <i>Sigmodon</i> 3, 20 |
| o + o + + | <i>Sigmodon hispidus</i> 11 |
| + + + + + | <i>Neotoma</i> 1, 2, 3, 5, 7, 17, 19, 20, 27 |
| o o + o o | <i>Neotoma floridanus</i> 15 cf |
| o + o + + | <i>Neotoma albigula</i> 6 cf, 11, 21 |
| o o + o o | <i>Neotoma stephensi</i> 16 (<i>N. lepida</i> ref) |
| o + o o + | <i>Neotoma mexicana</i> and/or <i>N. cinerea</i> 6 |
| o o + o + | <i>Neotoma mexicana</i> 16 ref |
| o o + o + | <i>Neotoma cinerea</i> 16 |
| + + + + + | <i>Microtus</i> 5, 19 |
| o o o + o | <i>Microtus pennsylvanicus</i> 20, 22, 27 |
| o o + + o | <i>Microtus montanus</i> 17 cf, 20, 27 |
| o + + o o | <i>Microtus longicaudus</i> 6, 7, 16 ref |
| o + + + + | <i>Microtus mexicanus</i> 6, 7, 10, 11, 16, 20, 27 |
| + + o + o | <i>Microtus ochrogaster</i> 3, 7, 20 |
| o + o o o | <i>Lagurus curtatus</i> 6, 7 |
| o + o o + | <i>Ondatra zibethicus</i> 6 |
| o + o o o | <i>Synaptomys cooperi</i> 11 |
| o + o + + | <i>Erethizon dorsatum</i> 5, 6, 11, 21 |
| | Carnivora |
| | Canidae |
| + + + o + | <i>Canis latrans</i> 3, 5, 6, 10, 16, 17, 18, 27 cf |
| + + + o + | <i>Canis lupus</i> 1, 2, 5, 16 |
| + + o + o | † <i>Canis dirus</i> 1, 10, 11, 12, 21 ref |
| + + + o + | <i>Vulpes</i> 15 |
| o o + o + | <i>Vulpes vulpes</i> 16 |
| o + o o + | <i>Vulpes macrotis</i> or <i>V. velox</i> 10 |
| + + + o o | <i>Vulpes velox</i> 1 gen. & sp. cf, 2 gen. & sp. cf, 5, 6, 7, 8, 14, 16, 19 |
| o o + + + | <i>Vulpes</i> or <i>Urocyon</i> 17, 20 |
| + o o + + | <i>Urocyon cinereoargenteus</i> 1, 2, 3, 21, 27 |
| | Ursidae |
| o + + o o | † <i>Arctodus</i> 10, 16 gen. ref |
| o + o o o | † <i>Tremarctos mexicanus</i> 11 |
| o + + + + | <i>Ursus americanus</i> 8, 11 nr, 18, 20 |
| o o o + + | <i>Ursus arctos</i> 21 ref |
| | Procyonidae |
| + + + o + | <i>Bassariscus</i> 1, 5 |
| o o + o + | <i>Bassariscus astutus</i> 16, 27 cf |
| o + o o o | † <i>Bassariscus sonoitensis</i> 11 |

TABLE 1. (Continued)

| OCCURRENCE | TAXON |
|---------------|---|
| >25,000 | |
| 25,000-12,500 | |
| 12,500-10,000 | |
| <10,000 | |
| Historic | |
| | Mustelidae |
| + + + o + | <i>Mustela</i> 10 |
| + + + o + | <i>Mustela frenata</i> 3, 5, 6, 8, 19 |
| o + o o o | † <i>Mustela reliquus</i> 11 |
| o o + o + | <i>Mustela nigripes</i> 16 |
| o + + o + | <i>Taxidea</i> 10 |
| o + + o + | <i>Taxidea taxus</i> 5, 11, 16, 17 |
| + + + + + | <i>Spilogale putorius</i> 3, 5, 11, 17, 20 |
| o + + o + | <i>Mephitis</i> 10 |
| o + + o + | <i>Mephitis mephitis</i> 5, 17, 11 |
| o + + o + | <i>Conepatus mesoleucus</i> 11 prob., 14, 16 |
| | Felidae |
| + + + + + | <i>Felis</i> 1, 2, 5 |
| + + o o + | <i>Felis onca</i> 2, 11 |
| o + + + + | <i>Felis concolor</i> 10, 16, 21 |
| o + o o o | † <i>Felis atrox</i> 5 ?, 11 |
| + + + + + | <i>Felis rufus</i> 3, 5, 8, 16, 17, 21 |
| o + o o o | † <i>Smilodon</i> 11 |
| | Proboscidea |
| | Elephantidae |
| o o + o o | † <i>Mammuthus columbi</i> 12 |
| | Perissodactyla |
| | Tapiridae |
| + o o o o | † <i>Tapirus</i> 3 |
| | Equidae |
| + + + + o | † <i>Equus</i> 2, 3, 5, 8, 9, 10, 12, 14, 15, 17, 19, 20, 27 |
| o + + o o | † <i>Equus conversidens</i> 6 ?, 7 cf, 11, 16 (<i>E. tau</i>) |
| o o + o o | † <i>Equus excelsus</i> 16 |
| o o + o o | † <i>Equus fraternus</i> 17 |
| o o o + o | † <i>Equus simplicatus</i> 21 |
| | Artiodactyla |
| + + + + o | Camelidae 2 ?, 11, 20 |
| + + + o o | † <i>Camelops</i> 1, 3, 8, 16, 17 |
| o o + o o | † <i>Camelops hesternus</i> 14 ?, 15 ? |
| o + + + o | † <i>Tanupolama</i> 5, 8, 10, 14, 19 |
| | Cervidae |
| o o o + + | † <i>Cervus merriami</i> 21 ref |
| + + + + + | <i>Odocoileus</i> 2 ?, 5, 11, 15 |
| o o + + + | <i>Odocoileus hemionus</i> 16, 21 |
| o o + + + | <i>Odocoileus virginianus</i> 16, 21 |
| o o + o o | † <i>Sangamona</i> 12 |
| o o + o o | † <i>Sangamona fricki</i> 16 |

TABLE 1. (Continued)

| OCCURRENCE | TAXON |
|---------------|---|
| >25,000 | |
| 25,000-12,500 | |
| 12,500-10,000 | |
| <10,000 | |
| Historic | |
| o + + + + | Antilocapridae |
| o + + + + | <i>Antilocapra</i> 6 gen. ? |
| o + + + + | <i>Antilocapra americana</i> 7, 16 ref, 21 |
| o + o o o | † <i>Stockoceros conklingi</i> 9 (presumably), 11, 17 |
| o o + o o | † <i>Tetrameryx onusrosagris</i> 16 |
| + + + o o | <i>Breameryx</i> 1, 2, 3, 5, 8, 10, 17 |
| | Bovidae |
| o + + o + | <i>Bison</i> 10 |
| o + + o o | <i>Bison antiquus</i> 7 cf, 16, 19 cf |
| o + + o o | <i>Preptoceras</i> 11 |
| o o + o o | <i>Preptoceras sinclairi</i> 16 |
| o o + o o | <i>Euceratherium collinum</i> 16 |
| o + o o o | <i>Oreamnos harringtoni</i> 9 |
| o + + + + | <i>Ovis canadensis</i> 5, 16 ref, 21 |

>25,000 B.P.

- 1 Sabertooth Camel Maze, Dry Cave, 4200 ft, Eddy County, N. M. MALB Loc. 2 and 5. 25,160±1730 B.P. (TX-1775), C¹⁴ on bone carbonate. Hurley 1972.
- 2 Room of the Vanishing Floor, Dry Cave, 4200 ft, Eddy County, N. M. MALB Loc. 26 and 27. 33,590±1500 B.P. (TX-1773), C¹⁴ on bone carbonate. Hornedo 1971; Hurley 1972.
- 3 Lost Valley, Dry Cave, 4200 ft, Eddy County, N. M. MALB Loc. 1 and 17. 29,290±1060 B.P. (TX-1774), C¹⁴ on bone carbonate. Hurley 1972.

25,000-12,500 B.P.

- 4 New Cave, Eddy County, N. M. >17,800 B.P., C¹⁴ on bat guano. Lawrence 1960.
- 5 Animal Fair, Dry Cave, 4200 ft, Eddy County, N. M. MALB Loc. 22. 15,030±210 B.P. (I-6201), C¹⁴ on bone collagen. Buckley 1973; Harris and Mundel 1974; Hornedo 1971; Hurley 1972.
- 6 Harris' Pocket, Dry Cave, 4200 ft, Eddy County, N. M. MALB Loc. 6. 14,470±250 B.P. (I-3365), C¹⁴ on *Neotoma* dung. Harris 1970b; Holman 1970; Hornedo 1971; Hurley 1972.
- 7 Bison Chamber, Dry Cave, 4200 ft, Eddy County, N. M. MALB Loc. 4. <14,470, >10,730 B.P. on stratigraphic grounds. Harris 1970b; Holman 1970; Hornedo 1971; Hurley 1972.
- 8 Early Man Corridor, Dry Cave, 4200 ft, Eddy County, N. M. MALB Loc. 31. <15,030, >11,880 B.P. on stratigraphic grounds. Hornedo 1971; Hurley 1972.
- 9 Dark Canyon Cave, ca. 3600 ft, Eddy County, N. M. <25,000, >12,500 B.P. (tentative, on faunal grounds). C. R. Harrington, pers. comm.; Howard 1971; E. L. Lundelius pers. comm.

TABLE 1. (Continued)

- 10 Conkling Cavern, 4590 ft, Bishop's Cap, Dona Ana County, N. M. <25,000, >12,500 B.P. (tentative, on faunal grounds). Brattstrom 1964; Bryan 1929; Conkling 1932; Howard and Miller 1933; Smartt 1972.
- 11 San Josecito Cave, 7700 ft, Aramberri Province, Nuevo Leon, Mexico. <25,000, >12,500 B.P. (tentative, on faunal grounds). Brattstrom 1955; Cushing 1945; Findley 1953; Furlong 1943; Hall 1960; Handley 1955; Hooper 1952; Howard 1940; Jakway 1958; Jones 1958; Miller 1940, 1941, 1942, 1943; Russell 1960; Stock 1942, 1950, 1953.
- 12,500-10,000 B.P.
- 12 Hermits Cave, ca. 6000 ft, Eddy County, N. M. 12,900±350, 12,270±450, 11,850±450 B.P. on charcoal and wood. Findley 1965; Hester 1960; Schultz 1968; Schultz et al. 1970.
- 13 Rocky Arroyo Cave, Eddy County, N. M. <12,500, >10,000 B.P. (tentative, on faunal grounds). Howard 1962; Howard and Miller 1933; Wetmore 1931, 1932.
- 14 Camel Room, Dry Cave, 4200 ft, Eddy County, N. M. MALB Loc. 25. Ca. 12,000 B.P. on stratigraphic grounds. Hurley 1972.
- 15 Stalag 17, Dry Cave, 4200 ft, Eddy County, N. M. MALB Loc. 23. 11,880±250 B.P. (I-5987), C¹⁴ on charcoal. Buckley 1973; Hornedo 1971; Hurley 1972.
- 16 Burnet Cave, 4600 ft, Eddy County, N. M. 7432±300 B.P., C¹⁴ on charcoal; date considered too young on archaeological grounds by Wormington (1957) and by myself on faunal grounds. Gehlbach and Holman 1974; Hester 1960; Howard 1932; Murray 1957; Schultz 1943, 1968; Schultz and Howard 1935; Schultz and Martin 1970; Schultz et al. 1970.
- 17 Shelter Cave, 4700 ft, Dona Ana County, N. M. <12,500, >10,000 B.P. in part (tentative, on faunal grounds); part of deposits post Pleistocene. Brattstrom 1964; Hall 1936; Howard 1931a, 1931b, 1962, 1964, 1971; Miller 1932; Smartt 1972; Stock 1930, 1932.
- 18 Aden Crater, Dona Ana County, N. M. MALB Loc. 42. 11,080±200 B.P. (also 9840±160 on contaminated tissue), C¹⁴ on sloth dung; non-sloth material may be of different age. Eames 1930; Lull 1929; Simons and Alexander 1964.
- 19 TT II, Dry Cave, 4200 ft, Eddy County, N. M. MALB Loc. 54 (includes some items originally catalogued under MALB 4). 10,730±150 B.P. (I-6200), C¹⁴ on bone collagen. Buckley 1973; Harris et al. 1973.
- <10,000 B.P.
- 20 Howells Ridge Cave, 5500 ft, Grant County, N.M. All Holocene? (see Van Devender and Worthington, this volume); on faunal evidence, >10,000 B.P. in part. Harris et al. 1973; Howard 1962, 1964; Smartt, 1972.
- 21 Williams Cave, Culberson County, Texas. Probably mixed late Wisconsin (<12,500, >10,000 B.P.) and Holocene. Ayer 1936.
- 22 Khulo Site, 4300 ft, Dona Ana County, N. M. MALB Loc. 21. Latest Pleistocene and Holocene or Holocene only; C¹⁴ dates conflict. Smartt 1972.
- 23 Wylde Cave, Bishop's Cap, Dona Ana County, N. M. LACMVP Loc. 1132. Late Wisconsin or Holocene. Brattstrom 1964.
- 24 Fosberg Cave, Bishop's Cap, Dona Ana County, N. M. LACMVP Loc. 1154. Late Wisconsin or Holocene. Brattstrom 1964.
- 25 Mule Ears Peak Cave, Brewster County, Texas. 1500-3000 B.P. (based on possible association with archaeological material). Wetmore and Friedmann 1933.

TABLE 1. (Continued)

26 Pratt Cave, Culberson County, Texas. <6000 B.P. (based on artifacts, pollen, stratigraphy, mollusks, and vertebrates). Gehlbach and Holman 1974.

NO AGE ESTIMATE

27 Anthony Cave, 5100 ft, Dona Ana County, N. M., and El Paso County, Texas. MALB Loc. 29. Pleistocene (possibly both stadial and interstadial material present); possible Holocene present. Smartt 1972.

in east-central or southeastern New Mexico—thus more effective warm-season precipitation is implied, perhaps produced in part by cool summer temperatures.

Thus interstadial conditions, insofar as recorded by these faunas, seem to have included temperatures less extreme than those of today and greater effective moisture, at least during the warm season.

The peak of late Wisconsin pluvial conditions may be absent from the record, though it could be represented in New Cave, Conkling Cavern, Dark Canyon Cave, or San Josecito Cave; the earliest definitive C^{14} date is on bone collagen from the Animal Fair site within Dry Cave (15,030 \pm 210 B.P., I-6201). Extralimital forms from the 16 sites considered likely to represent pluvial conditions are shown in Table 2.

Inspection of the present ranges of these extant, extralimital taxa is most instructive, for these forms were not drawn randomly from divers directions, but overwhelmingly represent kinds with major geographic distributions either to the northwest (particularly in the Great Basin) or across the Central or Northern Great Plains; a few show both patterns (e.g., *Lepus townsendi*). Approximately 22 of the 32 extralimital, pluvial taxa (excluding San Josecito Cave for the present) fall into these patterns (Table 2). At least two near-extralimital birds, the Western Grebe (*Aechmophorus occidentalis*) and the Black-billed Magpie (*Pica pica*), likewise have a dominant northwestern distribution; because they do occur casually near the site from which their remains are identified, they are not considered in the count.

One mammal (the dwarf shrew, *Sorex nanus*) seems to fit no general pattern, but can be described as a Southern and Central Rocky Mountain taxon. The Boreal Owl (*Aegolius funereus*) is a transcontinental, northern species. There remains only a smattering of forms to represent other geographic areas. The Passenger Pigeon (*Ectopistes migratorius*) and the eastern box turtle (*Terrapene carolina*) are eastern representatives. The desert tortoise and the antelope jack rabbit (*Lepus alleni*) are Sonoran animals (but see Brattstrom 1961, quoted above). *Lepus alleni* is an anomaly zoogeographically and it seems quite likely the tentative identification is incorrect. Schultz and Howard (1935) pointed out that

TABLE 2. Extralimital taxa in cave faunas in or near the Chihuahuan Desert by time interval and present geographic affinity.

| | >25,000 B.P. | 25,000-12,500 B.P. | 12,500-10,000 B.P. | <10,000 B.P. |
|--|--------------|--------------------|--------------------|--------------|
| Northwestern Distribution | | | | |
| <i>Pseudacris triseriata</i> | 0 | + | 0 | 0 |
| <i>Centrocercus urophasianus</i> | 0 | + | + | + |
| <i>Oreortyx pictus</i> | 0 | 0 | + | ? |
| <i>Sorex vagrans</i> | 0 | + | + | 0 |
| <i>Sorex merriami</i> | 0 | + | + | 0 |
| <i>Sylvilagus nuttalli</i> | 0 | + | + | 0 |
| <i>Lepus townsendi</i> | 0 | + | + | 0 |
| <i>Marmota flaviventris</i> | 0 | + | + | 0 |
| <i>Cynomys (Leucocrossuromys) and</i> | | | | |
| <i>Cynomys gunnisoni</i> | 0 | + | 0 | + |
| <i>Thomomys talpoides</i> | 0 | + | 0 | 0 |
| <i>Peromyscus crinitus</i> ? | 0 | + | 0 | 0 |
| <i>Neotoma stephensi</i> | 0 | 0 | + | 0 |
| <i>Neotoma cinerea</i> | 0 | 0 | + | 0 |
| <i>Microtus montanus</i> | 0 | 0 | + | + |
| <i>Microtus longicaudus</i> | 0 | + | + | 0 |
| <i>Lagurus curtatus</i> | 0 | + | 0 | 0 |
| Central and Northern Great Plains Distribution | | | | |
| <i>Sorex cinereus</i> | 0 | + | 0 | 0 |
| <i>Cryptotis parva</i> | 0 | + | + | + |
| <i>Lepus townsendi</i> | 0 | + | + | 0 |
| <i>Spermophilus richardsoni</i> ? | 0 | + | 0 | 0 |
| <i>Spermophilus tridecemlineatus</i> | 0 | + | 0 | 0 |
| <i>Neotoma floridanus</i> | 0 | 0 | + | 0 |
| <i>Microtus pennsylvanicus</i> | 0 | 0 | 0 | + |
| <i>Microtus ochrogaster</i> | + | + | 0 | + |
| <i>Synaptomys cooperi</i> | 0 | + | 0 | 0 |
| <i>Vulpes velox</i> | ? | + | + | 0 |
| Northern Distribution | | | | |
| <i>Histrionicus</i> | 0 | + | 0 | 0 |
| <i>Aegolius funereus</i> | 0 | 0 | + | 0 |
| Rocky Mountain Distribution | | | | |
| <i>Sorex nanus</i> | 0 | 0 | + | 0 |
| Eastern Distribution | | | | |
| <i>Terrapene carolina</i> | 0 | 0 | + | 0 |
| <i>Ectopistes migratorius</i> | 0 | + | 0 | 0 |
| <i>Dasyus</i> (or Southern ?) | + | 0 | 0 | 0 |
| Southern Distribution | | | | |
| <i>Dendrortyx</i> ? | 0 | + | 0 | 0 |

TABLE 2. (Continued)

| | > 25,000 B.P. | 25,000-12,500 B.P. | 12,500-10,000 B.P. | < 10,000 B.P. |
|--------------------------|---------------|--------------------|--------------------|---------------|
| <i>Burhinus</i> (2 spp.) | 0 | + | 0 | 0 |
| <i>Ciccaba virgatus</i> | 0 | + | 0 | 0 |
| Parrot | 0 | + | 0 | 0 |
| <i>Thomomys umbrinus</i> | 0 | 0 | + | 0 |
| Sonoran Distribution | | | | |
| <i>Gopherus agassizi</i> | 0 | + | + | 0 |
| <i>Lepus alleni</i> | 0 | 0 | + | 0 |

the specimen is heavier than any of the *L. alleni* specimens they had seen. They also stated that the fossil is "closely related to *L. giganteus* Brown from the middle Pleistocene of Arkansas and Nebraska." As I have suggested elsewhere (Harris 1970b), *L. callotis* (including *L. gailardi*) would make somewhat better sense, representing the high Mexican grasslands. An extinct species also is possible.

Several species may represent southern distributions: thick-knees (*Burhinus* spp.), the southern pocket gopher (*Thomomys umbrinus*, given as *Thomomys fulvus intermedius* referred), and parrot. All are suspect in terms of representing southern taxa, however. Although *Burhinus* now is southern in distribution, at least one of the species is extinct (Howard 1971) and possibly also the other—northern, now extinct species possibly may be involved; the parrot, likewise, has not been shown to be a southern species. The identification of *T. umbrinus* was tentative and, in view of the difficulties in identifying fragmentary gopher remains of this genus, may well represent a different species. Confirmation or rejection of these taxa as southern elements could help clarify the late- or post-Pleistocene picture considerably.

The traditional picture of late Pleistocene events in the Southwest has included the invasion of the lowlands by environments similar to those now found in the southwestern high mountains (particularly in the southern end of the Rockies in northern New Mexico), carrying the highland vertebrate fauna into the lower altitudes (cf. Stearns 1942; Murray 1957; Dalquest et al. 1969). Yet the distributions of the extralimital taxa clearly show that perhaps only one taxon (*Sorex nanus*) should be considered typical of that area. The other extralimital taxa that do occur in the Southern Rockies today are in a habitat that is

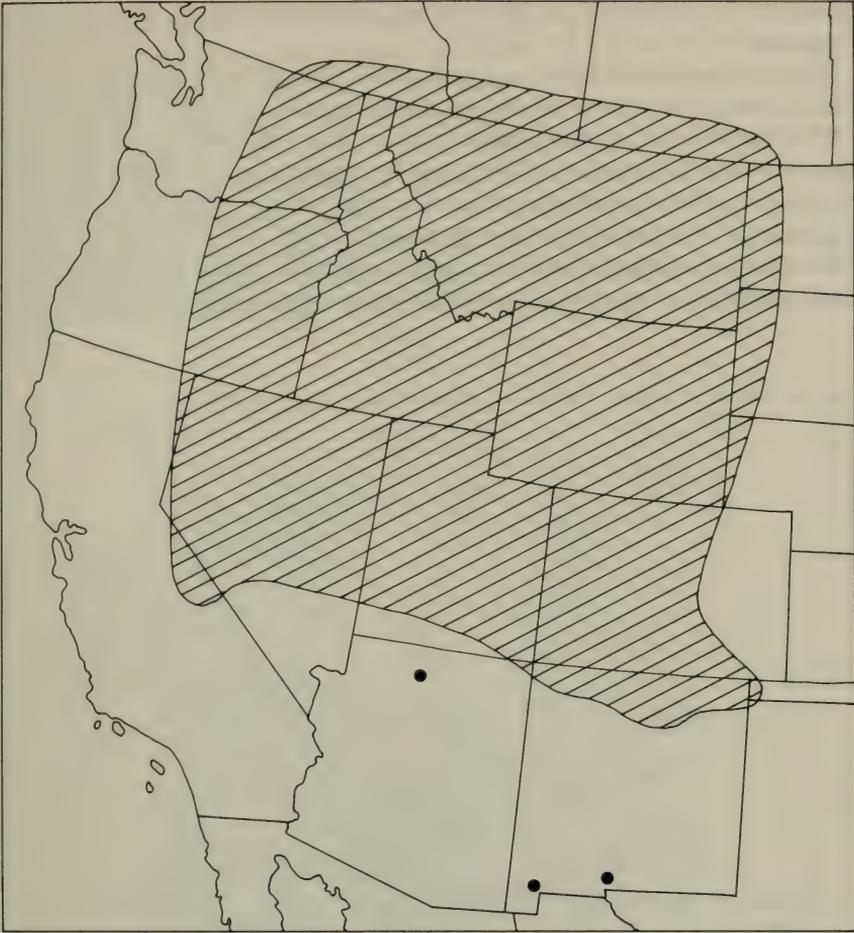


Fig. 2. Historic (hatched area) and Southwestern, late Pleistocene (dots) distribution of the Sagebrush Grouse (*Centrocercus urophasianus*).

anomalous for them—they are outlying populations of taxa living in low to moderate elevations over most of their ranges, but able at their southernmost periphery to meet their climatic requirements only in the high mountain masses. A picture more realistic than the traditional would seem to be advancement to the south of grassland forms now in the Central and Northern Great Plains and a southeasterly movement by cool, shrub desert vertebrates and associated higher-elevation faunal elements. Hibbard et al. (1965) have documented repeated southward movements of northern grassland forms into the Central Plains and others (e.g., Dalquest 1965; Dalquest et al. 1969) have shown these taxa reached far to the south. This invasion of a more northern type of

grassland fauna seems to be covered relatively well in the scientific literature.

The movement of sagebrush and other Great Basin elements far to the southeast has been hinted by pollen studies (e.g., Foreman et al. 1959; Hafsten 1961), but little faunal evidence has been apparent. The first breakthrough occurred with the recognition of the sagebrush vole (*Lagurus curtatus*) from the Isleta Caves in north-central New Mexico (Harris and Findley 1964) and then later at Dry Cave (Harris 1970b). With this focusing of attention to the northwest, other data, some new and some old but generally ignored, become meaningful. Many of these

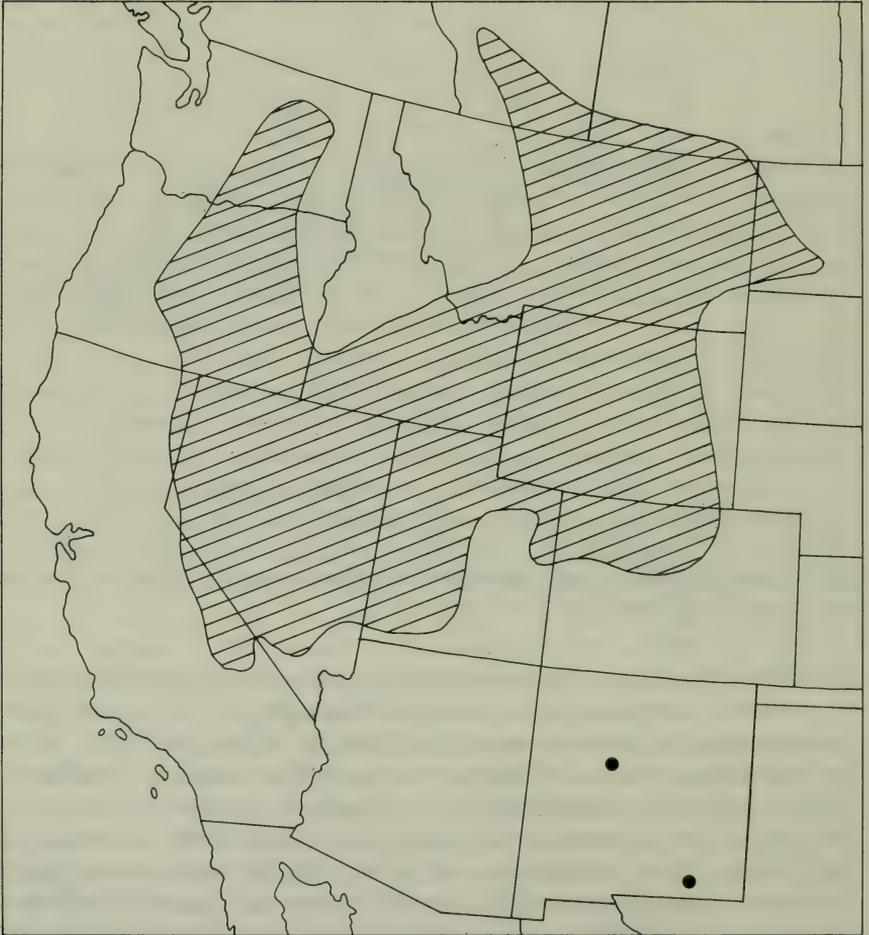


Fig. 3. Historic (hatched area) and Southwestern, late Pleistocene (dots) distribution of the Sagebrush Vole (*Lagurus curtatus*).

data are apparent in Tables 1 and 2; Figs. 2 and 3 illustrate some such data. Other pertinent information includes the recent recognition of another sagebrush-limited form, the pygmy rabbit (*Sylvilagus idahoensis*) from the Isleta Caves (Fig. 4). Presence of a relict population of the sagebrush lizard (*Sceloporus graciosus*) in the sandhills of southeastern New Mexico and western Texas (Degenhardt and Jones 1972) documents former sagebrush habitat in that general area (Fig. 5). J. S. Findley (pers. comm.) has pointed out that a number of birds (e.g., several forms of juncos) migrate southeasterly to winter in New Mexico and adjacent areas; possibly this reflects a pattern set up during stadial times.

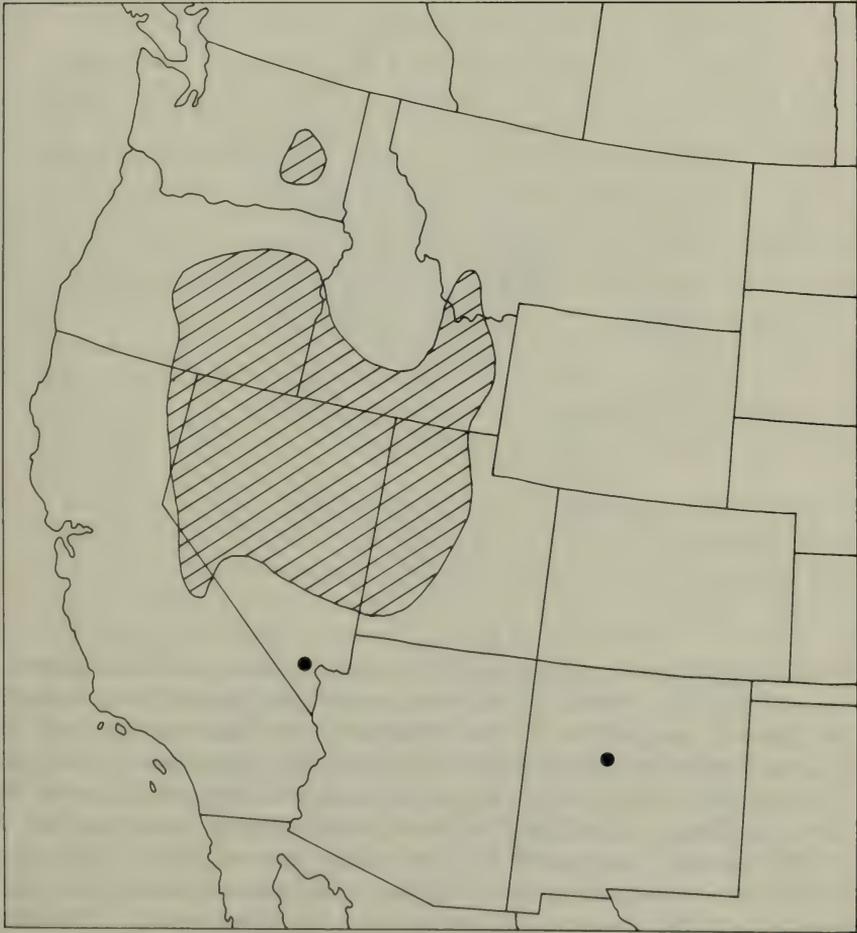


Fig. 4. Historic (hatched area) and Southwestern, late Pleistocene (dots) distribution of the pygmy rabbit (*Sylvilagus idahoensis*).

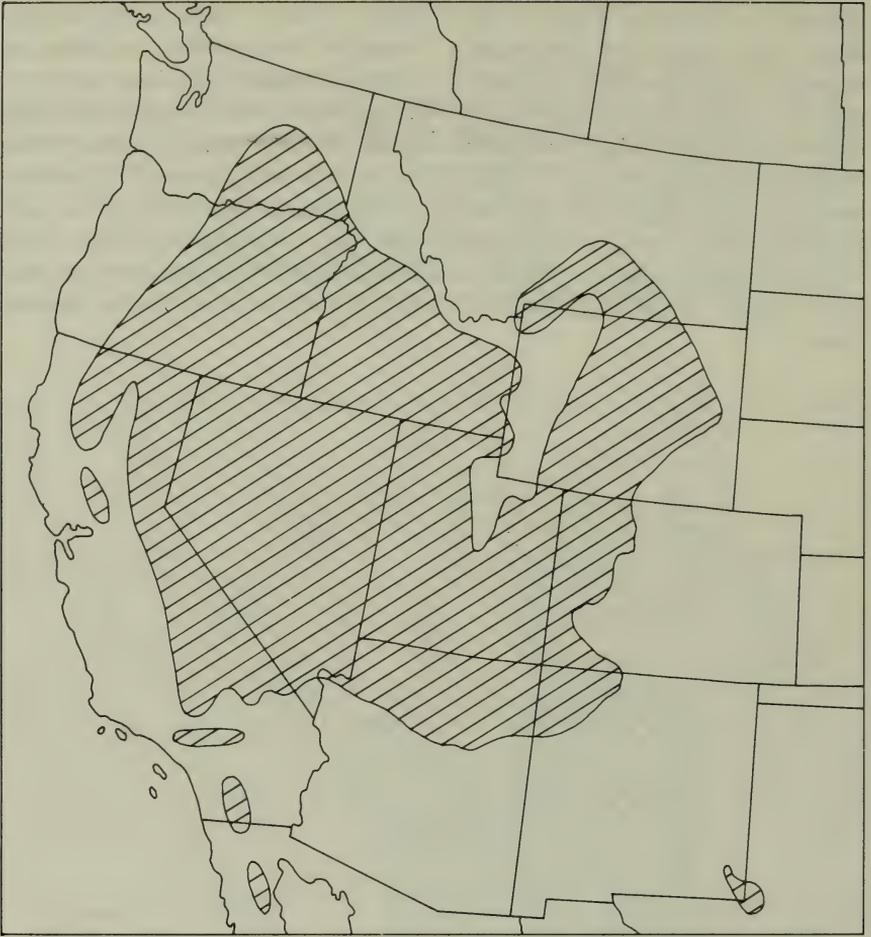


Fig. 5. Current distribution of the sagebrush lizard (*Sceloporus graciosus*).

The conditions in the northern Chihuahuan Desert area that allowed this pattern during the late Wisconsin would seem in part to be a result of different seasonality of precipitation from that now present. In general, winter precipitation becomes increasingly important to the west and northwest with distance from the northern Chihuahuan Desert. In the Great Basin, specifically, winter precipitation is dominant, but a healthy summer component also is present (Shreve 1942): "The low precipitation is, however, more uniformly distributed through the year than in the other desert areas. At most localities the rainfall is heaviest in the spring months, with June the dryest month. The rains of mid-summer are lighter, in most localities, than those of the autumn and

early winter." Displacement of present winter-storm tracks to the southward would go far toward bringing these conditions into our area; at the same time, summer precipitation, denied the Great Basin because of its distance from the Gulf of Mexico, may still have been available. Cool summer temperatures, possibly less extreme winter temperatures, increased winter and spring precipitation from the Pacific, and continued summer precipitation originating in the Gulf of Mexico all combined to allow the association within a limited geographic area of the forms noted in Table 1—that is, an overlapping of an appreciable part of the present fauna with elements of two other, now largely separate faunas. On the other hand, true forest forms of any type seem absent, and the dearth of eastern forms emphasize lack of forest continuity with the eastern woodlands.

In view of this hypothesis of intermingled and probably more complex communities during the late Pleistocene, the question arises as to how large a span of countryside is represented at any given site and how certain we can be that a given taxon actually occurred within the area rather than having been carried from afar. Data for distances through which raptorial birds, carnivores, scavengers, and the like may bring vertebrate remains are dishearteningly scanty, but some tentative material can be put forth. First, there seems no logical limit to the distance from which material could be carried by migrants, strays, and the like. However, it also seems (but with few hard data) that the amount of materials carried for long distances must be insignificant in most cave faunas, and that remains represented by more than a few hundredths of 1% in a large fauna can be assumed with a fair degree of confidence to have originated within the ranging radius of organisms which could bring them back to the site.

Large carnivores tend to have large home ranges, but presumably most carryback would be intestinal and subjected to digestion in large part before return from a long distance. Smaller carnivores are able to support themselves by hunting within a few miles of the den. Thus birds, rather than mammals, generally would be responsible for longer range transport. Even here, it appears that the hunting range of most small to medium raptorial birds can be measured in terms of a few miles; for example, Craighead and Craighead (1969) found among five species of hawks in Michigan (Red-tailed, Rough-legged, Red-shouldered, Sparrow, and Coopers hawks) that the maximum observed diameter of individual hawk ranges was 5 km (3.1 miles); that the maximum number of miles from the roost after morning dispersal of Marsh Hawks was 8.85 km (5.5 miles). In Wyoming, they report the maximum diameter of nesting-season ranges of various birds to vary as follows: Red-tailed Hawk, 3.05 km (1.9 miles); Swainson's Hawk, 4.82 km (3 miles); Cooper's Hawk, 2.25 km (1.4 miles); Sharp-shinned Hawk, 2.41 km (1.5

miles); Goshawk, 2.73 km (1.7 miles); Sparrow Hawk, 3.70 km (2.3 miles); Prairie Falcon, 7.07 km (4.4 miles); Great Horned Owl, 2.89 km (1.8 miles); Long-eared Owl, 1.60 km (1.0 mile); Raven, 5.79 km (3.6 miles); Great Gray Owl, 2.25 km (1.4 miles). Scavengers and the largest birds of prey generally range somewhat farther afield than these birds, but a practical limit of 24-32 km (15-20 miles) is reasonable from the limited data available.

Other than material specifically carried back to nestlings, the owls would be responsible for the vast majority of the small bird and mammal remains. Miller (1943) pointed out that falconiform birds tend "to pick the bones of the prey and then leave the carcass near the point of capture. Should the bone be swallowed, it is often dissolved by the gastric juices," but owls usually swallow their prey as whole as possible. The excellent preservation of bones in owl pellets is well known.

Some input on carrying ranges comes from two caves in New Mexico. The Khulo Site lies approximately 29 km (18 miles) from the Rio Grande. Two fish bones, unlikely to be obtainable other than from that river, were found among many thousands of bones scanned. Likewise, a total of eight fish bones (from about 18,000 catalogued bones and an estimated 100,000 scanned) from various Dry Cave sites has been noted; the Pecos River is about 24 km (15 miles) distant, though possible Pleistocene sources were somewhat nearer.

It seems clear, then, that the vast majority of vertebrate remains in most cave sites originated within a few kilometers of the cave, with lesser amounts coming from farther away; that only occasionally would the distance exceed 32 km (20 miles). We are seeing forms that actually were associated or at least closely approached each others' range. Some, today, are separated by hundreds of kilometers.

If the northern portions of the present Chihuahuan Desert were in cool grassland and shrubland (presumably with some trees moving out onto appropriate slopes), how far did such conditions extend? At Blackwater Draw, some 230 km (143 miles) to the NNE and dated at about 11,000 B.P., the Brown Sand Wedge Local Fauna (Slaughter 1964) reveals no northwestern elements. Instead, extralimital forms (Table 3) are western (ponderosa pine forest and pinyon-juniper woodland forms), Great Plains, and eastern (the record of *Sciurus arizonensis* is rejected on biogeographic grounds plus the lack of any indication that *Sciurus carolinensis* received consideration). Wells' (1966) evidence from wood-rat middens in the Big Bend seems to indicate increased effectiveness of precipitation at lower elevations but no evidence of northwestern floral influence; we may tentatively infer that the Big Bend lies beyond the effective sphere of influence of increased dominance of winter precipitation. If the tentative identification (Harris 1970b) of Gunnison's prairie dog (*Cynomys gunnisoni*) from along Hwy

TABLE 3. Extralimital taxa, Brown Sand Wedge Local Fauna, Blackwater Draw, Roosevelt County, New Mexico (Slaughter 1964).

| | |
|--|--------------------------------|
| <i>Terrapene carolina</i> | <i>Ondatra zibethicus</i> |
| <i>Didelphis virginianus</i> | <i>Microtus ochrogaster</i> |
| <i>Sorex cinereus</i> | <i>Microtus pennsylvanicus</i> |
| <i>Sciurus</i> sp. (given as <i>Sciurus arizonensis</i> cf.) | <i>Microtus mexicanus</i> cf. |
| <i>Peromyscus truei</i> cf. | |

118 ca. 8 km (5 miles) south of Alpine, Brewster County, Texas, is correct, some northwestern influence would seem to be indicated that far south and east.

The evidence for the remainder of the Chihuahuan Desert is based on the fauna from San Josecito Cave, Nuevo Leon, itself to the east and altitudinally higher than the Chihuahuan Desert today. Evidence of switches in geographic ranges of several taxa is present (Table 2), but particularly germane are three taxa, marmot (*Marmota* sp.), bog lemming (*Synaptomys cooperi*), and masked shrew (*Sorex cinereus*). The latter mostly is a cool grassland species in the Pleistocene, being absent from all New Mexican Quaternary sites except the Brown Sand Wedge. Its presence at San Josecito Cave implies the past presence of a cool grassland corridor into southern Nuevo Leon; presence of *Synaptomys cooperi* is best explained by the same concept. An approach from east of the Sierra Madre Oriental seems most acceptable. Presence of *Marmota* at San Josecito, however, tells a very different story. Assuming an extant species, the candidates are the eastern woodchuck (*M. monax*) and the yellow-bellied marmot (*M. flaviventris*). The former currently is the most distant from the site and is absent from Pleistocene sites in central and eastern Texas; *M. flaviventris*, on the other hand, has a relatively well documented late Pleistocene and Holocene distribution far to the southeast of its current range (Fig. 6). The range of *M. flaviventris* is thought to be governed by the amount of winter-early spring precipitation, at least in the south (Harris 1970a); its presence at San Josecito Cave would imply that increased effective moisture during the winter-spring interval occurred far enough east and south to allow this marmot to reach the Sierra Madre Oriental highlands and work southeasterly at least to the province of Aramberri, Nuevo Leon. Intuitively, this would not seem to allow sufficient aridity for true desert anywhere within the present day Chihuahuan Desert; the telescoping together of presently separated plant communities observed by Wells (1966) in the wood-rat material from Big Bend and as hypothesized here for southern New Mexico may have been the general rule throughout the Chihuahuan Desert. Vertebrate Quaternary sites within or near the Mexican portion of the desert

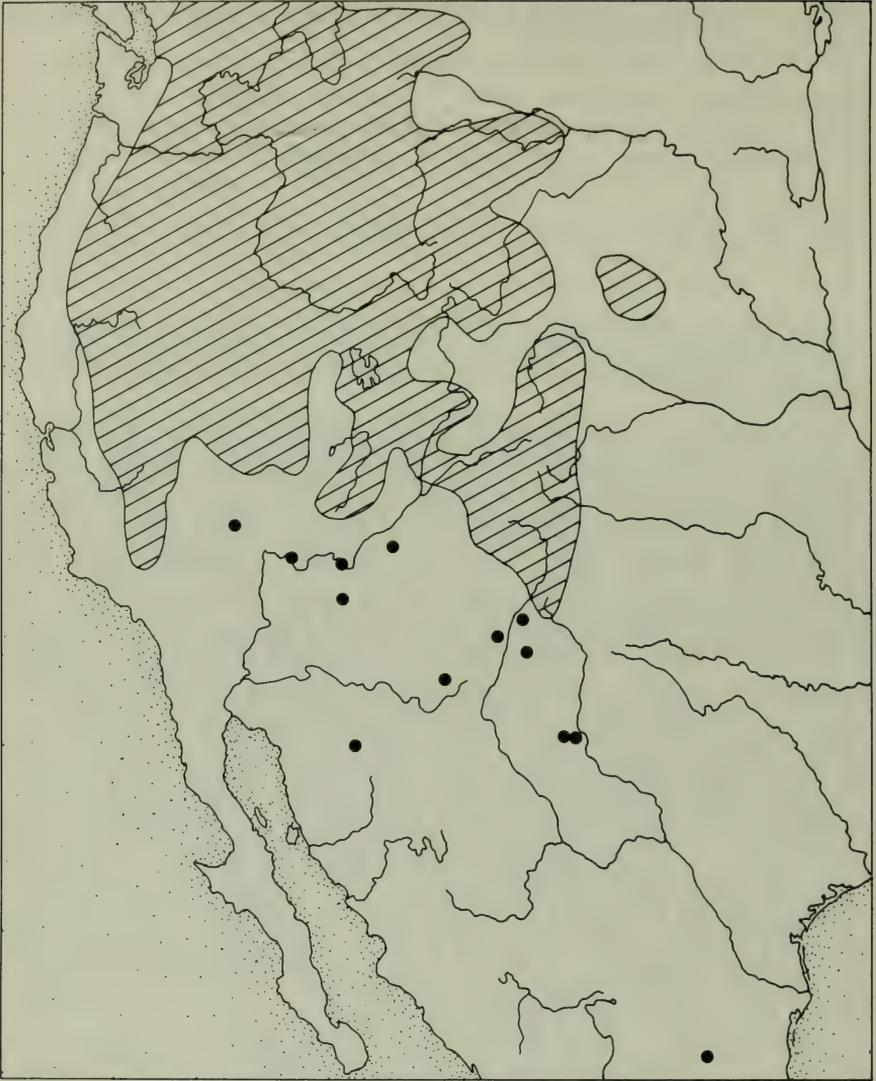


Fig. 6. Historic distribution (hatched area) and Southwestern distribution in the late Pleistocene and prehistoric Holocene (dots) of marmots (*Marmota*, probably all *M. flaviventris*).

now become vital to confirm (or destroy) the emerging model and to fill in details now only vaguely hinted.

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Some Quaternary Molluscan Faunas from the Northern Chihuahuan Desert and Their Paleoecological Implications

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INTRODUCTION

Little work has been done in regard to Quaternary mollusks, either living or fossil, of the southern and central part of the Chihuahuan Desert. Most work has been concentrated in the northern part, especially in those "peninsulas" of the desert that extend northward along the Rio Grande and Pecos River into New Mexico. Even here, work is largely of a reconnaissance nature. Lack of chronological control is an especially serious problem. Herein, Quaternary mollusks from the following situations are considered: (1) mountains within and bordering the Chihuahuan Desert; (2) present and ancient flood-plain deposits of the Rio Grande, the Pecos River, and a few of their tributaries; (3) cave deposits, mainly Dry Cave, Eddy County, New Mexico; and (4) lacustrine and spring deposits.

As temporal, guide fossils Quaternary fossil mollusks are of scant use because, as noted by Taylor (1965:598), "So far as fossil shells can demonstrate, nearly all species of mollusks have remained virtually unchanged throughout the Pleistocene." They have proven more useful as paleoecological indicators. Undoubtedly, they are best used in conjunction with as many other sources of paleoecological inference as possible. Hopefully, the future will see more team endeavors in the Chihuahuan Desert using paleomalacological indicators among a variety of approaches.

Assuming that ecology is the key to paleoecology, it follows that the study of living mollusks should precede that of fossil ones of the same or closely related species. Unfortunately, knowledge concerning living mollusks of the Chihuahuan Desert is still meager and knowledge of their ecology is practically nonexistent. Bequaert and Miller (1973:5-6) outlined the kinds of information that would be desirable for ecological

characterization of species of southwestern mollusks, but they concluded that probably not more than one species of the entire fauna considered by them had been analyzed in this way. Most available information consists simply of listings of species, collection localities, and some general remarks regarding biotopes. Even this kind of information is available for only a few areas in the Chihuahuan Desert. Pratt (1972) discussed the present malacofauna of the Chisos Mountains, Brewster County, Texas. Cheatum (1935) surveyed gastropods of the Davis Mountains in Texas. In far west Texas, Metcalf and Johnson (1971) reported living and fossil Quaternary mollusks from the Franklin Mountains. On the western and northwestern borders of the Chihuahuan Desert, Pilsbry and his co-workers investigated and made reports concerning the Big Hatchet, Florida, and Black ranges, New Mexico (Pilsbry 1915; Pilsbry and Ferriss 1917). Metcalf (1967) reported on living and fossil Quaternary mollusks from the Rio Grande Valley in southern New Mexico and adjacent Texas.

Although a knowledge of living mollusks is indispensable, here, as generally in the area of paleoecology, caution should be urged in interpreting the materials (shells) available to the paleontologist. Although shells may seem assignable to living species, it is possible that evolutionary changes may have taken place that were related to ecology but not necessarily to shell morphology. Conceivably, minute genetic changes might have far-reaching ecological effects in terms, for instance, of physiological tolerance, fecundity, and population and community interactions. In practice, however, students of Quaternary mollusks generally tend to assume that such changes have been minimal.

MONTANE MOLLUSKS

It is problematic to what degree faunas of the mountains occurring in a desert should be regarded as comprising part of a "desert fauna." The concept of life zones partially resolves the problem if there can be agreement as to which zones are "desertic." Nevertheless, the relationship even of higher mountains to the surrounding desert is an intimate one biogeographically and this is even more the case with lower ranges.

The interrelationship of desert basins and adjacent mountains assumes additional intimacy where there is evidence that life zones have fluctuated altitudinally in the Quaternary. In such cases one may be able to make reasonable inferences regarding biotas and biotopes simply by inferring vertical adjustments of life zones.

The Chihuahuan Desert comprises many mountains with limestone bedrock in which conditions conducive to preservation of shells of mollusks have prevailed. Shells are most commonly preserved in colluvial hillslope deposits, especially where these contain rock accumulations or talus deposits with interstices in which mollusks lived and were en-

tomed by calcareous silts. Such colluvial hillslope deposits often interdigitate downslope with alluvial deposits laid down by canyon streams.

Examples of mountain ranges of several different categories, altitudinally, are given below.

A HIGHER MOUNTAIN RANGE. The Guadalupe Mountains of Texas and New Mexico are one of the most salient ranges of the northern Chihuahuan Desert. The range has not been fully explored malacologically. However, at least 35 species of land snails are known to inhabit the range, with the greatest diversity of species in montane upland forests and along wooded canyons.

An especially impressive sequence of canyon fill comprising colluvial and alluvial deposits occurs and is exposed in Pine Spring Canyon west of the village of Pine Springs. The massiveness of the fill and occurrence of numerous facies changes and unconformities suggest a long and complex history for these deposits, although it seems probable that all are Quaternary. From this fill, 16 species of land snails have been taken. Three species are not known to live in the Guadalupe Mountains today.

The Sacramento, Guadalupe, Davis, and Chisos mountains may have served as major insular "staging areas" of an archipelago between the southern Rocky Mountains and the Sierra Madre Oriental of Mexico. The Guadalupe Mountains are the northern terminus of the range of the genus *Humboldtiana* in this archipelago and the southern terminus for the genera *Oreohelix* and *Discus* (both fossil).

MOUNTAINS OF MEDIUM ELEVATION. Pleistocene and living molluscan faunas have been investigated in two mountain ranges bordering, on the east, the "Rio Grande Valley Peninsula" of the Chihuahuan Desert. These are (1) the Franklin Mountains of El Paso County, Texas (Metcalf and Johnson 1971), and (2) the Caballo Mountains of Sierra County, New Mexico. Both ranges are narrow, elongate north to south, ca. 25 km (16 miles) long, and with the highest peak of the Franklins reaching 2192 m (7192 ft) and of the Caballos 2255 m (7400 ft). The ranges have much in common. The Caballo Range and the northern and southern parts of the Franklins are predominantly of limestone. However, some of the limestones of the Franklin Mountains are better producers of talus than any in the Caballo Mountains. Large quantities of rhyolitic talus also occur on North Franklin Mountain, in the central part of the range. For molluscan inhabitants of such arid mountains, accumulations of talus seem to have been a last refuge into which snails could withdraw as aridity increased in Holocene time. Thus, the Caballo Mountains, with fewer such refuges, has suffered a more marked decline in number of species. The present fauna of the Franklins (14 spp.)

greatly exceeds that of the Caballos (7 spp.) (Table 1). However, approximately 20 species of fossil land snails have been taken from hill-slope colluvium of probable late Wisconsinan age in each of the ranges (Table 1). Twelve species are common to both ranges. None of the species of the (larger) genera *Ashmunella* and *Oreohelix*, which are prone to endemism, is common to the two ranges. Several living and fossil species occurring in the Franklin but not in the Caballo Mountains seem to

TABLE 1. Living and Pleistocene fossil gastropods from the Franklin Mountains, El Paso County, Texas, and Caballo Mountains (west side of Brushy Mountain), Sierra County, New Mexico.

| Species | Franklins Living | Caballos Living | Franklins Fossil | Caballos Fossil |
|---|---------------------|--------------------|---------------------|--------------------|
| <i>Cochlicopa lubrica</i> (Müller) | | | X | X |
| <i>Gastrocopta pilsbryana</i> (Sterki) | | | X | X |
| <i>Gastrocopta quadridens</i> (Pilsbry) | | | | X |
| <i>Gastrocopta ashmuni</i> (Sterki) | X | X | | |
| <i>Gastrocopta procera</i> (Gould) | | | | X |
| <i>Gastrocopta pellucida</i> (Pfeiffer) | X | X | | |
| <i>Pupoides albilabris</i> (Adams) | X | X | | |
| <i>Pupilla sonorana</i> (Sterki) | | | X | X |
| <i>Pupilla blandii</i> Morse | | | X | |
| <i>Pupilla</i> sp. | | | X | X |
| <i>Vertigo gouldii</i> (Binney) | | | | X |
| <i>Vertigo modesta</i> (Say) | | | | X |
| <i>Vallonia perspectiva</i> Sterki | X | X | X | X |
| <i>Vallonia cyclophorella</i> Sterki | | | X | X |
| <i>Vallonia gracilicosta</i> Reinhardt | | | X | X |
| Succineidae | X | | X | |
| <i>Bulimulus d. pasonis</i> Pilsbry | X | | | |
| <i>Holospira roemeri</i> (Pfeiffer) | X | | X | |
| <i>Discus cronkhitei</i> (Newcomb) | | | | X |
| <i>Helicodiscus singleyanus</i> (Pilsbry) | X | | X | X |
| <i>Vitrina pellucida</i> (Müller) | | | X | |
| <i>Retinella indentata</i> (Say) | X | X | X | X |
| <i>Hawaiia minuscula</i> (Binney) | X | | X | X |
| <i>Zonitoides arboreus</i> (Say) | | | X | X |
| <i>Deroceras laeve</i> (Müller) | X | | | |
| <i>Euconulus fulvus</i> (Müller) | | | X | X |
| <i>Ashmunella pasonis</i> (Drake) | X | | X | |
| <i>Ashmunella Kochi caballoensis</i> Vag. | | X | | X |
| <i>Thysanophora horni</i> (Gabb) | X | X | X | |
| <i>Oreohelix caballoensis</i> Metcalf | | | | X |
| <i>Oreohelix socorroensis</i> Pilsbry | | | X | |
| <i>Oreohelix f. ferrissi</i> Pilsbry | | | X | |
| <i>Sonorella metcalfi</i> Miller | X | | X | |
| Total Number of Species | 14 | 7 | 21 | 19 |

have had a southern, eastern, or western derivation: *Bulimulus (Rabdotus) dealbatus pasonis*, *Holospira roemeri*, *Oreohelix f. ferrissi* and *Sonorella* sp. Several species of the Caballo Mountains seem to have been derived from the massive Black Range, 48 km (30 miles) to the west: *Gastrocopta quadridens*; *Vertigo modesta*; *V. gouldii*; and *Oreohelix caballoensis* (a probable derivative of *O. metcalfei* of the Black Range). The main area of evolution of *Gastrocopta quadridens* seems to have been in Arizona. It occurs (living) in a narrow band in New Mexico that includes the Mogollon, Black, and Capitan mountains. Fossils from the Caballo Mountains seem to have preserved evidence of a Pleistocene way-station once inhabited by the species in its penetration eastward from the Black Range to the Capitan Mountains.

Most of the species now extinct in the Caballo and Franklin mountains still occur along wooded canyons of the more massive and higher Sacramento, Organ, and Black ranges of south-central New Mexico, where moisture conditions are sufficient to support forest. Palynological information would be of value in indicating whether a former montane forest at lower elevations, which is suggested by the fossil snails, may have existed and what its components were.

MOUNTAINS OF LOW ELEVATION. More readily classifiable as "desert mountains" are low mountains such as the Hueco and Finlay mountains, El Paso and Hudspeth counties, Texas. Both generally rise only to elevations of 1676 m (5500 ft), although one small peak (Cerro Alto) attains 2042 m (6700 ft) in the Hueco Mountains.

The present land snail fauna of these low mountains and similar mountains in the northern Chihuahuan Desert generally comprises the small xeric species *Gastrocopta ashmuni*, *G. pellucida*, *Pupoides albilabris*, a succineid, *Hawaiiia minuscula*, *Retinella indentata*, and *Thysanophora horni*. However, in both ranges the following species occur in deposits, probably of late Wisconsinan age: *Gastrocopta cristata*; *Pupoides hordaceus*; *Pupilla blandii*; and *Vallonia gracilicosta*. In addition, in the Hueco Mountains, Pleistocene fossils of *Gastrocopta pro-cera*, *Vallonia perspectiva*, *Ashmunella* sp., and *Oreohelix s. socorroensis* occur. In sediments along arroyos (Holocene or latest Pleistocene) in both the Hueco and Finlay mountains the aquatic snails *Biophalaria obstructa* (Morelet) and *Promenetus umbilicatellus* (Cockerell) occur. (Identification of Hueco Mountains material by Dr. Dwight W. Taylor. The *Promenetus* is of the ribbed "carus Pilsbry and Ferriss 1906" form.) Neither occurs in the mountains at this time. The molluscan evidence strongly suggests that even low mountains at a time or times in the late Pleistocene were better watered and better vegetated than at present.

On Howells Ridge, Grant County, New Mexico, Metcalf and Smartt

(1974) found six species of gastropods in, or derived from, slope deposits and fissure fill probably of mixed Holocene and Pleistocene ages. Two of these species still inhabited the ridge in small favorable areas. Such small populations seem vulnerable to extinction should further deterioration of habitat occur. On the other hand, with improved conditions, they could serve as nuclei for repopulation of the ridge. Probably such processes of extinction or of repopulation have occurred repeatedly in low mountains of the northern Chihuahuan Desert.

FLUVIATILE DEPOSITS

Some Quaternary molluscan assemblages have been reported from stream-laid deposits along the two major rivers of the northernmost Chihuahuan Desert, the Rio Grande and the Pecos River, and some of their tributaries.

Metcalf (1967, 1969) investigated faunas of Pleistocene and Holocene ages in the Rincon and Mesilla Valley segments of the Rio Grande Valley in southern New Mexico and adjacent Texas. Along the Rio Grande, he discerned two Pleistocene and two Holocene assemblages. The older Pleistocene fauna occurred in sediments below the Tortugas geomorphic surface, a graded surface atop a thick caliche caprock. More species (21) were found in the Tortugas alluvium than in any of the younger units. All species were terrestrial and many characteristic of deciduous woodlands, suggesting presence of an extensive riparian gallery forest on the Rio Grande flood plain during what was probably a pluvial time. Approximately 75% of the species no longer occur so far south or at such low elevations in southern New Mexico as the Rio Grande Valley. The relatively ancient appearance and widespread occurrence of the Tortugas Surface suggest it is correlative of the Sangamon Surface, which has been widely reported in the central United States as an especially strong and salient feature, compared to later Pleistocene soils (Frye and Leonard 1965:203). Deposition of the Tortugas alluvium might, then, have occurred in Illinoian time.

In the northern Chihuahuan Desert, perhaps only the greatest glaciations left recognizable testimony to their existence. If this were the case, the next lower Pleistocene terrace complex, the Picacho, might reflect one or more maximally cold periods of the Wisconsinan. (The Picacho terrace is separated by a major episode of cutting and filling from the Tortugas terrace).

Ten of 16 terrestrial snails found in the Picacho alluvium now seem to occur only in montane forests in southern New Mexico, suggesting that the Picacho fauna, like that of the Tortugas alluvium, lived during a time of more effective precipitation than the present. Nine of the species of the Picacho alluvium are aquatic; five of these no longer live in this part of the Rio Grande Valley.

One assemblage of early Holocene age was reported in the Rincon Valley (Metcalf 1969:160). A radiocarbon date of 9360 ± 150 B.P. was obtained from associated charcoal. Shells of 14 species of terrestrial snails and of one aquatic snail were found associated with the charcoal. Several species (*Cochlicopa lubrica*, *Gastrocopta armifera*, *Vallonia perspectiva*, *V. gracilicosta*, and *Zonitoides arboreus*) suggest, paleoecologically, continued existence of a riparian forest at this early Holocene time. None of these species is found in younger Holocene sediments.

Holocene assemblages found in alluvium along arroyos tributary to the Rio Grande and dated at ca. 2500 B.P. to 7000 B.P. are poor in molluscan shells, with only seven species represented. Most of these are markedly xeric in their present-day tolerances and still occur in the Rio Grande Valley in this area. On the other hand, a young Holocene assemblage occurring in Rio Grande flood-plain deposits at the base of the Robledo Mountains and dated at less than 500 years contained 10 aquatic and several marsh-preferring species. This suggests a flood plain supporting a lush phreatophyte association and with marshes and pools probably like those described by early travelers to the area.

In the area of the Pecos River Valley in Texas, Leonard and Frye (1962) recognized four geomorphic surfaces. No mollusks were associated with sediments below the uppermost (I) surface (thought to be late Tertiary in age). Shells of succineid snails occurred under the second highest (II) surface, judged to be of early Pleistocene age. Sediments associated with Surface III yielded 17 species at Locality 13 and 14 species at Locality 6 of Leonard and Frye (1962:Fig. 4). They judged these deposits to be of Early Wisconsinan age. Locality 13 is indicated as being located at "E end bridge, E side Toyah, Reeves Co." (Fig. 4). Possibly this is at or near a locality known locally as the "Toyah Mammoth Locality."

In 1964, Dr. William Strain (Univ. Texas, El Paso) apprised me of the existence of a proboscidean skull at Toyah. I visited the locality on 17 April 1965, finding the skull protruding from sediments at the base of an arroyo bank 10 ft high. Two tusks, one intact and 34 inches long, and the other broken off a distance of one foot from its base were observed at that time. Subsequently, the skull was removed by personnel of Sul Ross State University, Alpine, Texas, and of the Paleo-Indian Institute of New Mexico Eastern University. From unionacean shells collected within close proximity of the skull, a radiocarbon determination of $12,140 \pm 140$ B.P. was obtained (Teledyne Isotopes, I-7088). Thus, these deposits, presumably appertaining to the Surface III complex of Leonard and Frye, seem to be late rather than early Wisconsinan in age.

A sample of sediments taken near the mammoth skull yielded skeletal elements of fishes (including catfish spines), reptiles, mammals, and 15 species of mollusks: 6 terrestrial gastropods (*Gastrocopta cristata*, *Pu-*

poides albilabris, *Pupilla blandii*, *Vallonia gracilicosta*, a succineid and *Hawaiiia minuscula*); 4 aquatic gastropods (*Biomphalaria obstructa*, *Gyraulus parvus*, *Helisoma anceps*, *Physa virgata*); and 5 aquatic bivalves (*Anodonta grandis*, a unionacean of uncertain affinities, *Sphaerium transversum*, *Pisidium casertanum*, and *P. compressum*). The assemblage suggests a permanent aquatic habitat. The arroyo today contains water only after rains. A striking change seems to have taken place in the past 12,000 years.

Deposits similar in appearance to those at the Toyah Mammoth Locality occur along other western tributaries of the Pecos River. Along Black River and Rocky Arroyo, Eddy County, New Mexico, there are rich molluscan assemblages preserved in late Quaternary flood-plain deposits. Multidisciplinary paleoecological approaches to such deposits should be rewarding.

Leonard and Frye (1962:16) noted that the most fossiliferous of the deposits examined by them in the Pecos Valley were those associated with their Surface IV. They noted (p. 12): "Surface IV is of relatively minor extent and consists mostly of the flood plain of Pecos River and its major tributaries . . ." and that "An age of late Wisconsinan and Recent is indicated for the deposits below Surface IV. . . ." Elsewhere (p. 16) they define this "Pleistocene" element as being post-Twocreekan; hence it would be considered Holocene by most present workers.

Radiocarbon age determinations from shells of mussels from two localities below Surface IV yield dates of 3660 ± 95 B.P. and 1135 ± 90 B.P. (Teledyne Isotopes I-6627 and I-6628). Holocene deposits are almost continuous from just above the lowermost canyon segment of the Pecos Valley upstream into New Mexico. Shells recovered from these deposits are mainly aquatic, including the unionacean mussels *Popenaias popeii* (Lea) and *Cyrtonaias tampicoensis* (Lea). Most of these aquatic mullusks do not live in this segment of the Pecos River at present, possibly because of pollution from adjacent oil fields and salinization.

Along the Pecos River at several localities in Eddy County, New Mexico, terrace gravels of Pleistocene age contain a unionacean mussel fauna of several species (Metcalf 1974:48). Some of these records represent extensions in range of 200 or more miles northwest of nearest present known localities of occurrence in the Rio Grande drainage. This assemblage is receiving further study.

DRY CAVE

Dry Cave is located ca. 24 km (15 miles) west of Carlsbad, Eddy County, New Mexico at an elevation of 1280 m (4200 ft). It contains extensive deposits of Pleistocene age that contain vertebrate and gastropod fossils. Mollusks taken at three localities in the cave were re-

ported previously (Metcalf 1970). Only one of these localities had an associated radiocarbon date. Subsequently, mollusks have been collected from additional localities in the cave and several additional radiocarbon dates have been determined.

Localities reported here are in two areas which received fill from different sources: Entrance Fissure and Bison Sink. The Entrance Fissure source area was at the present mouth of the cave and, when filling began, seems to have been a collapse sink some 18.29 m (60 ft) deep, probably with steep rocky walls. The locality designated Animal Fair (Loc. 22) lies near the bottom of this fill and has an associated date of $15,030 \pm 210$ B.P. The locality Stalag 17 (Loc. 23) lies higher and has an associated date of $11,880 \pm 250$ B.P.

Bison Sink is located 61 m (200 ft) south-southeast of the present mouth of the cave. From it have been derived sediments deposited in Bison Chamber (Loc. 4). Higher on a debris slope than Bison Chamber and younger than it is a locality designated Test Trench II (Loc. 54), with an associated date of $10,730 \pm 150$ B.P. Datable materials have not been found in Bison Chamber but position of its fill indicates that it is older than Test Trench II and younger than $14,470 \pm 250$ B.P. It is considered to be of late Woodfordian age.

Localities mentioned above and species and quantities of fossil snails recovered are indicated in Table 2. All Pleistocene assemblages differ greatly from the present fauna of the area, which comprises few species: *Gastrocopta pellucida*, *Pupoides albilabris*, *Hawaiia minuscula*, a succineid, and *Thysanophora horni*. There are also some differences between assemblages from different levels and source areas in the cave. It is difficult to discern which of these might reflect temporal changes in faunas and which might reflect slight differences in local habitats existing in the two source areas.

The Animal Fair (Loc. 22) assemblage has a much higher proportion of *Vallonia perspectiva* than have other assemblages and, unlike the others, contains *Cochlicopa lubrica*. Perhaps these species inhabited the rocky walls of the Entrance Fissure sink, mentioned above. At the present time these species are more common along valley walls of canyons in the Sacramento Mountains than they are on the adjacent valley flood plains.

Stalag 17 (Loc. 23) has yielded only a few fossils but does contain two species, *Gastrocopta contracta* and *Fossaria modicella*, not found at other localities. *Fossaria modicella* and *Stagnicola cockerelli* (this latter species found at the three other localities reported) are aquatic pulmonate snails. Their presence indicates presence of pools, at least temporarily, in the depressions in which fill was accumulating.

In Table 2, comparison is made to species of terrestrial gastropods from the Sacramento Mountains, Otero County, New Mexico, 121 km

TABLE 2. Fossil gastropods from four localities in Dry Cave, Eddy Co., New Mexico, indicated as percentages of the total number taken at each locality. Dry Cave species still living at 6600-7500 ft elevation along Penasco Canyon, Sacramento Mountains, N.M., are indicated. T. I. II=Test Trench II.

| Species | Entrance Fissure Source Area | | Bison Sink Source Area | | Penasco Canyon |
|---|------------------------------|------------------------|---------------------------|-----------------------|----------------|
| | Animal Fair (Loc. 22) | Stalag 17 (Loc. 23) | Bison Chamber (Loc. 4) | T. T. II (Loc. 54) | |
| <i>Stagnicola cockerelli</i> (Pilsbry) | 2.70 | | .14 | .07 | |
| <i>Fossaria modicella</i> (Say) | | 5.0 | | | X |
| <i>Cochlicopa lubrica</i> (Müller) | 1.17 | | | .83 | X |
| <i>Gastrocopta armifera</i> (Say) | .39 | 5.0 | .29 | | X |
| <i>Gastrocopta contracta</i> (Say) | | 10.0 | | | X |
| <i>Gastrocopta procera</i> (Gould) | 1.95 | | 21.28 | 3.76 | X |
| <i>Gastrocopta pellucida</i> (Pfeiffer) | | 20.0 | 5.00 | 1.04 | |
| <i>Pupoides albilabris</i> (Adams) | | | | .49 | |
| <i>Pupoides hordaceus</i> (Gabb) | | | .42 | .56 | |
| <i>Pupilla blandii</i> Morse | 1.17 | | 9.04 | | X |
| <i>Vallonia perspectiva</i> Sterki | 25.39 | 5.0 | 1.39 | .27 | X |
| <i>Vallonia cyclophorella</i> Sterki | | | 1.95 | .63 | X |
| <i>Vallonia gracilicosta</i> Reinhardt | 3.13 | | 14.74 | 6.33 | X |
| Succineidae (sp. indet.) | 32.03 | 5.0 | 39.64 | 73.41 | X |
| <i>Bulimulus dealbatus</i> (Say) | 1.95 | 5.0 | .14 | .14 | X |
| <i>Retinella indentata</i> (Say) | 20.70 | 25.0 | 1.25 | 1.46 | X |
| <i>Hawaitia minuscula</i> (Binney) | 9.38 | 20.0 | 4.45 | 10.44 | X |
| <i>Helicodiscus singleyanus</i> (Pilsbry) | | | .14 | .21 | |
| <i>Thysanophora horrii</i> (Gabb) | | | .14 | .35 | |
| Total Number of Specimens | 256 | 20 | 719 | 1437 | |

(75 miles) northwest of Dry Cave. Samples were taken at 91-m (300-ft) intervals along Penasco Canyon in the southern Sacramento Mountains from 1920 to 2926 m (6300 to 9600 ft). The faunas at 2012-2286 m (6600-7500 ft) most nearly resemble the Pleistocene faunas of Dry Cave (Locs. 4, 22, 23). The greatest number of shared species (10) was at 2195 m (7200 ft). Annual precipitation is estimated at 54.1 cm (21.3 inches) at 2195 m (7200 ft) by interpolating between amounts for Mayhill Ranger Station (50.29 cm [19.8 inches] at 1935 m [6350 ft]) and Cloudcroft (62.43 cm [24.58 inches] at 2640 m [8660 ft]). (Precipitation data from USDA Yearbook of Agriculture, 1941, *Climate and Man*).

Conditions of effective moisture perhaps similar to the 2195-m (7200-ft) locality in Penasco Canyon might be hypothesized for Dry Cave during late Wisconsinan times in which the assemblages at Localities 4, 22, and 23 existed. Annual precipitation at stations east, north, and northwest of Dry Cave at elevations of 975-1250 m (3200-4100 ft) range from 27.81 to 35.13 cm (10.95 to 13.83 inches).

Metcalf (1970) suggested, largely on the basis of the fauna from Bison Chamber (Loc. 4), that the Dry Cave area might have resembled the present rolling grasslands (*vegas*) in the vicinity of Las Vegas, San Miguel County, New Mexico. This surmise was based mainly on the prominent occurrence in the Bison Chamber assemblage of *Gastrocopta procera*, *Pupoides hordaceus*, *Pupilla blandii*, and *Vallonia gracilicosta*, species characteristic of the *vegas* at elevations of 1829 m (6000 ft) and above. *Pupoides hordaceus* is not known, except fossil, in the Sacramento Mountains. I previously stated (Metcalf 1970:43) that *Pupilla blandii* did not occur in the Sacramento Mountains. Further collecting reveals that I was in error and that it is, in fact, common there above 2134 m (7000 ft). Probably the present-day "xeric" species *Gastrocopta pellucida*, *Helicodiscus singleyanus*, and *Thysanophora horni* occupied the drier microhabitats in the source area in Bison Chamber time.

The assemblage from Test Trench II seems to be of early Holocene age, judging by the associated radiocarbon date. By Test Trench II time, *Pupilla blandii*, which I consider a "pluvial" indicator, no longer appears in the record and proportions of *Gastrocopta procera* and *Vallonia gracilicosta* have been reduced from those of the Bison Chamber assemblage. Shells of a succineid and of *Hawaiiia minuscula* dominate the fauna. Probably this is the same succineid (*Succinea grosvenori*?) that presently inhabits the area; however, shells of succineids do not allow for positive identification in many cases. A decline in "pluvial" indicators and an increase in some species common in the area today seems, then, to have occurred between Bison Chamber time and Test Trench II time. This suggests onset of a Holocene climatic trend toward less effective precipitation.

Molluscan fossils occur in other caves in the northern Chihuahuan

Desert but little attention has been given them. Fill taken from Conkling Cavern, at 1402 m (4600 ft) elevation on the east side of Bishop's Cap Mountain, Dona Ana County, New Mexico, contains specimens of *Gastrocopta procera* and *Vallonia gracilicosta*. These species were judged above, in the discussion of Dry Cave, to be probable "pluvial" indicators.

LACUSTRINE AND SPRING DEPOSITS

There are lacustrine deposits of various ages in the northern Chihuahuan Desert but they have received no malacological attention known to me. A small sample of sediments from a former pluvial lake in San Simon Sink, Eddy County, New Mexico, yielded several aquatic species of snails no longer found in the area. This fauna deserves further investigation.

Springs of the Chihuahuan Desert harbor numerous endemic species of snails, especially in northern Chihuahua, Mexico. What molluscan fossils might be found in Quaternary deposits laid down by these springs is unknown.

DISCUSSION

In the northern Chihuahuan Desert there are evidences of movements of faunas north and south and also up and down, altitudinally, during the Quaternary. *Gastrocopta holzingeri*, found in the Tortugas alluvium along the Rio Grande Valley, seems to be a more northern species, which at that time had penetrated southward. *Pupoides hordaceus* is presently found on plains and rolling hills at altitudes of 1524-2134 m (5000-7000 ft) in central and northern New Mexico. It is a common fossil in Pleistocene deposits in southern New Mexico and far western Texas at 1158-1372 m (3800-4500 ft). It has not retreated to montane habitats in southern New Mexico during the Holocene as have the species discussed in the next paragraph.

In most cases it is not possible to discern "northern" from "montane" species in characterizing Quaternary fossils of the northern Chihuahuan Desert, as these are, in many cases, one and the same. For such species, there was probably mingling during "pluvials" of stocks from both montane and northern refugia. I visualize movements both downward and southward from a number of refugia until concentric fronts of dispersal probably merged. Smaller species, such as the following, seem to have experienced such pluvial expansions and interpluvial contractions of range, both latitudinally and altitudinally: *Cochlicopa lubrica*, *Gastrocopta pilsbryana*, *G. procera*, *G. armifera*, *Pupilla blandii*, several *Vertigos* and *Vallonias*, *Discus cronkhitei*, and *Zonitoides arboreus*.

The larger snails that occur as endemic (precinctive) species or subspecies in mountains of the region show almost no fossil evidence of

having crossed from one mountain enclave to another. Possible modes of dispersal for these have been discussed by Bequaert and Miller (1973).

In the lower mountains discussed, the contrast between a Pleistocene pluvial and a Holocene interpluvial fauna is marked. As life zones shifted upward in the Holocene, some species became extinct and others suffered great restriction of habitat. At the same time, species rare or absent from pluvial assemblages in these mountains invaded upward. These include *Gastrocopta pellucida*, *G. ashmuni*, and *Thysanophora horni*.

Along the Rio Grande and Pecos River valleys, most Pleistocene terrestrial gastropods seem to appertain to categories discussed above. However, at least two, *Gastrocopta cristata* and *G. pellucida*, have a more southern or southeastern derivation. Several aquatic species seem to have had a southeastern derivation. Thus, *Biomphalaria obstructa* ascended both the Pecos and Rio Grande systems, probably from the southeast. From the southeast also, a number of unionacean mussels ascended the Pecos River into New Mexico but there is no fossil evidence that any ascended the Rio Grande mainstream as far as the El Paso area and New Mexico.

If present-day "southern" and "northern-montane" characterizations applied to these molluscan species have any relationship to temperature preferences, then the mingling of the two groups on a Wisconsinan flood plain of the Rio Grande and Pecos River suggests an environment with moisture conditions congenial to both groups and temperatures not too extreme to discourage either.

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Post-Glacial Origin of the Present Chihuahuan Desert Less Than 11,500 Years Ago¹

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INTRODUCTION

The Chihuahuan Desert is one of the highest North American deserts, in terms of both maximum and mean elevation above sea level. Physiographically, it is a high plateau between the two great mountain ranges of Mexico, the Sierra Madre Occidental and the Sierra Madre Oriental, both of which attain elevations in excess of 3048 m (10,000 ft). Thus partially defended against rain-bearing air masses and headward erosion by rivers draining into both oceans, the arid central plateau of northern Mexico maintains its basal plains or *bolsónes* at elevations of 914 to 2134 m (3000 to 7000 ft) or more above sea level, the most extensive areas lying above 1219 m (4000 ft). The outstanding exception is the anomalous valley followed by the through-flowing Rio Grande on its circuitous course from the snows of the Colorado Rockies to the Gulf of Mexico. In the Big Bend area of western Texas and adjacent Coahuila, elevation along the river drops to less than 610 m (2000 ft) above sea level, the lowest elevation in the entire Chihuahuan Desert province, which extends from southeastern Arizona and southeastern New Mexico to Zacatecas and southern San Luis Potosí (Fig. 1). Downstream and to the eastward, the Rio Grande escapes from its rain-shadowed defiles through the eastern barrier ranges of the Sierra Madre (namely, the Sierra del Carmen, the Dead Horse Mountains, and the offset Serranías del Burro) and enters a plain of low elevation (<610m or <2000 ft) with no obstructions to Gulf air. Here, there is a gradient of increasing precipitation toward the east, and the vegetation exhibits a transition to

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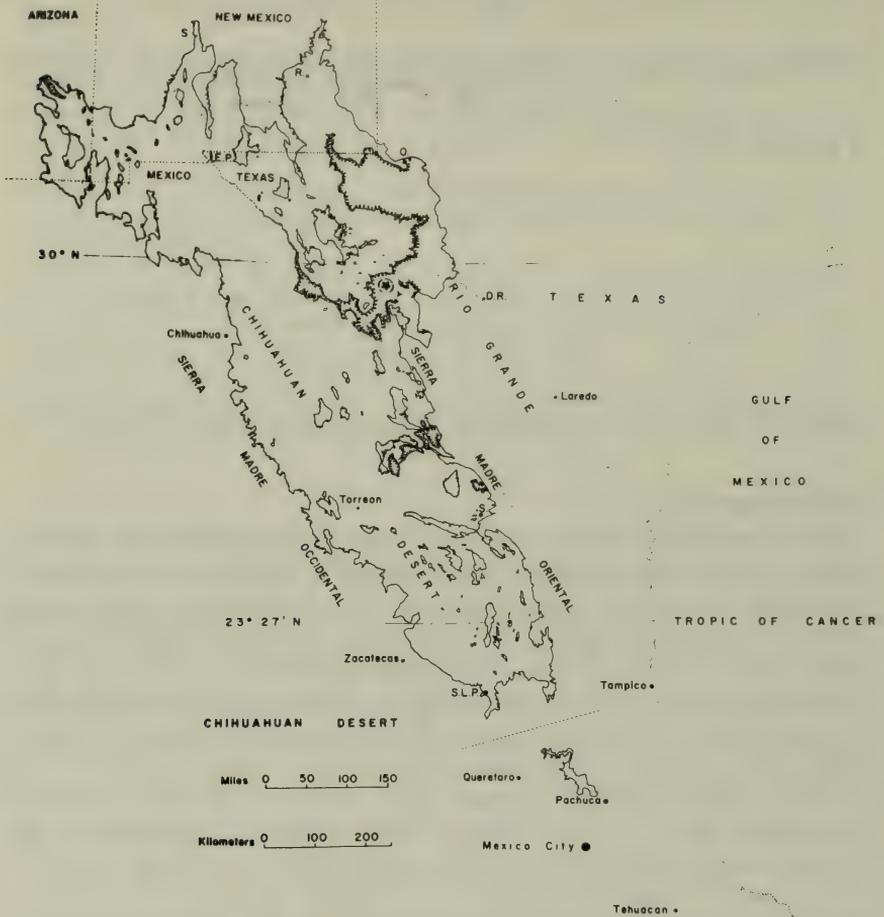


Fig. 1. The limits of the Chihuahuan Desert, according to Shreve (1942), Miranda (1955), Rzedowski and Leal (1958), and Wells (unpubl. data). Heavy, continuous lines delimit marginal boundaries of the desert province and its included mountains or other areas of higher elevation above the desert zone. Extent of areas below 915-m (3000 ft) are indicated within the boundaries of the province by the hachured 915 m contour. State and coast lines are faintly dotted. Thus delimited, the Chihuahuan Desert extends from southeastern Arizona and southern New Mexico to Zacatecas and southern San Luis Potosí. The isolated "island" of desert vegetation southeast of the dashed line is in Querétaro and Hidalgo and lies outside the accepted limits of the province. By far the largest area below 915 m is the Big Bend sector of the Río Grande drainage, extending from near Odessa (O.), Texas northwestward up the Pecos Valley into New Mexico, and from the mouth of the Pecos far up the Río Grande. At the Maravillas Canyon *Neotoma* site (marked ⊙), elevations drop below 610 m (2000 ft). The only other areas in the Chihuahuan Desert below 915 m (3000 ft) are much smaller, barely extending into the province along the upper Gila River in Arizona in the extreme northwest, and along the eastern boundary north of Saltillo (S.), Coahuila. However, these minor areas do not include elevations as low as the lowest *Neotoma* sites in the Big Bend area of Texas (Wells 1966).

the Tamaulipan thorn shrubland, which is taller and denser, and richer and more tropical in floristic composition than the desert scrub of the Chihuahuan Desert to the west of the mountains (Clover 1937).

Since the eastern limb of the Big Bend of the Rio Grande Valley is the lowest and one of the most arid sectors of the Chihuahuan Desert province, it would seem to be a likely place for survival of the existing desert vegetation zone during the full-glacial, pluvial conditions of the Pleistocene. At present, the treeless Chihuahuan Desert scrub, dominated by the creosote bush (*Larrea*) or other xerophytic shrubs, extends from this low point [at less than 610 m (2000 ft)] upwards to about 1524 m (5000 ft), or even more than 2134 m (7000 ft) above sea level in various parts of the province, before it overlaps with the variable lower limit of the montane pine-oak-juniper woodland. A pluvial, downward migration of the treeless desert zone to the eastward along the lower course of the Rio Grande Valley would be unlikely for a number of reasons. Although elevation declines in that direction, precipitation increases with decreasing distance from the source of warm, moist air masses over the Gulf of Mexico. As a result, the lower limits of Mexican pinyon pine (*Pinus cembroides* Zucc.) and juniper (*Juniperus pinchotii* Sudw.) drop from about 1372-1524 m (4500-5000 ft) in the mountains of the Big Bend area to less than 610 m (2000 ft) above sea level for the disjunct stands on the Balcónes Escarpment of the Edwards Plateau about 241 km (150 miles) to the east. Thus, an existing "downward displacement" of a vegetation zone amounting to at least 762 m (2500 ft) can be ascribed to the gradient of increasing precipitation at low elevations to the eastward of the Big Bend area. Any additional downward displacement due to pluvial effects during the glacials may have made what is now the Tamaulipan thorn woodland province of southernmost Texas and northeastern Mexico even less suitable for a regional dominance of the xerophytic shrubs characteristic of the Chihuahuan Desert than it is today.

VEGETATIONAL HISTORY OF THE CHIHUAHUAN DESERT

Fortunately, firm evidence is available to document the late Pleistocene vegetational history of the northern Chihuahuan Desert. The *Neotoma* macrofossil record precisely indicates the nature and magnitude of downward displacement of vegetation zones in the Big Bend area during the last great pluvial of the Wisconsin glacial (Wells 1966). The pinyon-oak-juniper zone was depressed at least 792 m (2600 ft) below its present lower limits at 1402 m (4600 ft) on the slopes of the higher mountains, such as the Chisos Mountains, because it occurred in what is now very arid *Larrea* desert on the east limb of the Big Bend of the Rio Grande, near the mouth of the broad, open Maravillas Canyon at an elevation of 610 m (2000 ft) above sea level (Fig. 1). Because the

Maravillas Canyon *Neotoma* sites are in the lowest sector of the Chihuahuan Desert, as discussed above, it appears probable that most edaphically suitable areas of the Chihuahuan Desert province were more or less wooded during the latest Wisconsinan pluvial, and as recently as about 11,500 years ago. In the Big Bend area, the principal species in the macrofossil record were a two-needled variety of Mexican pinyon (*Pinus cembroides* var. *remota* Little), redberry juniper (*Juniperus pinchotii*), and two species of shrubby live oak (*Quercus grisea* Liebm. and *Q. pungens* Liebm.). Remarkably, what appears to be exactly the same variety of Mexican pinyon pine occurs disjunctly on the southwestern escarpment of the Edwards Plateau, about 241 km (150 miles) to the east of existing stands in the Big Bend area (Little 1966). This strikingly disjunct distribution pattern almost certainly dates from the great pluvial expansion of the pinyon zone across the lowlands of west Texas.

The fossil evidence appears to exclude the possibility of a regional, treeless, desert scrub formation in what is now the Chihuahuan Desert during the most recent glacial of the Pleistocene. On the other hand, at least part of the "desert" flora coexisted with the pinyon-oak-juniper woodland then, as it characteristically does today. The same late Wisconsinan (radiocarbon age: 11,500-20,000 or more years B.P.) *Neotoma* deposits that document a pluvial dominance of now chiefly montane, woodland conifers and oaks in the vast lowlands of the Chihuahuan Desert also preserve a detailed, macrofossil record of obvious xerophytes. Several characteristic "Chihuahuan Desert" species are represented, in close, contemporaneous association with the more abundant remains of the woodland species. Some of the associated "desert" or semidesert species are the semisucculent rosette plants (*Agave lecheguilla* Torr.), sotol (*Dasyllirion*), sacahuista (*Nolina*), and arborescent *Yucca*; stem-succulents (*Echinocereus* and *Opuntia*); and the shrubs, *Acacia roemeriana* Scheele and *Ephedra aspera* Engelm. (Table 1). However, all of these species are equally characteristic of the lower or more open phases of the existing pinyon-oak-juniper zone on the high mountains of the Chihuahuan Desert province. Indeed, the most striking character-plants of the Chihuahuan Desert attain their maximal abundance and size in or just below the woodland zone. In some higher sectors of the desert, the arborescent species of *Yucca* or other Agavaceae segregate as a bizarre, rosette-tree zone below the woodland zone. Examples are the giant dagger/sotol zone dominated by *Yucca carnerosana*, as in the Dead Horse Mountains of Texas (Wells 1965), and the extensive forests or woodlands of *Y. australis* from Coahuila south, which are the physiognomic equivalent of the Joshua tree (*Y. brevifolia*) zone of the Mohave Desert. Hence, it is not at all anomalous, but rather to have been expected, that many "Chihuahuan Desert" species coex-

isted with pinyon-oak-juniper woodland in the lowlands of the province during the pluvials of the Pleistocene. The close association in the late Wisconsinan *Neotoma* record of macrofossils of woodland conifers and thermophilous plants, including a walnut (*Juglans microcarpa*), now restricted to the lower fringe of the woodland zone, and the several species of large semisucculents and succulents, places limitations on the degree of cooling in the lowlands. It rather suggests that enhancement of precipitation and its effectiveness were the prime climatic factors determining the pluvial expansion of woodland at this relatively low latitude (29° N).

The exact time of onset of desert conditions in the Chihuahuan province is not known, but a shift to drier climate may be inferred from compositional changes in the youngest series of *Neotoma* deposits in Maravillas Canyon, which is close to the minimal elevation for the entire province (Table 1). The $12,550 \pm 130$ B.P. deposit contains relatively more pinyon pine and juniper than scrub oak, and has comparatively few "desert" species. Moreover, the composition of this deposit is essentially the same as nearby deposits of more or less full-glacial age ($14,800 \pm 180$, $16,250 \pm 240$, and $20,000 \pm 390$ B.P.) at the same elevation [610 m (2000 ft)] or even higher [884 m (2900 ft)]. Hence, climatic conditions equivalent to the maximal pluvial effects of the Wisconsinan glacial in the Chihuahuan Desert region were still in force there at the lowest elevations about 12,500 B.P. In contrast, the two younger deposits in normal superposition in the series, with radiocarbon ages of $12,000 \pm 150$ and $11,560 \pm 140$ years, have much more scrub oak and juniper than pinyon pine, and contain several "desert" or semidesert species lacking in older deposits: *Acacia roemeriana* (armed shrub); *Yucca rostrata* and *Y. torreyi* (semisucculent rosette shrubs); *Echinocereus* cf. *dasyacanthus* (stem succulent). These changes clearly indicate that the climate already had begun to warm or to desiccate about 12,000 B.P. and this trend was still continuing about 11,500 B.P. It is as yet uncertain whether the apparent lack of further deposition by wood rats, immediately after 11,500 B.P. signifies the termination of pluvial woodland climate in the lowlands of the Chihuahuan Desert at about that time. Impoverished woodlands may have persisted later.

Significantly, the macrofossil record of pluvial age contains no trace of the extreme xerophytes of the lowest and most arid sectors of the existing Chihuahuan Desert, such as the creosote bush (*Larrea divaricata* Cav.) and the tar bush (*Flourensia cernua* DC.), two shrubs that dominate the sparse vegetation over many thousands of square miles of desert today. In fact, *Larrea* is consistently abundant or dominant throughout its vast range in North and South America (J. Hunziker unpubl. data), and *Larrea divaricata* ssp. *tridentata* is often the principal constituent of Holocene wood-rat deposits in the *Larrea* zone. Nor is

TABLE 1. Fossil plants and radiocarbon ages of wood-rat middens from three localities in the Chihuahuan Desert of western Texas.

| Site | Relative abundance in middens | | | | | | | | | |
|---|-------------------------------|---------|----------------|---------|----------------|----------------|----------------|----------------|----------------|----------------|
| | B-1 | B-2 | D-1 | D-2 | D-3 | M-1a | M-1b | M-1c | M-2 | M-3 |
| Elevation (m.) | 1200 | 1210 | 880 | 880 | 850 | 600 | 600 | 600 | 600 | 600 |
| Radiocarbon age (yrs.) | 18,750± 360 | >36,600 | 20,000± 390 | >40,000 | 16,250± 240 | 11,560± 140 | 12,000± 150 | 12,550± 130 | 13,350± 170 | 14,800± 180 |
| Trees | | | | | | | | | | |
| Species and structures in midden | | | | | | | | | | |
| <i>Pinus cembroides</i> , leaves, cones, seeds | ++ | ++ | ++ | ++ | ++ | + | + | ++ | ++ | ++ |
| <i>Juniperus pinchotii</i> , leafy twigs, seeds | ++ | ++ | ++ | ++ | ++ | ++ | ++ | ++ | ++ | ++ |
| <i>J. deppeana</i> , leafy twigs, seeds | ++ | | | | | | | | | |
| <i>Quercus grisea</i> , leaves, acorns | + | + | | | | | | | | |
| <i>Q. arizonica</i> x <i>Q.</i> <i>grisea</i> , leaves | + | | | | | | | | | |
| <i>Q. pungens</i> , leaves, acorns | | | | + | + | ++ | ++ | + | ++ | ++ |
| <i>Celtis reticulata</i> , endocarps | + | ++ | + | + | + | + | + | + | + | + |
| <i>Juglans microcarpa</i> , endocarps | | | + | + | + | | | + | | |
| Shrubs | | | | | | | | | | |
| <i>Acacia roemeriana</i> , twigs, legumes | | | | | | + | | | | + |

TABLE 1. (Continued)

| Site | Relative abundance in middens | | | | | | | | | |
|--|-------------------------------|---------|----------------|---------|----------------|----------------|----------------|----------------|----------------|----------------|
| | B-1 | B-2 | D-1 | D-2 | D-3 | M-1a | M-1b | M-1c | M-2 | M-3 |
| Elevation (m.) | 1200 | 1210 | 880 | 880 | 850 | 600 | 600 | 600 | 600 | 600 |
| Radiocarbon age (yrs.) | 18,750± 360 | >36,600 | 20,000± 390 | >40,000 | 16,250± 240 | 11,560± 140 | 12,000± 150 | 12,550± 130 | 13,350± 170 | 14,800± 180 |
| <i>Grasses and forbs</i> | | | | | | | | | | |
| <i>Bouteloua ramosa</i> , inflorescence | | | | | | | + | | | |
| <i>Buchloe dactyloides</i> , fruit | | + | | | | | | | | |
| <i>Heteropogon contortus</i> , fruits | | + | + | | | + | | | | |
| <i>Tridens muticus</i> , spikelets | | | + | | | + | | ++ | | |
| <i>Lithospermum</i> sp., nutlets | | | + | + | | | | + | | |
| <i>Machaeranthera</i> sp., heads | | | + | | | + | | + | + | + |

B. Burro Mesa; D. Dagger Mountain; and M. Maravillas Canyon. Symbols: +, present in midden but not abundant; ++, abundant or principal constituent of midden. The radiocarbon ages are from the UCLA series of radiocarbon dates, numbers 758, 934, 1039-1046, 1063, and 1064; determined at Institute of Geophysics, University of California; based on organic residue (chiefly cell-wall material) after treatment of fossiliferous strata from middens with HCl. M-1, a, b, and c, upper, middle, and lower strata of the largest Pleistocene wood rat deposit yet uncovered, measuring a few thousand liters in volume.

there any pluvial record of ocotillo (*Fouquieria splendens* Engelm.), candelilla (*Euphorbia antisyphilitica* Zucc.), or the subtropical bromeliad (*Hechtia scariosa* L.B.Sm). The ocotillo and other desert species do appear later in a mid-Holocene *Neotoma* midden with a radiocarbon age of 4200 ± 80 years (UCLA-1062) in Maravillas Canyon at an elevation of 610 m (2000 ft).

BIOGEOGRAPHIC HISTORY OF *LARREA*

The biogeography of *Larrea* during the Pleistocene is a particularly interesting enigma because there is an intriguing possibility of a late, intercontinental dispersal from South America, where the genus exhibits markedly greater morphological and ecological diversity than it does in North America (Hunziker et al. 1972). There are four very different species of *Larrea* in South America, but only one species is present in North America, namely, *L. divaricata* ssp. *tridentata* (Sesse & Moc. ex DC.) Felg. & Lowe, which is evidently a derivative of the South American *L. divaricata* Cav. In support of this derivation, an important phylogenetic point is that two of the South American species, *L. nitida* Cav. and *L. ameghinoi* Speg., have multifoliolate, pinnately compound leaves, which are ancestral traits in Zygophyllaceae. The bifoliolate leaf of *L. divaricata* and the more completely fused, virtually unifoliolate, leaf of *L. cuneifolia* Cav. are culminations of an evolutionary reduction series from the multifoliolate, pinnate leaf that survives today only in South America. It is unlikely that the striking, phyletic variation pattern of *Larrea* in South America has evolved as a result of a hypothetical introduction from North America of the relatively advanced taxon, *L. divaricata* ssp. *tridentata*, although this is a possibility that has been considered by a respected minority of botanists.

On the other hand, the North American *L. divaricata* ssp. *tridentata* exists as diploid ($n = 13$), tetraploid ($n = 26$), and hexaploid ($n = 39$) cytogeographic races in the Chihuahuan, Sonoran, and Mohave deserts, respectively (Yang 1968, 1970), whereas the South American *L. divaricata* is consistently diploid. But the latter taxon has putatively contributed a complement of chromosomes to the genome of the allotetraploid ($n = 26$) South American species, *L. cuneifolia*, the most xerophytic, and perhaps the most evolutionarily advanced member of the genus (Hunziker et al. 1972). The more or less parallel, morphological and cytological, geographic differentiation within *L. divaricata* ssp. *tridentata*, together with the complete distinctness of the insect faunas on *Larrea* in North and South America (C. D. Michener, pers. comm.), suggest that *Larrea* is also of some antiquity on the North American continent (Turner 1972; Porter 1974). However, recent studies of the chemistry of *Larrea* in both North and South America indicate that the extensive North American populations of *Larrea* are chemically more or

less uniform, whereas the South American species, including *L. divaricata*, show considerable geographic diversity in their chemistry, again indicating a greater antiquity for the genus in South America (T. J. Mabry et al. unpubl. data).

The remarkably annectant, largely allopatric, distributional areas of the diploid, tetraploid, and hexaploid chromosomal races of *Larrea divaricata* ssp. *tridentata* are nearly congruent with the boundaries of the Chihuahuan, Sonoran, and Mohave deserts, respectively, but all of these deserts are known to have undergone extensive vegetational and geographic changes during the Pleistocene (see details below). Most of the present areas of the warm deserts were occupied by pluvial woodlands until the waning phases of the Wisconsinan glacial, beginning perhaps as early as about 12,000 B.P. at the low, subtropical latitudes of the Sonoran and Chihuahuan deserts, but lingering till about 9000 or less B.P. at higher elevations of the northerly Mohave Desert (Wells and Berger 1967; Wells 1969). Hence, the present distributional range of *Larrea* in North America appears to be recent.

Indeed, the sharply delineated spatial pattern of its chromosomal races (Yang 1970) strongly suggests that the cytogeographic differentiation of *Larrea* in North America has developed *pari passu* with a northwestward migration from southern Mexico, the most likely point of immigration of the South American diploid. Since there is no evidence for more than one species of *Larrea* in North America, the doubling and tripling of its chromosome number amounts to autopolyploidy or "segmental allopolyploidy." The Mohavean hexaploid could have been derived from a combination of reduced and unreduced gametes stemming from meiotic irregularity in the Sonoran tetraploid at the cooler and drier northwestern limits of its range. Although the possibility of an earlier cycle of expansion of creosote bush deserts in North America cannot be ruled out on the present evidence, the major features of the existing geographic pattern of *Larrea divaricata* ssp. *tridentata* probably originated during the climatic transition from the late Wisconsin glacial to the Holocene, when a desiccating climate gripped the immense lowlands of the Southwest, opening a vast and varied desert niche into which a burgeoning population of *Larrea* could have expanded and differentiated explosively.

The weight of biogeographic evidence supports a South American origin for the genus *Larrea* and the related, endemic genera, *Plectrocarpa*, *Bulnesia*, and *Metharme*. If the extremely xerophytic species *Larrea divaricata* had been able to follow the hypothetically continuous overland migration route across the now wet tropics of northern South America and Central America during a period of drier climate, then a much greater amphitropical disjunction of zygophyllaceous genera would be expected between North and South America. As it is, the only

real disjunctions are in *Larrea* and *Fagonia*. Absence of the genus *Bulnesia* in North and Central America is a particularly difficult anomaly for the continuity theory, because *Bulnesia* has an array of eight species adapted to extremely different precipitation regimes in South America, ranging from *B. retama* in desert scrub too arid for *Larrea* to *B. arborea* in relatively humid tropical woodlands north of the equator in Columbia and Venezuela (Porter 1974; Hunziker unpubl. data). Any continuous route across the tropics hypothetically traversed by *Larrea* should have been more readily negotiated by *Bulnesia*. Only the least xerophytic genus *Guaiacum* is more or less continuous through the wet tropics between North and South America today. These biogeographic data defeat the idea of transtropic continuity for *Larrea* or most other Zygophyllaceae in the Americas, whether the family originated in the Northern or Southern Hemisphere or diverged north and south from conveniently extinct, hypothetical ancestors, formerly centered within the tropics.

There remains the major question as to how *Larrea divaricata* reached North America. Long distance transport across the wet tropics by bird dispersal seems to be the most feasible possibility. Among the available carriers would have been the Golden Plover (*Pluvialis dominica*), which has been an enormously abundant and frequently nonstop migrant between South and North America. In the northern spring season, when the bird departed from the arid steppes of Argentina for its breeding grounds in the Arctic tundra, it was autumn in the southern hemisphere, and the hairy mericarps of *Larrea* were available for epizoid dispersal, possibly cemented to the undertail coverts by the birds' own excrement (the "slovenly plover" mechanism of G. Ledyard Stebbins). On its spring migration the Golden Plover flies northwestward from the Pampas across Bolivia and the Peruvian Andes, and more or less nonstop across Central America, whence it proceeds northward through Mexico, including the arid interior plateau (A.O.U. 1957:172). With millions of birds flying this route for thousands of years, even a seemingly highly improbable event would have been feasible. Thus, diploid South American *Larrea divaricata*, which is apparently self-compatible (Hunziker et al. 1972), could have reached the Chihuahuan Desert of North America by a single, direct dispersal.

As to the timing of the event, the paleobotanical evidence in North America is as yet incomplete. Whether *Larrea* arrived in southern Mexico before or during the Wisconsinan glacial—and a glacial would be a favorable time to disperse across a wet tropical belt, considerably narrowed by an equatorward shift of the dry, subtropical high pressure cells—there is conclusive evidence that the present wide dominance of the *Larrea* zone throughout southwestern North America was not attained before the Holocene. *Larrea* has not been detected in the full-gla-

cial *Neotoma* record from any part of the Mohave Desert, nor from the Sonoran Desert in southeastern California, central Baja California, and central Sonora, nor from the Chihuahuan Desert in Texas. During the height of the Wisconsinan-age pluvials, any extensive creosote bush deserts must have been displaced far to the south by the great expansion of the woodland zone throughout most of the vast area presently dominated by *Larrea* in southwestern North America (Wells 1966; Wells and Jorgensen 1964; Wells and Berger 1967; Wells 1969, 1970, and unpubl. data). Of course, the current inadequate state of knowledge does not preclude the existence of *Larrea* in one or more North American refugia during the glacials of the Pleistocene, but the available evidence is in agreement with a relatively recent, perhaps Wisconsinan, age for *Larrea* in North America.

The oldest, well-documented *Neotoma* record of *Larrea* in North America is dated at $10,580 \pm 550$ B.P. (the radiocarbon age was determined on *Larrea* macrofossils) from the Wellton Hills east of Yuma in southwestern Arizona, at an elevation of 162 m (530 ft) (T. Van Devender, dissertation, Univ. of Arizona, 1973:138). The deposit contains a desert assemblage similar to the xerophilous Sonoran Desert scrub presently growing at the site, except for the abundant macrofossils of an *Ephedra* which is now rare or absent in the area. An early occurrence of desert conditions slightly different from today seems to be established. However, other deposits obtained by Van Devender at the same locality have a similar content of *Larrea* and *Ephedra*, but have yielded much younger dates, ranging from 6600 ± 370 (on *Larrea* fossils) and 8150 ± 260 (on *Ephedra* fossils) to 7950 ± 370 (on *Larrea*) and 8750 ± 320 (on *Ephedra*). The younger dates suggest that the entire series of deposits from the Wellton Hills is early Holocene in age. If the $10,580 \pm 550$ B.P. date (A-1407) is indeed accurate, it indicates an early onset of modern desert conditions at a very low elevation in the Sonoran Desert. In any case, 18 dated *Neotoma* records of pluvial, juniper woodland vegetation within the Sonoran Desert show a range in age from 10,250 (most are $>11,000$) to $>38,000$ B.P., but none show an authenticated contemporaneity of *Larrea* and *Juniperus*. One *Neotoma* deposit from the arid New Water Mountains in Yuma County, Arizona, contained *Larrea* together with juniper and oak, but separate dating of macrofossils of each gave an age of only 2710 ± 280 years for the *Larrea* in contrast to $11,000 \pm 505$ years for the *Juniperus* (Van Devender unpubl. data).

FULL-GLACIAL ZONATION OF WOODLANDS IN THE WARM-DESERT PROVINCES

The pluvial woodlands that displaced the *Larrea* zone varied geographically in composition. In the relatively arid Mohave Desert region

there was a well-marked zonation within the woodland zone, as follows: (1) Higher elevations. *Pinus monophylla*, *Juniperus osteosperma*, *Acer glabrum* (a xerophytic maple), *Ceanothus greggii* (an evergreen sclerophyll of chaparral), *Chamaebatiaria millefolium*, *Coleogyne ramossissima*. (2) Lower elevations. *Juniperus osteosperma*, *Yucca brevifolia* (Joshua tree), *Purshia glandulosa*, *Atriplex confertifolia* (shadscale). The lower juniper-Joshua tree zone extended south into what is now the northwestern Sonoran Desert along the trough of the lower Colorado River valley, where it descended to an elevation of only 260 m (850 ft). A *Neotoma* midden containing this relatively xerophilous juniper-woodland assemblage, but without a trace of *Larrea*, was found at this elevation between Needles and Parker in the midst of the extremely arid *Larrea* zone of the Colorado sector of the Sonoran Desert. The deposit has a radiocarbon age of $16,900 \pm 190$ (UCLA-1666), which is equivalent to full-glacial age. Presence of juniper and absence of *Larrea* is also recorded at >38,000 years ago in *Neotoma* deposits from the plains of the southern Sonoran Desert at 457 m (1500 ft) in the latitude of Hermosillo, Sonora (29°N), amidst the typical saguaro-paloverde vegetation of the existing desert (Wells and Berger unpubl. data).

The higher elevation pluvial woodland zone along the northern fringe of the Sonoran Desert province was dominated by the Mohavean *Pinus monophylla* and *Juniperus osteosperma*, as on the east base of the Turtle Mountains, California, at an elevation of 732 m (2400 ft) in what is now paloverde-ironwood-ocotillo desert (Wells and Berger 1967). From the Colorado River valley eastward, shrubby live oaks (*Quercus turbinella*, *Q. palmeri*) were an important component of the pluvial woodlands at elevations above 610 m (2000 ft) in the northern Colorado or Sonoran Desert (P. H. Leskinen unpubl. data; T. Van Devender unpubl. data), suggesting more mesic conditions to the east of the modern Mohavean province. Far to the southeast, the Chihuahuan Desert developed this trend to a greater degree, with a different set of evergreen oaks (*Quercus pungens*, *Q. grisea*) present in the Wisconsinan-age *Neotoma* middens down to the lowest available elevations, together with the different pinyon pine (*Pinus cembroides*) and junipers (*Juniperus pinchotii*, *J. deppeana*) that still dominate the existing, montane woodlands of that region (Wells 1966).

Hence, the pluvial woodlands of the Chihuahuan Desert province differed significantly from those of the Sonoran and Mohavean regions in having a much lesser degree of zonation with elevation (that is, no evidence of downward segregation of a juniper zone). In fact, the *Neotoma* record shows a dominance of pinyon, juniper, and scrub oak over the entire span of elevation available in the northern Chihuahuan Desert. Again, as in the other deserts, no trace of *Larrea* was detected in *Neotoma* deposits of pluvial age. Absence of a segregated juniper or ju-

niper-yucca zone at lower elevations and the consistent presence of evergreen oaks indicate that the Chihuahuan province enjoyed an even more mesic, pluvial woodland climate in its vast, now arid lowlands than the Sonoran, which, in turn, was more mesic or equable than the cool-arid, oakless Mohavean province. The apparent east-west, paleoclimatic gradient of increasing aridity may have been caused by decreasing summer rainfall in the westward direction, as a function of decreasing penetration of moist air masses with increasing distance from the Gulf of Mexico, essentially as in the modern pattern. Also, the Chihuahuan province undoubtedly has been subject to invasion by outbursts of cold, polar air masses moving southward across the Great Plains because there is no effective orographic barrier along the northeastern border of the province in Texas.

FULL-GLACIAL REFUGIA FOR WARM-DESERT SPECIES

The decidedly high elevation [1524-2286 m (5000-7500 ft)] of the southern sector of the Chihuahuan Desert in Zacatecas and San Luis Potosí would seem to render it even less suitable as a warm-desert *refugium* under a full-glacial climate. The strongly meridional atmospheric circulation during the glacials would have greatly augmented the present wintry visitations of frigid air (the *Norte* or norther), which would have had a telling effect on any thermophilous vegetation at high elevations. Moreover, the 792 m (2600-ft) pluvial downward displacement of the pinyon-oak-juniper woodland zone, firmly established by abundant macrofossil evidence in the much lower and presently hotter and more arid Big Bend area of the Rio Grande, would have been more than enough to shift the main body of the woodland zone down onto the high intermountain plateau of the southern Chihuahuan Desert province.

Suitable full-glacial *refugia* for the extremely xerophilous, warm-desert vegetation of the province might be sought where there is a combination of low elevation, tropical latitude, orographic protection from outbursts of polar air, and local or regional aridity. One example might be the arid rain-shadow pocket on the Extorax-Tula drainage in eastern Querétaro at 21°N, which now harbors a remarkably isolated, but extensive, area of *Larrea*-dominated landscape at elevations ranging from 1067 m (3500 ft) or less to about 1524 m (5000 ft) (northwestern sector of desert "island" in Fig. 1). There is also a further disjunction of creosote bush to the Valle del Mezquital on another branch of the same drainage at about 1829 m (6000 ft) in Hidalgo, north of Mexico City (southeastern part of desert "island" in Fig. 1), reported by Rzedowski and Leal (1958). A significantly large number of Chihuahuan Desert species are known to share this distribution. For example, Quintero (1968) lists 47 species in 34 genera that are important elements of the

Chihuahuan Desert vegetation, and which occur in the Valle del Mezquital area of Hidalgo. These include *Agave lecheguilla*, *A. striata*, *Ephedra aspera*, *Euphorbia antisiphilitica*, *Flourensia cernua*, *Hechtia glomerata*, *Jatropha dioica*, *Koeberlinia spinosa*, *Opuntia imbricata*, *Parthenium incanum*, *Salvia ballotaeflora*, and *Sophora secundiflora*. No doubt, an even more diverse list could be generated by more intensive collecting in Querétaro and Hidalgo, but the present information clearly indicates that the Chihuahuan Desert flora has extended into this southeasterly pocket in full force.

The mild but arid climate in Querétaro and Hidalgo is indicated by the rich diversity of succulents, including about 18 genera and 77 species of cacti (Bravo 1936, 1937; Britton and Rose 1920). The fact that many of the cacti are narrowly endemic strongly suggests that the distribution of desert plants in this area is of considerable antiquity, and undoubtedly antedates the Wisconsinan glacial. In this connection, there are several species of large, temperature-sensitive cacti in the same area, namely, the columnar *Cephalocereus senilis* (endemic), *Pachycereus marginatus* (endemic), *Lemaireocereus dumortieri*, and *Myrtillocactus geometrizans*; and enormous barrel cacti of the genus *Echinocactus*. Large, succulent-tissued cacti are known to be extremely sensitive to frost (Shreve 1951). The relatively hardy saguaro (*Carnegiea gigantea*), which has the most northerly distribution of any of the columnar giants of Mexico, is nevertheless subject to damage from frost in Arizona if temperatures drop below -5°C (23°F) for a short period or below -2°C (28°F) for a longer period; death may result from exposure to frost for 29 consecutive hours (Shreve 1911). It may be inferred that the giant succulents of southern Mexico are at least as good indicators of mild winter climate as the saguaro, and that the narrowly endemic columnar giants are located in areas that have not been subjected to severe frost during the evolutionary history of these types of cacti. Hence, it seems likely that the lower elevation range of the Querétaro-Hidalgo rain-shadow pocket had a relatively mild, frost-free climate during the glacials of the Pleistocene. At the same time, the climate must have been arid enough to harbor the rich and partly endemic assemblage of xerophytes presently sequestered there. Until macrofossil evidence is obtained from Querétaro, one can only conjecture whether the aridity during the glacial maxima was sufficient to favor the local dominance of *Larrea* which characterizes the lower range of elevation in the area today. Toward the close of a glacial, a southerly, tropical, warm-desert *refugium* such as this, with or without a physiognomic dominance of microphyllous scrub, could have restocked the entire Chihuahuan Desert province with the more xerophytic species that were unable to survive the cooler, pluvial woodland conditions on the elevated intermountain plateau or in the northerly Rio Grande drainage.

Much of the existing landscape of the Chihuahuan Desert, its vast expanses of low desert scrub and numerous dry lakes, is a product of the Holocene interglacial climate, and the vegetation pattern is demonstrably less than 11,500 years old in its current incarnation, even at the lowest possible elevations within the accepted limits of the province. Some elements of the present desert flora and fauna are known to have coexisted with the erstwhile pluvial woodlands in the lowlands, and these species may have had an uninterrupted history in the province during the glacials and interglacials of the Pleistocene, although no doubt suffering vicissitudes involving geographic or edaphic restrictions and drastic shifts in abundance. However, it is apparent from the macrofossil record that some of the more xerophytic desert species, including even the now enormously dominant *Larrea divaricata*, have entered or reentered the Chihuahuan Desert province during the Holocene, after having survived the Wisconsinan glacials elsewhere.

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The Herpetofauna of Howell's Ridge Cave and the Paleoecology of the Northwestern Chihuahuan Desert

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Howell's Ridge Cave is a vertical chimney in the marine reef-limestone of the Lower Cretaceous U-Bar Formation located at 1790 m elevation on Howell's Ridge, Little Hatchet Mountains, Grant County, New Mexico (Fig. 1). The chimney has been filled to within 1 m of the opening with a matrix that is extremely rich in the bones of various vertebrates including birds (Howard 1962), mammals (Smartt 1972; Harris et al. 1973), reptiles, and amphibians. This site is the Museum of Arid Land Biology, University of Texas at El Paso locality number 32, and the University of Arizona Laboratory of Paleontology locality number 7444.

The herpetofauna in samples collected from a 1.8-m (5.9-ft) stratigraphic column in undisturbed cave fill is reported here. The faunal list, changes in reptile and amphibian community composition and structure, and inferences for the paleoecology (biotic and climatic) and zoogeography of the northwestern Chihuahuan Desert are also presented.

HISTORY

Howell's Ridge Cave was discovered by the late Robert A. Zeller, Jr., during a geological reconnaissance of the Little Hatchet Mountains (Zeller 1970). He found some interesting bones on the surface which were sent to Hildegard Howard at the Los Angeles County Museum. The bird bones from this and subsequent collections by Zeller were reported by Howard (1962). She thought that the accumulation contained materials of both Holocene and Pleistocene ages. Howell's Ridge Cave received no further attention until Arthur Harris of the Museum of Arid

Land Biology relocated and excavated a portion of the cave in 1971. The materials discussed here were collected by the authors in 1972. Metcalf and Smartt (1974) reported on a collection of Pleistocene and Holocene snails collected from alluvial deposits on Howell's Ridge, but snails are rare in the cave deposit.

TECHNIQUES AND BIASES

Cave deposits are notorious for their confused stratigraphy; in many cases, the stratigraphy is disturbed through the mixing action of burrowing rodents. Yet, it is obvious that if cave deposits are excavated with an assumption of no stratigraphy, none will be observed. These deposits should be excavated in close stratigraphic levels to prove or disprove the presence of dependable stratigraphy. In most cases, the added vertical time control achieved by this technique is desirable.

The Howell's Ridge Cave herpetofaunal sample reported here was taken from a vertical profile to a depth of 1.8 m (5.9 ft); standard volume samples were collected at each 10 cm. Additional samples taken at every 5 cm (2 inches) for pollen analyses will be reported later. The matrix contains an extremely rich fauna mixed with various materials including rock fragments, fecal pellets, and plant fragments. The deposit has recognizable stratigraphy, i.e., horizontal layering and vertical changes in sediment color, rock-fall content, and a degree of decomposition of organic materials (Table 1). The upper portion of the cave fill is dry, but the water content increases with depth. In the lower, moist levels, most of the plant materials are decomposed.

The cave is located on the scarp face of a steep limestone block. The cave is a vertical chimney with a lateral entrance that is well above the ground (Fig. 2). The cave configuration is such that the faunal materials were probably carried in by predators or packrats and does not represent a natural trap. This type of accumulation can reflect the actions of wide-ranging predators rather than a detailed, local record. The fauna probably represents the accumulated efforts of a number of different raptorial predators of several sizes, including both nocturnal (owls) and diurnal (hawks, passerines) species. The vertebrae of several snakes, including *Leptotyphlops* sp. (blind snake) and juvenile *Sonora semiannulata* (ground snake), are so small that raptorial collectors are unlikely. These may have been brought into the cave in the guts or feces of small mammalian carnivores such as *Bassariscus astutus* (ring-tailed cat) or reptile carnivores such as *Lampropeltis getulus* (kingsnake) or *Crotaphytus wislizeni* (leopard lizard). The only types of reptiles that could have been in the past faunas and were not sampled were *Heloderma suspectum* (Gila monster), *Kinosternon* (mud turtle), and *Terrapene ornata* (box turtle).

Radiocarbon dates on the endocarps of *Celtis reticulata* (netleaf

TABLE 1. Radiocarbon dates, age estimates, stratigraphic data, and the presence of *Microtus* in a 1.8-m stratigraphic column from Howell's Ridge Cave, Grant County, New Mexico.

| Depth (cm) | C-14 dates, age estimates (B.P.) | Matrix | Rock Fall | gm water kg matrix (dry) | <i>Microtus</i> |
|------------|--|--|-----------|--------------------------------|-----------------|
| 0-10 | (0-) 495 | Tan color, abundant plant materials | | | 0 |
| 10-20 | 990 | | | | + |
| | | | | 19 | |
| 20-30 | 1485 | <u>Neotoma</u> midden | | | - |
| 30-40 | 1980 | | | | 0 |
| 40-50 | 2470 ± 120 | Tan color, abundant plant materials | | 48 | - |
| 50-60 | 2757 | | | | + |
| 60-70 | 3044 | | | 54 | + |
| | | | | 63 | |
| 70-80 | 3330 ± 170 | | | 78 | 0 |
| | 3910 ± 80 | | | 93 | |
| 80-90 | 4151 | | | 103 | + |
| | | | | 83 | |
| 90-100 | 4972 | Brownish black color, moderate amounts plant materials | | 148 | + |
| | | | | 117 | |
| 100-110 | 5793 | | | 166 | + |
| | | | | 143 | |
| 110-120 | 6410 ± 1270, 6820 ± 550 | | | 171 | + |
| 120-130 | 7436 | | | 179 | + |
| 130-140 | 8257 | | | | + |
| | | Red color with variable brown mottling, little plant material left | | | |
| 140-150 | 9078 | | | 196 | + |
| 150-160 | 9899 | | | | + |
| 160-170 | 10720 | | | | + |
| 170-180 | 11541 | | | | + |

Data on water content of cave matrix provided by W. Geoffrey Spaulding, Department of Geosciences, University of Arizona. B.P. = years before present, 0 = absent, + = present, ± = standard deviation on radiocarbon dates.

hackberry) are available for levels 70-80 cm (28-32 inches) (A-1354 [Radiocarbon Laboratory, University of Arizona, laboratory number]: 3330 ± 170 B.P.) and 110-120 cm (44-48 inches) (A-1429: 6820 ± 550 B.P. and A-1430: 6410 ± 1270 B.P.). The two dates from level 110-120 cm on stained and unstained endocarps are very close and suggest that at least for this level mixing is not great. A date on *Juniperus* (juniper) twigs and seeds from 40-50 cm (16-19 inches) is 2470 ± 120 B.P.

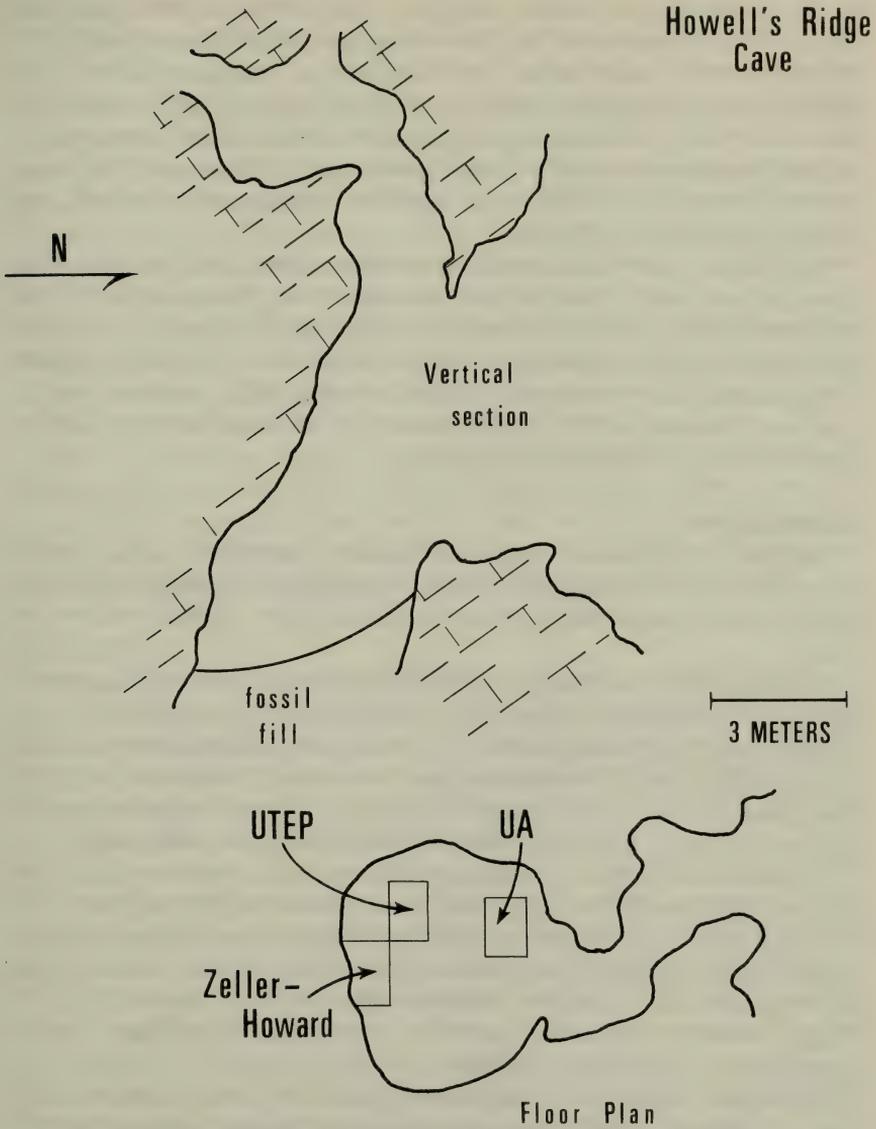


Fig. 2. Vertical section and plan view of Howell's Ridge Cave, Little Hatchet Mountains, Grant County, New Mexico (modified after Smartt 1972).

(A-1574). A date on a sotol (*Dasyilirion wheeleri*) stalk from 70-90 cm (28-35 inches) is 3910 ± 80 B.P. (A-1619). Table 1 gives age estimates for all levels extrapolated from these radiocarbon dates and the deposition rates derived from them (495 years/10 cm [4 inches] for the upper five levels, 287 years/10 cm between levels 40-50 cm and 70-80 cm, and 821 years/10 cm below). There is undoubtedly a gradual compaction with depth due to

the decomposition of organic materials: e.g., the lower levels probably represent more time per 10 cm than the upper levels. The 1.8-m (5.9-ft) column in this study spans the Holocene (= post-glacial) with the Pleistocene boundary about 160-170 cm (63-67 inches). The samples from levels 20-30 cm (8-12 inches) and 40-50 cm (16-20 inches) were lost. A radiocarbon date on whole bone of *Gymnogyps californianus* (California Condor) from the UTEP pit without stratigraphic control was $13,460 \pm 220$ B.P. (A-1557).

The entire lizard and amphibian samples from the Howell's Ridge Cave column were identified and are presented. The snake bones from six levels (70-80, 80-90, 130-140, 150-160, 160-170, and 170-180 cms) were identified; the remainder will be reported later. The fauna includes 163 specimens and nine species of amphibians, 1431 specimens and 17 species of lizards, and 973 specimens and 19 species of snakes. This is a total of 2567 specimens and 45 species.

AMPHIBIANS

Ambystoma tigrinum (tiger salamander): vertebrae (53), dentary fragments (2), maxilla, premaxilla. *A. tigrinum* apparently does not occur in the modern herpetofauna (see discussion, faunal analyses section).

Scaphiopus couchi (Couch's spadefoot toad): vertebrae (30), premaxillae (6), maxillae (6), humeri (4), tibiofibulae (8), sacrococcyges (3), fibulare, ilia (7), frontoparietals (2), radioulna. Skeletal elements from larger individuals of this species are distinctive. The species is present throughout most of the column. *S. couchi* is a xeric-adapted species although it lives in more mesic areas in the eastern part of its range.

Scaphiopus bombifrons (plains spadefoot toad): vertebrae (5). The anterior vertebrae of large individuals can be distinguished from those of *S. hammondi* on the basis of centrum shape. The centrum of *S. bombifrons* is proportionately larger and more massive than in *S. hammondi*. We were not able to use the character described by Holman (1970) to assign several small *Scaphiopus* ilia to species. *S. bombifrons* lives in grassland and desertscrub habitats.

Scaphiopus hammondi (Hammond's spadefoot toad): vertebrae (3). This species is locally common today, but also lives in more mesic grassland, woodland, and forest habitats to the south in Chihuahua.

Bufo debilis (green toad): posterior vertebra. This species was found only in level 120-130 cm (48-52 inches). The vertebrae of this small-sized species are easily distinguished from other local species of *Bufo*. *B. debilis* lives in grassland and desertscrub habitats.

Bufo punctatus (red-spotted toad): 5th vertebra. This species was found only in level 70-80 cm (28-32 inches). The vertebrae of this small-sized species are also distinctive in comparison with other *Bufo*. This species lives in rocky habitats in many plant communities up to

elevation of 2000 m (6560 ft).

Bufo sp. (toad): ilia (4), vertebrae (12), urostyles (2), sacral vertebrae (4), fragment of cranial crest, tibiofibula. These elements represent the larger-sized species of *Bufo*. The ilia have the high ilial crest characteristic of the *B. americanus* species group (Tihen 1962). *B. cognatus* is common in the area today, but *B. woodhousei* and *B. speciosus* are also possibilities. We have not been able to use the sacral character described by Holman (1971) to separate *B. cognatus* from *B. speciosus* and *B. woodhousei* or to find any additional characters that would enable us to separate them.

Rana cf. *pipiens* (leopard frog): posterior vertebra, premaxilla, tibiofibula. *R. pipiens* is an ubiquitous species that lives in many types of aquatic habitats, but needs relatively permanent water of some type. It presently occurs locally in the nearby Playas Valley.

Hyla cf. *arenicolor* (canyon treefrog): 3rd vertebra. This species was found only in level 150-160 cm (60-64 inches). The vertebra appears to represent *H. arenicolor* rather than *H. eximia wrightorum* on the basis of a proportionately larger neural canal. This species occurs to the west of Howell's Ridge across the Playas Valley in rocky, canyon habitats.

LIZARDS

Cnemidophorus cf. *tigris* (western whiptail lizard): frontals (3), dentaries (7), maxillae (8). *C. tigris* is a large-sized species that is locally common in desertscrub communities. The frontals can be identified to *C. tigris* as they have the characteristically rugose dorsal surface. Other large-sized species such as *C. burti* cannot be ruled out on the other elements, but these also probably belonged to *C. tigris*.

Cnemidophorus sp. (whiptail lizard): frontal, dentaries (17), premaxilla, maxillae (13). These represent species of smaller size than *C. tigris* which cannot be separated into different species. Local species of this size include *C. exanguis*, *C. inornatus*, *C. tessellatus*, and *C. uniparens*.

Eumeces obsoletus (Great Plains skink): dentary, premaxilla, maxillae (4). *E. obsoletus* is a mesic canyon species that may occasionally occur away from the mountains in riparian habitats.

Gerrhonotus kingi (Arizona alligator lizard): frontals (2), osteoderms (2). *G. kingi* is basically a montane species that may also enter the desert in riparian habitats. Two specimens collected from the wash below Howell's Ridge represent an unusually low-elevation xeric record for this species.

Crotaphytus collaris (collared lizard): frontals (3), parietals (5), pterygoids (3), skull, dentaries (17), premaxillae (5), maxillae (23). *C. collaris* is a large predator that lives in rocky habitats in xeric to mesic habitats. It may be locally abundant in rocky areas within grassland habitats.

Crotaphytus wislizeni (leopard lizard): frontal, dentaries (4), maxillae

(3). *C. wislizeni* is a large predator that is restricted to nonrocky, desert-scrub habitats.

Sceloporus cf. *clarki* (Clark's spiny lizard): frontal, dentaries (2), premaxilla, maxillae (4). *S. clarki* is a large-sized woodland species that does not occur in the vicinity of Howells' Ridge today. It lives in the higher mountains (Animas and Peloncillos) to the west.

Sceloporus cf. *jarrovi* (Yarrow's spiny lizard): dentaries (4), premaxilla, maxillae (2). *S. jarrovi* is a medium-sized crevice-dweller in montane, rocky habitats. It now lives no closer to Howell's Ridge than the higher mountains to the west.

Sceloporus cf. *magister* (desert spiny lizard): frontals (2), parietals (2), dentaries (2), maxillae (2). *S. magister* is a large-size species that lives in desertscrub habitats. It probably occurs in the Howell's Ridge vicinity today.

Sceloporus cf. *undulatus* (western fence lizard): frontals (14), dentaries (28), maxillae (33). *S. undulatus* is a small-sized species that lives in grassland, woodland, and occasionally desertscrub. It is uncommon in the Howell's Ridge vicinity today. The bones of the closely related woodland and forest species, *S. virgatus*, are very similar. Some elements of *S. scalaris*, *S. grammicus*, and *S. graciosus* could be confused as well. All of the fossils compare favorably with the reference material of *S. undulatus*.

Phrynosoma cornutum (Texas horned lizard): parietals (48), frontals (55), preorbitals (10), jugals (14), squamosals (86), angulars (55), dentaries (90), premaxillae (3), maxillae (64), basioccipital. *P. cornutum* is a large-sized species that lives in grassland and desertscrub habitats. This is the most common species of *Phrynosoma* in the Howell's Ridge area today.

Phrynosoma douglassi (short-horned lizard): parietals (27), frontals (38), preorbitals (3), jugals (2), squamosals (22), angulars (2), dentaries (96), premaxillae (12), maxillae (76), basioccipital. *P. douglassi* is a large-sized species that lives in mesic grasslands, woodlands, and forest habitats. It does not live in the Howell's Ridge area today. The nearest populations are to the west in the Animas and Peloncillo mountains. *P. douglassi* could possibly occur in the nearby Big Hatchet Mountains, but has not been collected. Any trend toward mesic or cool conditions would probably result in an increase of this species.

Phrynosoma modestum (round-tailed horned lizard): parietals (21), frontals (22), preorbitals (12), jugals (19), squamosals (45), angulars (45), dentaries (28), maxillae (17). *P. modestum* is a small- to moderate-sized species that is restricted to desertscrub communities. It presently occurs in the Howell's Ridge vicinity.

Cophosaurus texanus (greater earless lizard): parietal, frontals (9), dentaries (97), premaxilla, maxillae (40). *C. texanus* is a medium-sized lizard that lives in rocky habitats in desertscrub and lower elevation grassland. It is common near Howell's Ridge today.

Holbrookia maculata (lesser earless lizard): parietal, frontals (21), dentaries (75), premaxillae (6), maxillae (29). *H. maculata* is a grassland and woodland species that may occasionally occur in desert areas. It has not been collected in the immediate vicinity of Howell's Ridge, but does occur in the grassland near Hachita to the east.

Urosaurus ornatus (tree lizard): dentaries (4), maxillae (21). *U. ornatus* is a small-sized lizard that lives on trees and rocks in many different habitats well into woodland and forest communities. It is common on Howell's Ridge today.

Uta stansburiana (side-blotched lizard): parietal, frontal, dentaries (5), premaxilla. *U. stansburiana* is a widespread desert species that lives in most of the southwestern deserts, but also in woodland and chaparral in some portions of its range. In the Howell's Ridge area, it appears to be relatively restricted to the desertscrub plant communities.

Arizona elegans (glossy snake): vertebrae (31). *A. elegans* is a medium-sized, nocturnal species which lives in desertscrub and desert-grassland habitats.

Crotalus sp. (rattlesnake): vertebrae (27), dentary. These vertebrae represent both a medium-sized and a small-sized species. The large vertebrae resemble *C. viridus*, but *C. scutulatus* is also a possibility. *C. viridus* is in the Playas Valley today, and *C. scutulatus* is just to the west in the Animas Valley. The small vertebrae resemble *C. lepidus*, but some of them would represent *C. pricei*, *C. willardi*, or *Sistrurus catenatus*. The three small *Crotalus* are montane species. *C. lepidus* occurs lower than the other two species, and a specimen from Howell's Ridge may be a low-elevation record for this region. The crotalid vertebrae will be reexamined in detail later.

Diadophis punctatus (ringneck snake): vertebrae (30). In Trans-Pecos, Texas, New Mexico, and Arizona, ringnecks are found in mountain or scarp woodlands mainly between 1200 and 2200 m (1320-2420 yards), but are known to disperse along riparian lowland corridors surrounded by desertscrub or grassland (Gehlbach 1974). They are strictly limited by desertscrub. Some of the fossils are large enough to be the large-sized western subspecies, *D. p. regalis*, which lives in the region today.

Ficimia cana (western hook-nosed snake): vertebrae (53). *F. cana* is a small-sized, nocturnal, secretive species that is more common in desertscrub and grassland, but is occasionally found in more mesic habitats.

Heterodon nasicus (western hog-nosed snake): vertebrae (9). *H. nasicus* is a small- to medium-sized, crepuscular species that is common in grasslands, less so in desertscrub.

Hypsiglena torquata (Night snake): vertebrae (80). *H. torquata* is a small-sized, nocturnal species that occurs in all habitats up to and in-

cluding pine forests. It is probably most abundant in desertscrub habitats.

Lampropeltis getulus (common, or grassland kingsnake): vertebrae (41). *L. getulus* is a large-sized, nocturnal species that is most common in mesic grassland habitats. It can also occur well into the desert along riparian washes or arroyos.

Lampropeltis cf. *pyromelana* (Arizona mountain kingsnake): vertebrae (10). *L. pyromelana* is a medium-sized diurnal species that is restricted to mesic or riparian montane habitats. The nearest populations to Howell's Ridge are in the Animas Mountains to the west across Playas Valley, and the Big Hatchet Mountains to the south.

Leptotyphlops sp. (blind snake): vertebrae (152). *Leptotyphlops* is a very small, burrowing form that is rarely found above ground unless the surface is wet. Two species, *L. dulcis* and *L. humilis*, may occur in the area today.

Masticophis sp. (whipsnake, coachwhip): vertebrae (15). *Masticophis* are large, diurnal snakes that live in desertscrub and grassland (*M. flagellum*) or rocky habitats in the mountains (*M. bilineatus*, *M. taeniatus*). The species of *Masticophis* are not determinable using the vertebrae. In many cases, they cannot be distinguished from *Coluber constrictor* (racer), which may be a possible component in the Pleistocene samples.

Pituophis melanoleucus (bull snake): vertebrae (98). *P. melanoleucus* is a large-sized, nocturnal or crepuscular species that lives in most habitats from the lowest deserts to the highest mountains in this region.

Rhinocheilus lecontei (long-nosed snake): vertebrae (118). *R. lecontei* is a medium-sized, nocturnal species that lives in desertscrub and xeric grassland habitats.

Salvadora sp. (patch-nosed snake): vertebrae (38). *Salvadora* is a medium-sized, diurnal snake that lives in desertscrub and xeric grassland (*S. hexalepis*) or up into the woodland and forest (*S. grahamiae*). The vertebrae of the two species are indistinguishable.

Sonora semiannulata (ground snake): vertebrae (230), articular. *S. semiannulata* is a very small, nocturnal snake that lives in most habitats below woodland communities. It presently lives on Howell's Ridge.

Tantilla sp. (black-headed snake): vertebrae (8). *Tantilla* are very small, nocturnal, secretive species found in many habitats at most elevations. Some of the vertebrae are large enough to represent the large-sized race of *T. nigriceps* which presently occurs locally. The smaller vertebrae may be of subadult *T. nigriceps*, or of the smaller-sized species, *T. planiceps*.

Thamnophis cf. *cyrtopsis* (black-neck garter snake): vertebrae (2). *T. cyrtopsis* is a medium-sized, diurnal, semi-aquatic species that is common in montane, riparian habitats. It occasionally may be found some

distance from the mountains in riparian habitats, but does not live in xeric grassland or desertscrub.

Trimorphodon biscutatus (lyre snake): vertebrae (29). *T. biscutatus* is a medium-sized, nocturnal species that lives in rocky habitats ranging from desert elevations into lower woodland. The Little Hatchet Mountains are located on the present eastern edge of the subspecies, *T. b. lambda*. *T. b. wilkinsoni* occurs in isolated populations to the east into the Big Bend of Texas. *T. biscutatus* has been present in the Little Hatchet Mountains since the Pleistocene. Perhaps there was gene flow between the isolated populations at that time.

FAUNAL ANALYSES

The reptile and amphibian bones in the 10-cm (4-inches) interval samples from Howell's Ridge Cave are numerous enough that the samples were analyzed quantitatively. The specific skeletal elements identified for this purpose were mid-dorsal vertebrae in snakes, skull bones in lizards, and skull, limb, and vertebral elements in amphibians. The fossil reptiles and amphibians will be deposited in the Museum of Arid Land Biology, University of Texas at El Paso. A representative sample will be deposited in the University of Arizona Laboratory of Paleontology. The fauna includes most of the herpetofauna in all habitats from the higher-elevation mesic forest, woodland, and grassland to the lowest, xeric, desertscrub plant communities. The predators that collected the faunal materials appear to have been sampling a regional rather than a local area. Even aquatic and semi-aquatic amphibians are present. Table 2 lists the modern reptile and amphibian fauna as compiled from specimens in the collections of the University of Arizona, Department of Biological Sciences (UAZ), the Museum of Arid Land Biology (MALB), University of New Mexico (UNM), and the American Museum of Natural History (AMNH).

Certain biases are apparent in the fossil fauna, but are probably consistent within the entire column. Specific examples include the consistently dominant percentages of *Phrynosoma* (three species) which are only moderately abundant in the present fauna. *Cnemidophorus* (several species) are common lizards in the present fauna, but are only moderately represented in the fossil fauna. The predators bringing the bones to Howell's Ridge Cave appear to have been differentially selecting species as preferred food, or selecting those that have behavior patterns allowing easy capture. Another possible bias is that the species of predator-collectors could have changed, thus creating apparent changes in the fauna. If this occurred, it was probably in response to a change in climate and would not necessarily negate any changes reflected in the fossil herpetofauna. The fossils also show a size bias in that few specimens of animals larger than rabbit are present.

TABLE 2. The modern herpetofauna of the Howell's Ridge, Little Hatchet Mountains, Grant County, New Mexico, and nearby areas.

A. Species collected in the Little Hatchet Mountains and/or Playas and Hachita valleys.

| | |
|--------------------------------|----------------------------------|
| <i>Scaphiopus bombifrons</i> | Plains spadefoot toad |
| <i>S. couchi</i> | Couch's spadefoot toad |
| <i>S. hammondi</i> | Hammond's spadefoot toad |
| <i>Bufo cognatus</i> | Great Plains toad |
| <i>B. debilis</i> | Green toad |
| <i>Rana pipiens</i> | Leopard frog |
| <i>Terrapene ornata</i> | Ornate box turtle |
| <i>Kinosternon flavescens</i> | Yellow mud turtle |
| <i>Crotaphytus wislizeni</i> | Leopard lizard |
| <i>Sceloporus undulatus</i> | Fence lizard |
| <i>Phrynosoma cornutum</i> | Texas horned lizard |
| <i>P. modestum</i> | Round-tailed horned lizard |
| <i>Cophosaurus texanus</i> | Greater earless lizard |
| <i>Holbrookia maculata</i> | Lesser earless lizard |
| <i>Urosaurus ornatus</i> | Tree lizard |
| <i>Uta stansburiana</i> | Side-blotched lizard |
| <i>Cnemidophorus exanguis</i> | Chihuahua whiptail lizard |
| <i>C. tigris</i> | Western whiptail lizard |
| <i>C. uniparens</i> | Desert-grassland whiptail lizard |
| <i>Gerrhonotus kingi</i> | Arizona alligator lizard |
| <i>Arizona elegans</i> | Glossy snake |
| <i>Diadophis punctatus</i> | Ringneck snake |
| <i>Heterodon nasicus</i> | Western hog-nosed snake |
| <i>Hypsiglena torquata</i> | Night snake |
| <i>Lampropeltis getulus</i> | Common kingsnake |
| <i>Masticophis flagellum</i> | Coachwhip snake |
| <i>M. taeniatus</i> | Striped or ornate whipsnake |
| <i>Pituophis melanoleucus</i> | Bullsnake |
| <i>Rhinocheilus lecontei</i> | Long-nosed snake |
| <i>Salvadora grahamiae</i> | Mountain patch-nosed snake |
| <i>S. hexalepis</i> | Western patch-nosed snake |
| <i>Sonora semiannulata</i> | Western ground snake |
| <i>Tantilla nigriceps</i> | Black-headed snake |
| <i>Thamnophis marcianus</i> | Marcy's gartersnake |
| <i>Trimorphodon biscutatus</i> | Lyre snake |
| <i>Crotalus atrox</i> | Western diamond-back rattlesnake |
| <i>C. lepidus</i> | Rock rattlesnake |
| <i>C. molossus</i> | Black-tailed rattlesnake |
| <i>C. viridus</i> | Prairie rattlesnake |

B. Species possibly in local herpetofauna of Little Hatchet Mountains; specimens have been collected in similar habitats to the east and to the west.

| | |
|-------------------------------------|------------------|
| <i>Bufo punctatus</i> | Red-spotted toad |
| <i>B. woodhousei</i> | Woodhouse's toad |
| <i>Hyla arenicolor</i> | Canyon treefrog |
| <i>Rana catesbiana</i> (introduced) | Bullfrog |
| <i>Ambystoma tigrinum</i> | Tiger salamander |
| <i>Crotaphytus collaris</i> | Collared lizard |

TABLE 2. (Continued)

| | | |
|---|--------------------------------|------|
| <i>Sceloporus magister</i> | Desert spiny lizard | |
| <i>S. poinsetti</i> | Crevice spiny lizard | |
| <i>Cnemidophorus inornatus</i> | Little striped whiptail lizard | |
| <i>C. tessellatus</i> | Checkered whiptail lizard | |
| <i>Leptotyphlops dulcis</i> | Texas blind snake | |
| <i>L. humilis</i> | Western blind snake | |
| <i>Tantilla planiceps</i> | Black-headed snake | |
| <i>Sistrurus catenatus</i> | Massasauga | |
| C. Additional species occurring within a 150 km radius of the Little Hatchet Mountains. Direction of the nearest populations are given. | | |
| <i>Bufo alvarius</i> | Colorado river toad | W |
| <i>B. microscaphus</i> | Arizona toad | NS |
| <i>B. speciosus</i> | Texas toad | E |
| <i>Hyla eximia</i> | Arizona treefrog | NS |
| <i>Rana tarahumarae</i> | Tarahumara frog | S |
| <i>Kinosternon sonoriense</i> | Sonoran mudturtle | WS |
| <i>Phrynosoma douglassi</i> | Short-horned horned lizard | WNS |
| <i>Sceloporus clarki</i> | Clark's spiny lizard | W |
| <i>S. jarrovi</i> | Yarrow's spiny lizard | WS |
| <i>S. scalaris</i> | Bunch grass lizard | WS |
| <i>S. virgatus</i> | Striped plateau lizard | WS |
| <i>Cnemidophorus burti</i> | Giant spotted whiptail lizard | W |
| <i>C. neomexicanus</i> | New Mexican whiptail lizard | NE |
| <i>Coleonyx variegatus</i> | Banded gecko | W |
| <i>Eumeces multivirgatus</i> | Many-lined skink | NS |
| <i>Heloderma suspectum</i> | Gila monster | W |
| <i>Elaphe subocularis</i> | Trans-Pecos ratsnake | E |
| <i>E. triaspis</i> | Green ratsnake | W |
| <i>Lampropeltis pyromelana</i> | Arizona mountain kingsnake | WS |
| <i>Masticophis bilineatus</i> | Sonoran whipsnake | W |
| <i>Micruroides euryxanthus</i> | Arizona coral snake | W |
| <i>Natrix rufipunctatus</i> | Narrow-headed watersnake | NS |
| <i>Thamnophis cyrtopsis</i> | Black-necked gartersnake | NESW |
| <i>T. elegans</i> | Wandering gartersnake | NS |
| <i>T. eques</i> | Mexican gartersnake | EWS |
| <i>T. sirtalis</i> | New Mexican gartersnake | NS |
| <i>Crotalus pricei</i> | Twinspotted rattlesnake | WS |
| <i>C. scutulatus</i> | Mohave rattlesnake | WS |
| <i>C. willardi</i> | Ridge-nosed rattlesnake | WS |

The samples were analyzed in several different ways in order to ascertain the best quantitative method for use in the interpretation of the Howell's Ridge faunal remains. The simplest method is to calculate percentages of the total number of identifiable specimens (NS). This method is best applied when the samples are such that the minimum number of individuals (MNI) cannot be determined. The snake fauna from Howell's Ridge was analyzed using percentages of NS because the

TABLE 3. Percentages of total number of identifiable specimens of fossil snakes from six 10 cm levels in Howell's Ridge Cave, Little Hatchet Mountains, Grant County, New Mexico. Most of the identifications were made from vertebrae.

| Species | 70-80 | 80-90 | 130-140 | 150-160 | 160-170 | 170-180 |
|---|-------|-------|---------|---------|---------|---------|
| <i>Arizona elegans</i> | 5.8 | 2.4 | 5.3 | 0.6 | 6.3 | 0.5 |
| <i>Crotalus</i> sp. (large) | 1.2 | 0.6 | 0.3 | 0.6 | — | 0.5 |
| <i>Crotalus</i> sp. (small) | 7.0 | 1.2 | 3.2 | 0.6 | — | 0.5 |
| <i>Diadophis punctatus</i> | 2.3 | 1.8 | 4.7 | 4.7 | 4.2 | 2.0 |
| <i>Ficimia cana</i> | 4.7 | 2.4 | 7.3 | 10.6 | 8.3 | 3.0 |
| <i>Heterodon nasicus</i> | — | 1.2 | 0.3 | — | — | 3.0 |
| <i>Hypsiglena torquata</i> | 7.0 | 13.2 | 7.9 | 2.9 | 8.3 | 9.0 |
| <i>Lampropeltis getulus</i> | 5.8 | 4.9 | 3.8 | 6.5 | 2.1 | 2.0 |
| <i>Lampropeltis</i> cf. <i>pyromelana</i> | — | — | 1.3 | 1.2 | — | 2.0 |
| <i>Leptotyphlops</i> sp. | 1.2 | 9.1 | 18.3 | 10.0 | 6.3 | 29.0 |
| <i>Masticophis</i> sp. | 4.7 | 1.2 | 1.3 | 1.8 | 4.2 | — |
| <i>Pituophis melanoleucus</i> | 9.3 | 10.4 | 7.6 | 12.9 | 6.3 | 12.0 |
| <i>Rhinocheilus lecontei</i> | 15.1 | 11.6 | 10.7 | 15.9 | 6.3 | 12.0 |
| <i>Salvadora</i> sp. | 9.3 | 5.5 | 3.2 | 3.5 | — | 2.5 |
| <i>Sonora semiannulata</i> | 24.4 | 25.0 | 23.0 | 24.1 | 34.4 | 19.0 |
| <i>Thamnophis</i> cf. <i>cyrtopsis</i> | — | — | 0.3 | — | — | 0.5 |
| <i>Tantilla</i> sp. | — | 1.8 | — | — | 4.2 | 1.5 |
| <i>Trimorphodon biscutatus</i> | 2.3 | 7.3 | 1.3 | 4.1 | 8.3 | — |
| Number species | 14 | 16 | 17 | 15 | 12 | 16 |
| Number specimens | 86 | 164 | 317 | 170 | 48 | 200 |

mid-dorsal vertebrae are very numerous; e.g., most taxa would unrealistically be recorded as single individuals (Table 3).

A refinement of this method is to use percentages of a corrected number of identifiable specimens (CNS) as suggested by Shotwell (1955, 1958). This method involves weighting the species differences in the number of recognizable elements. The seven easily recognizable lizard elements (left and right dentaries and maxillae, premaxilla, frontal, and parietal) provide a standard number of identifiable elements per species (SN). Ratios of SN to actual numbers of identifiable elements per species (AN) provide weighting values enabling the derivation of CNS, e.g., $\frac{SN}{AN} \times NS = CNS$. Some of the lizards in the Howell's Ridge Cave fauna have a few more recognizable elements in the skull than the SN of seven. The squamosals in *Phrynosoma douglassi* are easily recognized and the frontal and premaxilla in *Eumeces obsoletus* are paired. These two species have nine recognizable skull bones and a weighting ratio of 0.78. The squamosals and angulars are identifiable in *Phrynosoma cornutum* and *P. modestum*, giving an AN of 11 and a weighting ratio of 0.64. The faunal abundances can then be expressed as percentages of identifiable specimens.

Shotwell's (1955, 1958) method of reconstructing past communities does not appear to be meaningful in faunal assemblages such as the Howell's Ridge Cave samples. He used a ratio of the corrected number of specimens and the MNI to give a relative completeness (RC). The RC value was used as a measure of the distance of transport and as a means of allotting portions of his fauna to "distal" and "proximal" communities. Relative completeness in the lizard samples in Howell's Ridge Cave appears to reflect the durability of lizard skulls (*Phrynosoma* has high values) rather than any community parameter. Moreover, the bone accumulations of wide-ranging predators could well reflect many parameters, e.g., distance from cave, abundance of animals, behavior of animals, habitat of animals and/or size, and dietary preferences of the predators. We feel that the factors represented by the RC value do not include enough variables to be meaningful.

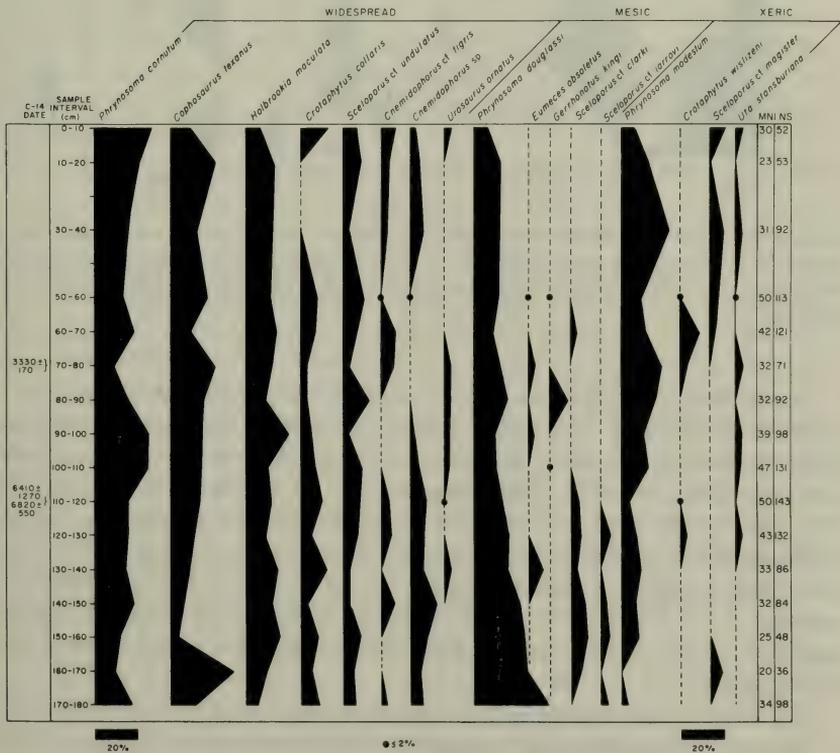


Fig. 3. Percentages of minimum numbers of individuals of fossil lizards in standard volume samples collected at 10 cm intervals from a 1.8 m stratigraphic column in Howell's Ridge Cave, Grant County, New Mexico. MNI = minimum number of individuals, NS = number of identifiable specimens.

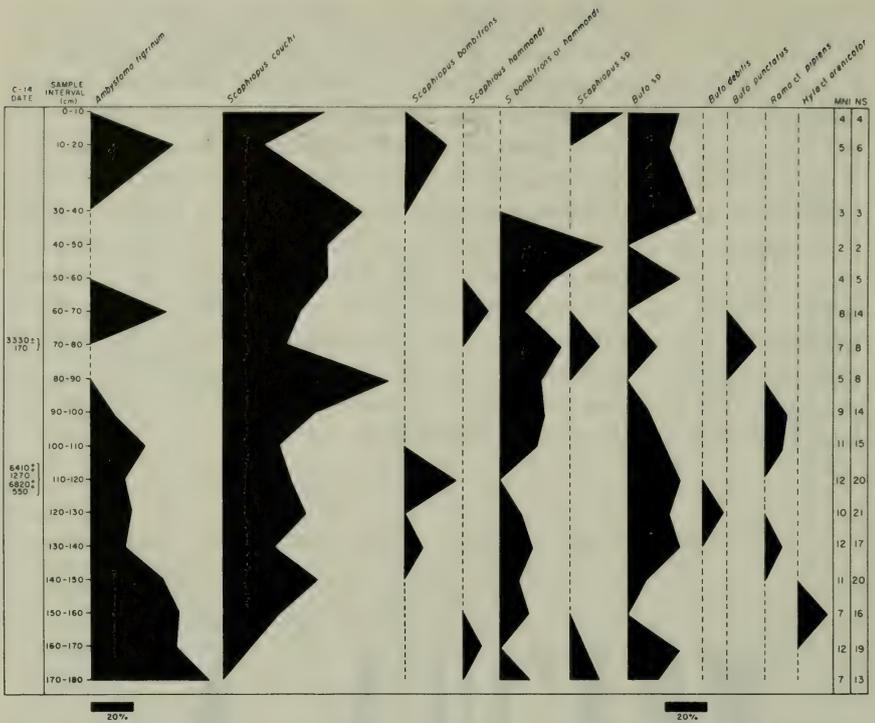


Fig. 4. Percentages of minimum numbers of individuals of fossil amphibians in standard volume samples collected at 10 cm intervals from a 1.8 m stratigraphic column in Howell's Ridge Cave, Grant County, New Mexico. MNI = minimum number of individuals, NS = number of identifiable specimens.

Shotwell did restrict his relative abundance (RA) calculations to a percentage of MNI. This value appears to reflect the sample compositions in a fairly accurate, conservative way and was used by us in the analyses of the Howell's Ridge lizards (Fig. 3) and amphibians (Fig. 4). The conversion from NS or CNS to MNI involves a reduction in the numbers used to calculate RA so that sample sizes appear small. Yet, these percentages are probably more robust and more realistic than percentages from NS or CNS. We feel that percentages of MNI are a better estimate of population changes than the percentages of NS used in pollen analyses.

The MNI in the lizards and the total number of identifiable elements in the snake fauna are large enough to reflect accurately changes in the faunal composition in different samples. The MNI in the amphibian fauna are lower and there is almost certainly some variance due to sampling errors. Yet some of the changes in the amphibian fauna appear to be real. Inferences about past vegetations and past climates from such

quantitative samples imply that these samples accurately reflect changes in the populations and distributions of the animals involved. The relationship between the changes reflected in these samples and the structure of the populations is difficult to establish. However, we feel that the population changes recorded in the fossil samples are directly related to changes in climate and vegetation.

FAUNAL CHANGES

At a basic level, the herpetofauna remained stable throughout the Howell's Ridge stratigraphic column. No major change in structure or composition analogous to a change from forest or woodland to grassland or desertscrub occurred at the beginning of or during the Holocene. The flora of this area probably underwent a greater change in composition similar to the 1000-m (3280-ft) depression of vegetation zones recorded to the west at Willcox Playa, Arizona (Martin 1963). Similarly, Van Devender (1973) recorded a 400-600 m (1450-2150 ft) lowering of woodland plant species into the present Sonoran Desert of Arizona in response to late Wisconsinan Ice Age climates farther to the west. The general stability in the herpetofauna of the Howell's Ridge region is probably due to the fact that predator-collectors sampled a large area.

Yet, there are interesting correlated changes discernible in this record. The changes in percentages of the more mesic-adapted and more xeric-adapted species show concomitant increases and decreases. The percentages of such mesic forms as *Phrynosoma douglassi* and *Ambystoma tigrinum* increase with depth, while the xeric *Phrynosoma modestum* and *Scaphiopus couchi* decrease with depth. Several relatively mesic taxa, including *Lampropeltis* cf. *pyromelana*, *Thamnophis* cf. *cryptopsis*, *Sceleoporos* cf. *clarki*, *S.* cf. *jarrovi*, *Rana* cf. *pipiens*, and *Hyla* cf. *arenicolor*, were found only in the lower levels. Xeric species found only in the upper levels include *Crotaphytus wislizeni*, *Uta stansburiana*, and *Bufo punctatus*. The trend toward a more mesic fauna (and climate) can be readily seen in the ratio of mesic-adapted lizards shown in Fig. 5. These types of changes in the populations of reptiles and amphibians would logically be expected under climatic changes resulting in shifts in the plant communities in which the animals live.

Ambystoma tigrinum is a salamander found in either mesic or xeric climates, but it needs relatively permanent water situations for the development of its larvae. In xeric environments, *A. tigrinum* may be neotenic and never metamorphose into terrestrial adults. The most likely habitat for this animal in the Howell's Ridge area is in the playa (= barrial) in Playas Valley, 13 km (8 miles) to the west. The presence of *A. tigrinum* in Howell's Ridge Cave implies that the playa was wet (permanently, or intermittently with few extended droughts) during the

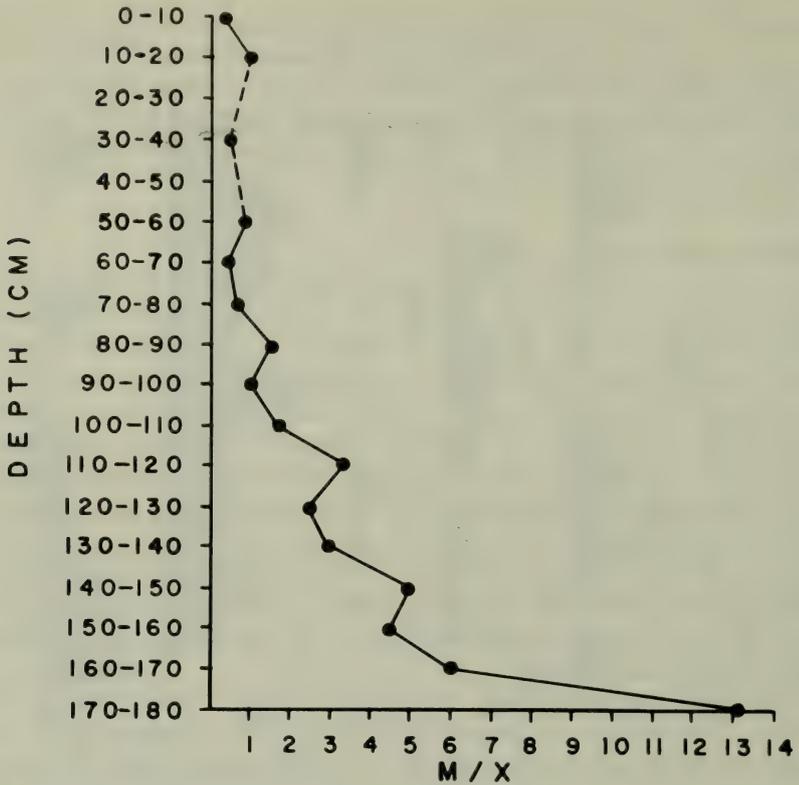


Fig. 5. Ratio of percentages of minimum numbers of individuals of mesic-adapted (M) versus xeric-adapted (X) species of lizards in the 1.8 m stratigraphic section in Howell's Ridge Cave, Grant County, New Mexico. Species included in ratio indicated in Fig. 3.

time of deposition. The presence and percentages of *A. tigrinum* reflect alternate wet and dry conditions in the playa (see Fig. 4). Specifically, we infer that the playa was wet from the Pleistocene until about 4000-5000 years ago (levels 90-100 cm to 170-180 cm). Two subsequent wet periods are suggested at about 3000 and again less than 1000 years ago. The absence of *A. tigrinum* in the dry periods suggests that it became extinct locally or that population levels were very low. The reappearance of *A. tigrinum* in younger, wet periods implies that the climate was again mesic enough to allow population buildup and/or the dispersal of terrestrial adult salamanders from distant populations (probably the north end of Playas Valley near Silver City). A vertebra from a moderate-sized fish in level 60-70 cm (24-28 inches) was identified as *Gila cf. robusta* (Cyprinidae, Colorado chub) by William J. Koster, University of New Mexico. This large minnow lives in fresh-water streams, rivers, and springs and also suggests permanent water in the Playas Valley at the time of deposition. The nearest present population

of *Gila robusta* is in the headwaters of the Gila River to the north. Neither moderate-sized fish nor *A. tigrinum* are known to occur in the vicinity of Howell's Ridge today.

Other faunal records in the Howell's Ridge column are of particular interest. Voles of the genus *Microtus* are fairly mesic-adapted rodents. They have been used as indicators of Pleistocene climate and age throughout the semi-arid southwest. *Microtus* is present in all samples in the column except 70-80 cm (3330 ± 170 B.P.), 30-40 cm (ca. 1664 B.P.) and probably the top 5 cm (Table 1). *Microtus* does not live in the Howell's Ridge vicinity today, and was not found in two modern owl-pellet assemblages from Howell's Ridge examined by the senior author. There is a possibility that relict populations of *M. mexicanus* could exist on Big Hatchet Peak or in the Animas Mountains, but these have not been collected. The *Microtus* fossils in the cave may represent as many as four species with somewhat different mesic adaptations (R. Smartt, pers. comm. 1974), and will be identified and reported later. For the present discussion, we wish to say only that the time distribution of *Microtus* in the stratigraphic column is very similar to that of *Ambystoma* (Fig. 4) and probably reflects mesic, grassy habitats.

Harris et al. (1973) reported *Cryptotis parva* (least shrew) from Howell's Ridge Cave with no depth provenience given. This shrew presently lives no closer than central Texas and is probably a member of the Pleistocene fauna in the lower levels. In her study of the avian fossils from Howell's Ridge Cave, Howard (1962) found several forms referable to Pleistocene species (usually larger than modern species) including *Gymnogyps amplus* (condor). Several species of ducks and geese were identified, again suggesting wet playa conditions. Most of the bird bones were collected from the top meter of the deposit. Our radiocarbon dates and time estimates suggest that most of the bird bones are Holocene in age. Perhaps condor did not become extinct until well into the Holocene and not synchronously with the megafauna (Martin 1973). Metcalf and Smartt (1974) suggested that several species of snails which no longer occur on Howell's Ridge did not become extinct locally until fairly late in the Holocene based on their presence in Holocene alluvial deposits. Extinct species of large mammals in the original Zeller-Howard collections include *Equus* cf. *conversidens* (horse; lower molar) and Camelidae (camel; tooth fragments). These were tentatively identified by T. Downs, Los Angeles County Museum of Natural History, but the specimens were lost (G. T. Jefferson, pers. comm. 1974). No specimens of extinct mammals were found in association with our stratigraphic column in Howell's Ridge Cave.

PALEOECOLOGY

The biotic communities of the Little Hatchet Mountains and Playas Valley appear to have undergone a gradual change from the Pleistocene

cool, moist climate to the modern hot, dry climate. This was not a simple transition to a hot, dry climate at the beginning of the Holocene (ca. 10,000 B.P.), but rather a transition to a warm, moist period which ended only 4000-5000 years ago. A hot, dry "Altithermal" period from 4000 to 7500 years ago is not recorded. Perhaps this term should be discarded or restricted to use in the Great Basin where dendrochronologic evidence for it exists (La Marche 1973).

The biotic changes accompanying such a gradual transition may not have been as abrupt as in other areas where the climate became hot and dry at the beginning of the Holocene. The more mesic plant communities probably retreated up the elevational gradient, but the remaining communities were still a great deal more mesic than the present ones. Perhaps the only reliable microfaunal record of the beginning of the Holocene would be the disappearance of the most mesic forms, such as *Cryptotis parva*, and decreased percentages of the more tolerant mesic forms. The dramatic change in the Howell's Ridge fauna occurred when the climate finally dried up at 4000-5000 years ago. At about 3300 years ago, the climate appears to have been hotter and drier than the present and probably caused local extinctions of most of the mesic forms. However, the top level (0-10 cm [0-4 inches]) integrates the present hot, dry climate with the more mesic period that preceded it. During two later periods, the climate was again relatively mesic, thus allowing the reexpansion of some of the mesic forms, e.g., *Ambystoma*, *Microtus*, and *Gila*. The fauna probably reached its present composition and structure less than a thousand years ago. The overall Holocene faunal record can be characterized as a major change occurring about 4000-5000 years ago, with minor fluctuations since. In contrast, the major extinctions of the Pleistocene megafaunas occurred from 10,000-11,000 years ago (Martin 1973).

The implication of this biotic record for the Chihuahuan Desert is that the sensitive ecotone between the Chihuahuan desertscrub communities and the more mesic, desert-grassland communities has not been stable. The relative areas of these have fluctuated in response to climatic changes during the Holocene. We suggest that the recent invasion of grassland by desertscrub involved both the recent climatic warming and the environmental perturbations by man (overgrazing, reduced fire frequency, lowering of the water table, etc.; see discussion in Hastings and Turner 1965). Further, the Chihuahuan Desert communities in high-elevation areas in New Mexico, Arizona, and northwestern Chihuahua must be relatively new to those areas.

ZOOGEOGRAPHY

The faunal evidence for relatively moist conditions in the Holocene suggests the following scenario of drainage connections. The present

(hot, dry) Playas and Hachitas valleys have only ephemeral water in their playas and arroyos. During the early Holocene (warm, moist or hot, moist) the Playas Valley system probably joined the Hachita Valley system (at least occasionally) through the pass between the Big and Little Hatchet Mountains. The combined systems drained southeastward into the Laguna Moscos in Chihuahua (Morrison 1969). During the latest Wisconsin pluvial period (cold, moist or cool, wet), the Playas-Hachita-Laguna Moscos system was probably permanently connected. At this time, Laguna Moscos probably overflowed (at least occasionally) into the Rio Casas Grandes. During the last full-glacial period (cold, moist or wet), the entire system was probably connected with Pluvial Lake Palomas in north-central Chihuahua (Reeves 1969). This would provide drainage connections for the internally drained portion of New Mexico between the Rio Grande drainage (Atlantic) and the Gila River drainage (Pacific) with Pluvial Lake Palomas in Chihuahua. The Mimbres River system east of the Hachitas Valley also drained into Pluvial Lake Palomas from the north.

This scenario of drainage connections is very interesting because of the disjunct distributions of aquatic, semi-aquatic, and riparian-dwelling reptiles and amphibians in Chihuahua (Rio Casas Grandes, Rio Santa Maria, Rio Carmen). The closest northern populations to these species are usually in the montane areas of Arizona and New Mexico that are drained by the Gila River or that portion of New Mexico drained by the Rio Grande. Perhaps the Playas-Hachitas-Laguna Moscos system and the Mimbres system were dispersal routes for these animals from the Gila River and Rio Grande drainages, respectively. *Natrix rufipunctatus* (narrow-headed watersnake), *Thamnophis elegans* (wandering garter-snake), and *Hyla eximia wrightorum* (Arizona treefrog) are species exhibiting the Gila River-Chihuahua disjunction. *Thamnophis sirtalis ornata* (New Mexican gartersnake) and *Chrysemys picta belli* (western painted turtle) are disjunct in Chihuahua from the Rio Grande system. A specimen of *Opheodrys vernalis* (smooth greensnake) from a mesic grassland on the continental divide (2185 m elevation) near Cuahatemoc [1 km (0.6 mile) NW Pedernales; 14 km (8.4 miles) SE Guerrero on Mexico 16 (UAZ 34416)], Chihuahua, documents a similar connection and dispersal of a terrestrial species from north-central New Mexico into highland Chihuahua. The nearest population of *O. vernalis* to the Chihuahua locality is in the Sacramento Mountains, 440 km to the northeast in New Mexico.

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Late Pleistocene Biotic Communities from the Guadalupe Mountains, Culberson County, Texas

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Deposits of perishable organic materials preserved in caves of the Guadalupe Mountains are providing rich records of the late Pleistocene biotic communities of west Texas. These deposits are being excavated and studied with permission and support of the National Park Service and the Guadalupe Mountains National Park. Dung of the extinct Shasta ground sloth (*Nothrotheriops shastense*) and plant macrofossils from William's (or "Indian") Cave and three additional caves are reported here.

SLOTH DUNG

Dung of *Nothrotheriops shastense* has been recovered from the following caves in the Guadalupe Mountains National Park: William's Cave and Upper Sloth Cave (C-05 and C-08). A sample of the dung from Cave C-05 was radiocarbon dated at $11,590 \pm 230$ radiocarbon years before present (B.P.) by the Laboratory of Isotope Geochemistry (= Radiocarbon Laboratory), University of Arizona (S-1519; Table 1). Additional dates are being processed on dung samples with William's Cave and Cave C-08. The sloth dung in Cave C-08 is associated with fecal pellets of a large artiodactyl (possibly *Cervus merriami*, Merriman's elk) which have been dated at $11,760 \pm 610$ B.P. (A-1522). The dung of *Nothrotheriops shastense* is known from only four other North American sites: Rampart Cave and Muav Caves in the Grand Canyon of Arizona, Gypsum Cave, Nevada, and Aden Crater, New Mexico. Radiocarbon dates presently available for these localities are all 11,000 B.P. or older, with a clustering of the stratigraphically youngest material at about 11,000 years ago.

TABLE 1. Radiocarbon dates from the Guadalupe Mountains, Culberson County, Texas, B.P. = radiocarbon years before present.

| Site | Material | Number | Date (B.P.) |
|----------------|---|--------|--------------|
| William's Cave | Packrat midden: <i>Juniperus</i> sp. twigs | A-1540 | 12,040 ± 210 |
| Cave C-05 | Sloth dung | A-1519 | 11,590 ± 230 |
| Cave C-08 | Artiodactyl fecal pellets | A-1533 | 11,760 ± 610 |
| Cave C-08 | Packrat midden: <i>Picea</i> sp. needles | A-1549 | 13,060 ± 280 |
| Cave C-09 | Cave fill: <i>Picea</i> sp. needles | A-1539 | 13,000 ± 730 |

The timing of the extinction of the Shasta ground sloth is viewed by Martin (1973) as a critical test of the theory of overkill.

PLANT MACROFOSSILS AND PALEOCOMMUNITIES

William's Cave.

William's Cave is located at 1500-m elevation on the south end of the Guadalupe Mountains below El Capitan Peak. The cave was originally excavated in 1934 and 1935 by the University Museum, Philadelphia, and the Academy of Natural Sciences, Philadelphia. Ayer (1936) reported on the vertebrate fossils and archaeological materials. Insufficient attention was given to stratigraphy, including possible reworking by packrats (*Neotoma* sp.), and the fauna is not clearly separable into Pleistocene and Holocene components.

Remnants of two indurated packrat middens still cling to the cave walls and mark two old, compacted surfaces. The upper midden (William's Cave #1) contained only fragments of the desert vegetation presently growing near William's Cave. Several pieces of Indian twine were also in this midden. In contrast, the lower midden (William's Cave #2) contained macrofossils of plant species very different from those in the present desertscrub (Table 2). The late Pleistocene plant community near the mouth of William's Cave included *Pinus edulis* (Colorado pinyon), *Juniperus* sp. (juniper), *Celtis reticulata* (netleaf hackberry), *Quercus* sp. (oak), and *Robinia neomexicana* (New Mexican locust). The present Chihuahuan Desert community near the cave includes *Larrea divaricata* (creosote bush), *Parthenium incanum* (mariola), *Viguiera stenoloba* (skeleton-leaf golden-eye), *Aloysia wrightii* (Wright lippia), *Agave lechuquilla* (lechuquilla), *Opuntia imbricata* (cane cholla), *Yucca torreyi* (Torrey yucca), and *Y. elata* (soap-weed yucca). The species

TABLE 2. Late Pleistocene plant macrofossils recovered from cave fill and fossil packrat middens in the Guadalupe Mountains, Culberson County, Texas.

| Species | Common Name | WC2 | C-08(F) | C-08(M) | C-09(F) |
|--|----------------------|-----|---------|---------|---------|
| <i>Agave</i> sp. | Century plant | | X | | X |
| <i>Arctostaphylos</i> sp. | Manzanita | | | | X |
| <i>Artemisia</i> cf. <i>ludoviciana</i> Nutt. | Estafiata | X | | | X |
| <i>Atriplex canescens</i> (Pursh) Nutt. | Four-winged saltbush | X | X | | |
| <i>Berberis haematocarpa</i> Wootan | Algerita | | X | X | X |
| <i>Berberis</i> sp. | Barberry | X | | | |
| <i>Brickellia</i> sp. | Brickell-bush | | X | X | X |
| <i>Ceanothus</i> sp. | Buck-brush | | | | X |
| <i>Celtis reticulata</i> Torr. | Netleaf hackberry | X | X | | |
| <i>Cercocarpus breviflorus</i> Gray | Mountain mahogany | | X | | X |
| <i>Chenopodium</i> sp. | Goosefoot | | X | | |
| <i>Chrysothamnus</i> sp. | Rabbit bush | | | X | |
| <i>Echinocereus</i> sp. | Hedgehog cactus | | X | | X |
| <i>Ephedra</i> sp. | Mormon tea | | | X | |
| <i>Fallugia paradoxa</i> (D. Don) Endl. | Apache plume | | X | | |
| <i>Fendlera</i> sp. | Fendler-bush | | | | X |
| <i>Gutierrezia</i> sp. | Snake-weed | X | | X | |
| <i>Helianthus</i> sp. | Sunflower | X | | | |
| <i>Juniperus communis</i> L. | Dwarf juniper | | | X | X |
| <i>Juniperus</i> sp. | Juniper | X | X | X | X |
| <i>Lappula</i> sp. | Stick-seed | | | | X |
| <i>Lesquerella</i> sp. | Bladder-pod | | | X | |
| <i>Lithospermum</i> sp. | Puccoon | | | | X |
| <i>Mentzelia</i> sp. | Stick-leaf | X | | | |
| <i>Mortonia scabrella</i> Gray | Sandpiper bush | | X | | X |
| <i>Nolina</i> sp. | Bear-grass | | X | | |
| <i>Opuntia imbricata</i> Haw. | Cane cholla | X | X | | X |
| <i>O. (Platyopuntia)</i> sp. | Prickly pear cactus | X | X | | X |
| <i>Ostrya knowltoni</i> Coville | Hop hornbeam | X | X | X | X |
| <i>Phacelia</i> sp. | Wild heliotrope | X | | | X |
| <i>Phoradendron</i> sp. | Mistletoe | X | | | |
| <i>Physalis</i> sp. | Ground-cherry | X | | | X |
| <i>Picea</i> sp. | Spruce | | | X | X |
| <i>Pinus edulis</i> Engelm. | Colorado pinyon | X | X | X | X |
| <i>P. flexilis</i> James | Limber pine | | | X | X |
| <i>Prunus serotina</i> Ehrh. | Wild-cherry | X | | | |
| <i>Pseudotsuga menziesii</i> (Mirbel) Franco | Douglas fir | | X | X | X |
| <i>Quercus gambelii</i> Nutt. | Gambel oak | | X | | |
| <i>Quercus</i> sp. | Oak | X | | | X |

TABLE 2. (Continued)

| Species | Common Name | WC2 | C-08(F) | C-08(M) | C-09(F) |
|----------------------------|--------------------|-----|---------|---------|---------|
| <i>Rhus</i> sp. | Sumac | X | | | X |
| <i>Robinia neomexicana</i> | | | | | |
| Gray | New Mexican locust | X | X | X | X |
| <i>Rubus</i> sp. | Raspberry | | | | X |
| <i>Sphaeralcea</i> sp. | Globe mallow | X | | | |
| <i>Yucca</i> sp. | Yucca | | | | X |
| N = | | 19 | 19 | 14 | 31 |

WC = William's Cave, C-08 and C-09 = High Sloth Caves, F = cave fill, M = fossil *Neotoma* sp. midden.

of plants in the Pleistocene midden that do not occur in the vicinity of William's Cave today are found at higher elevations in the Guadalupe Mountains. A radiocarbon date on juniper twigs places the age of this paleocommunity at $12,040 \pm 210$ B.P. (A-1540).

The William's Cave record of pinyon-juniper at 1500-m elevation on an exposed south-facing slope may not be the lowest glacial-age extent of this vegetation type. The playa (Salt Flat) in the valley to the west is about 660-m (2160 ft) elevation. Wells (1966) recorded woodland vegetation as low as 600 m (2000 ft) in the Big Bend National Park of Texas to the south. Perhaps pinyon-juniper or more xeric woodland covered much of the lower elevations surrounding the Guadalupe Mountains.

High Sloth Caves.

Three caves are located at 2000-m elevation on a steep, exposed west slope of the mountains below Bartlett Peak. In a recent survey of the Guadalupe Mountains National Park, the caves were numbered C-05, C-08, and C-09. These caves were referred to as the High or Upper Sloth caves by Howard (1932). Little previous work has been done in Cave C-05 and C-09, but C-08 was excavated in the 1930s. Only small areas of C-08 are undisturbed. Lloyd Logan of the Museum of Texas Tech University recently undertook excavation of test trenches in all three caves; he found abundant bones of small vertebrates. Some of the materials presented here were collected through his cooperation during his excavation.

The caves are located at the base of cliffs in Permian limestone. The present vegetation is a very diverse, succulent Chihuahuan desertscrub community with some intermixed woodland species including *Rhus* (sumac), *Quercus*, *Ptelea* (hop-tree), *Berberis* (barberry), *Opuntia*, *Fouquieria* (ocotillo), and *Mortonia* (sandpaper bush). No conifers presently grow in the immediate vicinity, but *Pinus edulis* presently

grows both above and below the caves in isolated, mesic microhabitats. A flat ledge habitat just below the crest of Bartlett Peak and 350 m (1150 ft) above the caves supports an isolated stand of trees probably including *Pseudotsuga menziesii* (Douglas fir) and *Pinus edulis*.

Two samples of late Pleistocene plant macrofossils were recovered from Cave C-08 (Table 2). One sample was in an indurated ancient packrat midden from a crevice 4 m (13.1 ft) above the entrance to the cave. The fossils in this midden record a mixed-conifer forest including *Picea* sp. (spruce), *Pinus flexilis* (limber pine), *Pinus edulis*, *Pseudotsuga menziesii*, *Juniperus communis* (dwarf juniper), and *Juniperus* sp. A radiocarbon date on *Picea* sp. needles establishes the age of this fossil community at $13,060 \pm 280$ B.P. (A-1549). Neither *Picea* nor *Juniperus communis* presently occurs in Texas. To our knowledge, they have not been recorded as macrofossils previously. The nearest spruce (*Picea pungens* and *P. engelmanni*) is in the Sacramento Mountains, New Mexico, 110 km to the north. *Picea* also occurs 450 km (280 miles) to the southwest as a relict in the Sierra Madre Occidental near Creel, Chihuahua. The species, *P. chihuahuana*, is not closely related to *P. pungens* or *P. engelmanni*. The nearest *Juniperus communis* is 325 km (200 miles) to the northwest in the southern end of the Rocky Mountains of central New Mexico.

The second sample from Cave C-08 was taken from unconsolidated cave fill in a shallow pit excavated by Lloyd Logan near the front of the cave. The pit had an interesting stratigraphy and showed the following layers: (1) an upper layer with archaeological materials (quids and charcoal); (2) a layer containing sloth dung; (3) a layer of wood; and (4) a layer of wind-accumulated leaves and organic debris. The plant macrofossils listed in Table 2 were collected from the lower debris unit. The plant macrofossils have not been dated, but a radiocarbon date on artiodactyl fecal pellets from the sloth unit above was $11,760 \pm 610$ B.P. (A-1533). The high-elevation forest species found in the midden, *Picea* sp., *Pinus flexilis*, and *Juniperus communis*, were absent from the cave fill sample. Lower-elevation forest and woodland species such as *Pseudotsuga menziesii*, *Pinus edulis*, *Juniperus* sp., *Quercus gambelii*, and *Ostrya knowltoni* (Knowlton hop-hornbeam) grew at the mouth of the cave at the time the cave fill was deposited. This sample predates stratigraphically the extinction of the ground sloth and represents a flora intermediate between subalpine forest and the present upper Chihuahuan Desert community.

A very rich sample of plant macrofossils were recovered at a shallow depth (0-7.5 cm or 0-3 inches) in Cave C-109. The flora recorded in this sample was similar to that in the Cave C-08 midden; i.e., a subalpine forest community of *Picea* sp., *Pinus flexilis*, and *Juniperus communis*. A radiocarbon date on *Picea* sp. needles from this sample is $13,000 \pm 730$ B.P. (A-1539), apparently contemporaneous with the date for the C-08

midden. This sample is rich enough to show that the last Pleistocene community was diverse and contained species both from the more mesic subalpine forests and the present high-elevation, desertscrub community. The independent records of *Picea* sp., *Pinus flexilis*, and *Juniperus communis* from Caves C-08 and C-09 suggest that the fossils represent more than isolated trees. The well-developed conifer forest community probably existed just above the caves on a relatively level, sandy area and the cave samples were "window-box" populations. Presumably, subalpine forest was widespread over the top of the Guadalupe Mountains about 13,000 B.P.

DISCUSSION

These deposits record a transition from a mesic, subalpine forest dominated by spruce and limber pine to a relatively more xeric forest with *Pseudotsuga menziesii*, *Pinus edulis*, and *Quercus gambelii*. The transition occurred between 13,000 and approximately 11,500 B.P. The transition from dominance by species of the xeric forest to dominance by the present desertscrub vegetation occurred later. If the climate remained fairly wet in the Chihuahuan Desert until 4000-5000 years ago, as suggested by Van Devender and Worthington (this volume), the more xeric-adapted of the woodland species may have survived at low elevations until much later. This probably would have been a pinyon-juniper community near the High Sloth Caves and a juniper woodland near William's Cave. If the climate changed to one similar to the present (hot, dry) at the beginning of the Holocene, the plant communities may have been similar to those of the present for the last 10,000 years.

The absence of *Pinus ponderosa* (Ponderosa or yellow pine) and *Abies concolor* (white fir) in these paleocommunities is intriguing. *Pinus ponderosa* is a widespread dominant in most forest communities that occur between pinyon-juniper woodland and mixed-conifer forrests along the elevational-moisture gradient of the Southwest. *Abies concolor* is a common member of southwestern forest communities from the ponderosa pine to the subalpine forest zones that does not presently grow in the Guadalupe Mountains, but would be expected to accompany *Picea* sp. A similar situation is apparent in high-elevation sites in southern Nevada. Pleistocene-age packrat middens record such montane conifers as *Pinus longaeva* (Intermountain bristlecone pine), *P. flexilis*, and *Abies concolor* at elevations as low as 1860 m (6100 ft) in more mesic sites and 2000 m in more xeric sites (Mehringer and Ferguson 1969; Spaulding, unpubl. data). Again, *Pinus ponderosa* was not found. Perhaps *P. ponderosa* is better adapted to sites where deep soils develop and the other montane conifers are better adapted to rocky slopes of shallow or negligible soil.

While Pleistocene fossils of *P. ponderosa* may eventually be found, it

is already obvious that these montane trees behaved individualistically rather than in any manner that can be attributed to movement of an entire community. The concept of a dynamic plant community pioneered by Gleason (1926) and recently modified and expanded by McIntosh (1958), Whittaker (1967), and Whittaker and Niering (1965) appears to be a more realistic expression of the observed movements of plants during the last Ice Age. In this concept, the plant community is viewed as an assemblage of individual species occurring together along independent gradients in time and space.

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A Reconnaissance Survey of Pollen Rain in Big Bend National Park, Texas: Modern Control for a Paleoenvironmental Study

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INTRODUCTION

During June 1969, a series of soil-surface pollen samples were gathered on a reconnaissance basis in Big Bend National Park. The purpose of the collections and subsequent laboratory analyses of the samples was to determine whether or not pollen could be recovered from soil samples from the park and whether or not pollen rain would serve as a workable measure of local vegetation and climatic conditions. The findings of the survey, which were affirmative on both counts, are presented here. This report will serve as groundwork for more detailed studies of both pollen rain and the ecological factors controlling pollen rain in the Big Bend region. It establishes the feasibility of developing a body of modern palynological control data upon which to base paleoecological interpretations of any Quaternary fossil pollen records that are developed in the future for the Big Bend area.

This paper is one of a series (Meyer 1973, 1975) dealing with pollen rain in the Chihuahuan Desert.

THE STUDY AREA

Big Bend Park (Fig. 1) is located at ca. 29°15' N, 103°15' W, in Brewster County, Texas. The area includes roughly 283,200 ha (708,000 acres) of land, and was purchased by the state of Texas and deeded to the federal government to be preserved as national parkland in 1935 (Maxwell 1968). Big Bend Park exhibits some of the most spectacular mountain and desert landscapes to be found in North America,

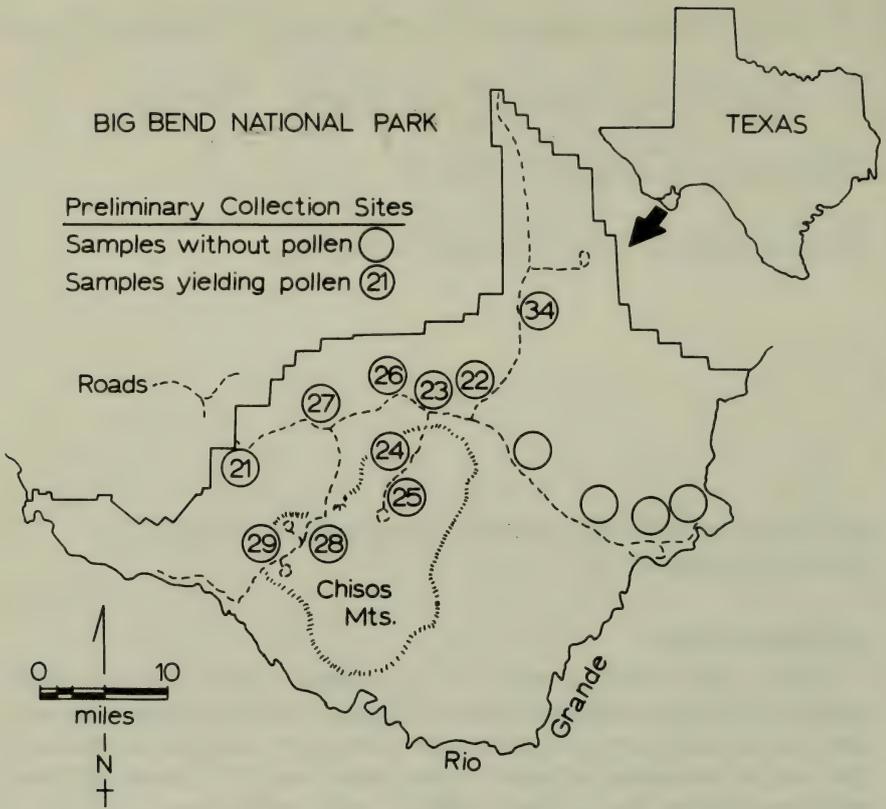


Fig. 1. Map of Big Bend National Park showing locations of pollen sample collection sites.

and is one of the few near-natural examples of the Chihuahuan Desert ecosystem remaining in the United States.

Geology and Climate

The major landforms in the park are formed of precipitously folded, faulted, and eroded Cretaceous sedimentary rocks, predominantly limestones, interrupted by numerous Tertiary and early-Quaternary igneous intrusions. Elevation in the area ranges from ca. 670 m (2200 ft) on desert flats and floors of intermontane basins to 2370 m (7777 ft) at the summit of Emory Peak, the highest point in the Chisos Mountains. The Chisos range covers more than 48 km² (30 miles²) and is the largest and most noticeable physiographic unit in the park. The mountains are formed of massive early- to late-Tertiary volcanic intrusions covered by a disjunct veneer of sedimentary and metamorphic rocks (Maxwell 1968).

Precipitation in lowland sections of the park averages less than 25.4 cm/yr (10 inches/yr), and increases with increasing elevation to about 40.6 cm/yr (16 inches/yr) at high elevations in the Chisos Mountains. Most rainfall comes during summer. Summer temperatures in local desert areas often exceed 38°C (100°F), while those at upland locations average 27-29°C (80-85°F). Winters are mild. Park lowlands may never receive frost, but snow has been reported from the Chisos Mountains (Maxwell 1968; Wauer 1971).

Vegetation

A flora for the Chisos Mountains was presented by Muller (1937). Maxwell (1968) provided a general description of vegetation in Big Bend Park and Wauer (1971) described ecological zonation of vegetation in the area.

Arid lowlands in the park bear a xerothermic desert flora. Dominant species include creosote bush (*Larrea divaricata*), lechuguilla (*Agave lechuguilla*), candelilla (*Euphorbia antisiphylitica*), ocotillo (*Fouquieria splendens*), Torrey yucca (*Yucca torreyi*), prickly pear and cholla (*Opuntia* spp.). Mountain foothills support dense stands of sotol (*Dasyilirion leiophyllum*), yucca (*Yucca* sp.), lechuguilla, agave (*Agave* sp.), beargrass (*Nolina erumpens*), a variety of cacti, and a number of grass species. Middle montane elevations are occupied by scrubby, chaparral-like woodland communities dominated by several species of scrub oak (*Quercus* spp.), alligator juniper (*Juniperus deppeana*), pinyon (*Pinus cembroides*, *P. edulis*), and different kinds of shrubby legumes (*Acacia* spp., *Mimosa* spp.). Summits and high-elevation basins in the Chisos Mountains support a coniferous forest that includes pinyon, ponderosa pine (*Pinus ponderosa*), Arizona cypress (*Cupressus arizonica*), Douglas fir (*Pseudotsuga menziesii*), and Gambel's oak (*Quercus gambelii*).

METHODS

Fourteen soil-surface pollen samples were collected in Big Bend Park on 4-5 June 1969. Collection sites were selected so that samples would be obtained from as many different environmental situations as possible within the time available for field work. Locations and elevations of collection sites were read from the USGS 1:250,000 "Emory Peak" topographic quadrangle.

Vegetation association names applied to communities occupying collection sites were taken from Wauer (1971). Wauer's association names were also used to arrange pollen spectra in pollen diagrams.

Pollen samples were collected in multiple subsamples as described by Mehringer (1967) and returned to the laboratory for analysis in sealed plastic bags. In the laboratory all samples were subjected to Mehringer's

TABLE 1. Pollen count data from surface samples collected in Big Bend National Park, Texas.

| Sample | Pollen Types | | | | | | | | | | | | | | | | total grains | | | |
|--------|--------------|------------------|----------------|--------------|-----------|-----------|---------------------------|--------------------------|------------------|----------------|-------------------|--------------|--------------------|----------------|-------------------|-----------|--------------|------------------|---------------|--------------------------|
| | <i>Pinus</i> | <i>Juniperus</i> | <i>Quercus</i> | <i>Picea</i> | Gramineae | Cheno-ams | High-spined Compositae | Low-spined Compositae | <i>Artemisia</i> | <i>Ephedra</i> | cf. <i>Celtis</i> | <i>Agave</i> | <i>Tidestromia</i> | Caprifoliaceae | <i>Sarcobatus</i> | Liliaceae | | Type "A" unknown | <i>Larrea</i> | unidentifiable grains |
| BBM 21 | 54 | 02 | 043 | 0 | 070 | 55 | 15 | 078 | 81 | 12 | 1 | 00 | 0 | 0 | 0 | 00 | 1 | 2 | 11 | 425 |
| BBM 22 | 34 | 02 | 034 | 0 | 083 | 41 | 66 | 144 | 17 | 16 | 1 | 02 | 0 | 0 | 2 | 01 | 0 | 0 | 07 | 450 |
| BBM 23 | 19 | 03 | 052 | 0 | 052 | 43 | 65 | 114 | 25 | 14 | 3 | 00 | 0 | 1 | 0 | 00 | 0 | 0 | 09 | 400 |
| BBM 24 | 38 | 11 | 086 | 0 | 125 | 19 | 30 | 066 | 18 | 03 | 1 | 03 | 1 | 0 | 0 | 00 | 0 | 0 | 09 | 400 |
| BBM 25 | 97 | 18 | 122 | 1 | 075 | 24 | 25 | 027 | 01 | 03 | 1 | 00 | 0 | 0 | 0 | 00 | 0 | 0 | 06 | 400 |
| BBM 26 | 75 | 02 | 035 | 0 | 102 | 27 | 31 | 087 | 21 | 10 | 1 | 02 | 0 | 0 | 0 | 00 | 0 | 0 | 07 | 400 |
| BBM 27 | 14 | 02 | 016 | 0 | 040 | 68 | 15 | 057 | 03 | 02 | 2 | 00 | 0 | 0 | 1 | 00 | 0 | 0 | 05 | 225 |
| BBM 28 | 47 | 05 | 014 | 0 | 179 | 39 | 15 | 047 | 12 | 07 | 2 | 10 | 0 | 0 | 0 | 17 | 0 | 0 | 06 | 400 |
| BBM 29 | 28 | 02 | 038 | 0 | 098 | 32 | 29 | 070 | 92 | 04 | 3 | 00 | 1 | 0 | 0 | 00 | 0 | 0 | 04 | 401 |
| BBM 34 | 03 | 04 | 021 | 0 | 045 | 49 | 30 | 133 | 05 | 06 | 0 | 00 | 0 | 0 | 0 | 00 | 1 | 0 | 12 | 309 |

(1967) extraction sequence and those containing organic debris also received a 1.5 min hot acetolysis (Gray 1965). Residues were stored in 5 dram shell vials. Preparations for counting were suspended in glycerol, stained with basic fuchsin, and mounted under 20 × 60 mm, no. 0, glass cover slips. Counting was done under a Leitz "Ortholux" microscope at 540 X. During counting, identifiable fragments of pollen grains were tabulated as single grains. Fragments of grains and intact grains too battered or eroded to be identified, together with pollen types that could not be assigned to an available taxon or category, were grouped as unidentifiables.

RESULTS

Ten of the 14 pollen samples contained sufficient pollen for 225-450 grain counts. Pollen was abundant and well preserved in those samples and 18 pollen types appeared during the analyses. Count data are presented in Table 1. A limited amount of pollen was present in the remaining four samples, but the grains were too scarce to permit completion of statistically meaningful counts and generally too battered to be identified.

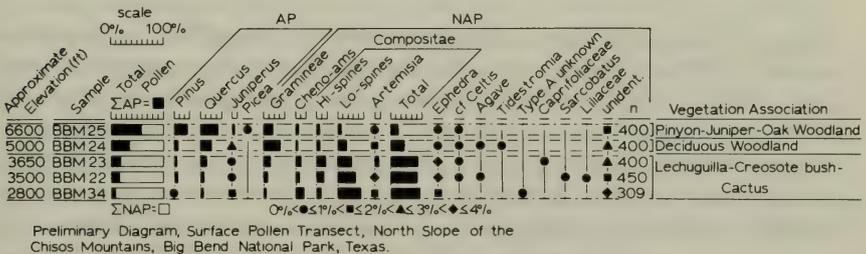


Fig. 2. Diagram for the surface pollen transect up the north slope of the Chisos Mountains.

Five samples formed a transect up the north slope of the Chisos Mountains. The series extended from ca. 853-m (2800-ft) elevation in an arid section of the north-central portion of the park to roughly 2012-m (6600-ft) elevation in the coniferous forest occupying higher slopes of the Chisos range. Pollen spectra from the transect are diagrammed in Fig. 2. Elevational trends in pollen proportions were most apparent when counts were separated as total NAP (= nonarboreal pollen types) and total AP (= arboreal pollen types). The AP group consisted primarily of *Pinus* and *Quercus*, with *Juniperus* playing a lesser role. Arboreal pollen frequency exceeded 59% in the uppermost sample of the transect, reflecting local abundances of conifers and oaks, and decreased moving downhill to less than 10% in the basal sample of the

series. The NAP proportions exhibited a reciprocal trend. Patterns within the NAP were controlled by the Compositae group, and the Compositae were dominated by low-spined pollen types. Gramineae pollen and Chen-ams (= *Chenopodiaceae* + *Amaranthus*; Martin 1963) were present in all samples forming the transect, but Chen-am proportions did not exceed 16% in any sample and grass frequency fell below 19% in all samples except BBM 24 from the mid-elevation deciduous woodland.

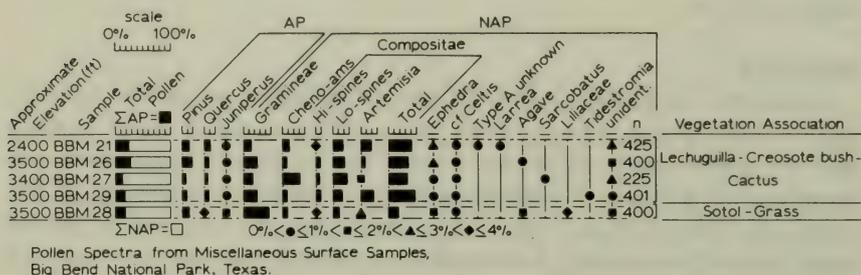


Fig. 3. Pollen spectra from miscellaneous surface samples from Big Bend Park.

Figure 3 presents pollen spectra from the remaining five samples that contained sufficient pollen for analysis. All of those samples were collected in arid and semi-arid sections of the park at or below 1067-m (3500 ft) elevation. The AP proportion did not exceed 28% in any sample. Spectra from extremely arid sites occupied by the xerophytic lechuguilla-creosote bush-cactus vegetational association were dominated by Compositae pollen, and the spectrum from the single sample obtained in the semi-arid, sotol-grass association was dominated by grass pollen. Chen-ams were present in all samples, but the Chen-am proportion was greater than 13% in only one sample.

A number of rare pollen types also appeared in the surface samples, but their proportions fell consistently below 4%. The rare types did not exhibit significant patterns in the elevational transect and could not be used as indicators to separate pollen spectra from arid and semi-arid environments. The rare pollen types included a single *Picea* grain observed in sample BBM 25. Spruce does not grow in Big Bend Park, and the grain is evidence of transport of exotic pollen into the area from distant sources.

The pollen spectra from the vegetational associations sampled during this study are separable on the basis of proportional composition, and fluctuations of proportions within the spectra can be used as measures of both elevation and aridity of local environments. Arboreal-pollen frequency was greater than 33% only in samples from relatively mesic

woodland habitats at or above 1524-m (5000-ft) elevation in the Chisos Mountains; AP frequency did not exceed 28% in the samples from lower elevations. The Compositae proportion exceeded 30% in each sample from the arid, low-elevation lechuguilla-creosote bush-cactus association and fell below 27% in all other samples. Grass-pollen frequency was greater than 44% in the sample from the semi-arid, sotol-grass association and less than 32% in all remaining samples.

DISCUSSION

Although the proportionate pollen spectra were good indices of elevation and degree of aridity at collection sites in Big Bend Park, the spectra did not reflect accurately species composition of the plant associations occupying the areas sampled. The spectra include far fewer taxa than were present in the associations sampled, and pollen proportions did not seem to relate to the proportionate species composition of plant communities occupying the collection sites. This discrepancy appears to be a function of the pollen-producing capabilities of plants occupying a given area. Wind-pollinated species release far more pollen than do plants that are pollinated by insects and other animals. Because of this, pollen spectra from a given area are often composed either completely or almost entirely of pollen types produced by wind-pollinated plants even though a variety of species producing less pollen, including perhaps the dominant species at the site, are also present (Martin 1963). Since, however, there was a reasonable degree of consistency in the proportional composition of the spectra from the lechuguilla-creosote bush-cactus association (the only community yielding more than one spectra during this project) it is possible that pollen profiles can be used carefully as gross indirect measures of, if not species composition, at least appearance of vegetation communities in Big Bend Park.

It is interesting to compare the pollen diagram from the surface transect in the Chisos Mountains to those presented by Meyer (1973) for transects from Sierra de la Madera and Sierra de San Marcos, two ranges located about 289 km (180 miles) SSE from Big Bend Park in central Coahuila, Mexico. Although the Mexican ranges are slightly higher and more massive than the Chisos Mountains, the ranges are of comparable overall physiographic dimensions. The Mexican ranges support vegetation communities similar to those occupying the Chisos Mountains. The similarities are both structural, in terms of elevational zonation of plant associations, and compositional, at least in terms of dominant species in communities occupying equivalent elevation zones on the three ranges. The composition and proportionate structure of the pollen diagrams from these ranges are also quite similar. Spectra from relatively mesic coniferous forests located at high-elevation sites in all three situations were dominated by an AP composed primarily of pine

pollen. Pollen spectra from xeric sites at lower elevations were dominated by Compositae pollen at each of the three locations. Spectra from intermediate elevations in these mountains were also comparable in most respects, as were elevational trends apparent both within and between the AP and NAP. This comparison suggests a degree of uniformity in pollen rain on mountain ranges in the Chihuahuan Desert seldom found in ecosystems of similar geographic dimensions.

Other than Wells' (1966 and this volume) plant macrofossil studies, little information is available concerning the Quaternary environmental history of the Big Bend area. There is also a paucity of information about the environmental history of the Chihuahuan Desert as a unit. The value of local pollen rain studies as bases for controlling interpretations of Quaternary fossil pollen sequences from arid regions of western North America is well established (Martin 1963; Martin and Mehringer 1965), and this report documents the feasibility of a detailed study of pollen rain in Big Bend Park. The results of the investigation would be of immediate value in furthering the understanding of modern vegetational and climatic relationships within the park and would provide a sound basis for ecological interpretations of any Quaternary fossil pollen records developed in the future from the Big Bend region and adjacent sections of the Chihuahuan Desert.

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Session II
Mammalogy

The Status of Mammals in the Northern Region of the Chihuahuan Desert

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What, if anything, is the Chihuahuan Desert mammal fauna? We may attempt to answer this question in two ways. We may list the mammals occurring in some arbitrarily selected geographic area, such as the state of Chihuahua or within the geographic range of tarbush (*Flourensia*) or lechuguilla (*Agave lecheguilla*). A fauna so defined has relatively little biological significance. Chance primarily dictates the composition of such a fauna, not common ancestry, common history, common adaptation to a pervasive environmental force, or some other biologically meaningful factor. Study of such a collocation of organisms is unlikely to be very rewarding scientifically. A second way of defining the Chihuahuan Desert mammalian fauna is to search for a distinctive assemblage of mammalian species which co-occur over a substantial geographic area which to some extent coincides with those regions of the Mexican Plateau where aridity is the overriding environmental factor to which mammals must adapt. Such an assemblage may or may not exist, but if it does, we would then be dealing with a real natural entity which would be subject to rational analysis as are other natural phenomena. There may, of course, be an arid-adapted fauna on the Mexican Plateau which is not significantly different from that of the Sonoran or Coloradan lowlands, or of the southern Great Plains. To characterize that as a Chihuahuan desert fauna would indeed be inaccurate.

We undertook to attempt a definition of the second kind, focusing our attention on the northern part of the Mexican Plateau, that part centered on the Bolson de Mapimi, the arid heartland of what many biologists refer to as the Chihuahuan Desert. Here we present evidence that there is indeed a recognizable mammalian fauna centered on this area, that it has close ties with recognizable arid-adapted faunas of the Great Plains, and is more distantly related to the fauna of the Sonoran Desert. Having identified and mapped the Chihuahuan or Mapimian

fauna, we then consider the current status of some of the faunal elements, concluding that the less arid-adapted the species the more precarious is its present existence in the Chihuahuan Desert area.

METHODS

We delineated 94 quadrangles, 160.9 km (100 miles) on a side, covering the southwestern United States and northern Mexico (Fig. 1).

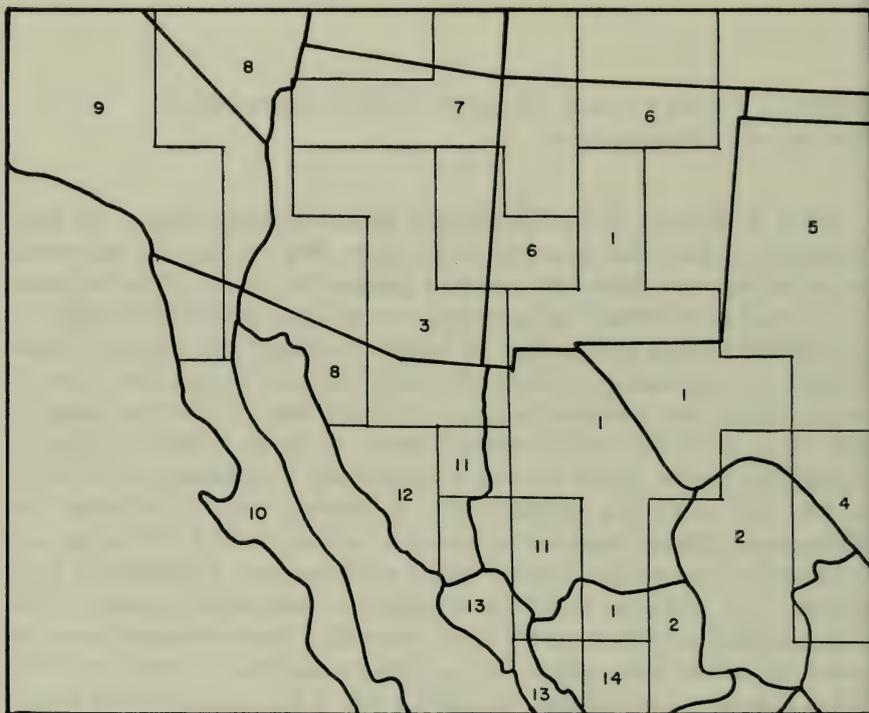


Fig. 1. Mammalian faunal provinces of the arid Southwest based upon 160×160 km (100×100 mile) quadrats grouped into similar clusters by distance analysis. (1) Mapimian; (2) Lower Mapimian; (3) Upper Mapimian (= Yaquinian of Hagmeier 1966); (4) Tamaulipan; (5) Balconian; (6) Coloradan; (7) Uintian; (8) Mohavian; (9) San Bernardinoian; (10) Bajan; (11) Northern Madrean; (12) Trans Sonoran; (13) Sinaloan; (14) Southern Madrean.

Using published faunal reports and original data gathered by Caire on Sonora, we listed all the mammals reported to occur in each quadrat. Then, treating each quadrat as an OTU (Operational Taxonomic Unit, see Sneath and Sokal 1973), and the fauna of each quadrat as its suite of characteristics, we computed 94×94 distance and correlation matrices. From these we constructed phenograms using the unweighted

pair group method with arithmetic averages (UPGMA; see Sneath and Sokal 1973). Clusters revealed by the phenograms suggested the existence of homogenous associations of mammals extending over two or more quadrats. Additionally, we drew the range boundaries of all mammals occurring in our area on one map. This technique also revealed the existence of areas where few distributions terminate, that is, of relatively homogenous faunal areas. We then applied phenon lines to successively lower levels on both phenograms until we reached collocations of clustered quadrats which approximated the homogenous areas revealed by superimposing range boundaries. These units constituted the natural faunas used in discussions beyond.

RESULTS

Range Overlap Map

A simplification of this map is depicted in Fig. 2. The homogenous areas revealed coincide generally with mammalian faunal areas delineated by Hagmeier (1966) for the United States. We have extended these areas into Mexico where appropriate, or have delineated and named those areas which lie wholly south of the border. Faunal areas delineated in this fashion may enclose centers of differentiation of an endemic fauna, as perhaps is the case with the Sonoran fauna, or they may be areas where two or more distinctive faunas overlap, producing a homogenous area containing a mixture of two or more independently developed assemblages. Such, we believe, is the case with the San Matean Province. The biogeographic significance of these two kinds of provinces is quite different; in one case we may be dealing with the result of a long period of isolation, in the other with the result of recent faunal migration resulting from climatic or physiographic change. In attempting to identify a Chihuahuan Desert fauna, we are much more interested in learning of the possible existence of the former kind of province because it might suggest to us something about the history of the desert regions of the Mexican Plateau. In any event, this method does reveal the existence of a natural faunal area, the Mapimian, centered on the arid sector of the Mexican Plateau.

Cluster Analyses

Correlation and distance phenograms reveal the same clustering of quadrats. Boreal montane faunas are distinctly set off from all others (the Coloradan fauna), followed in distinctiveness by the grouped faunas of the Sierra Madre Occidental and the tropical Sinaloan lowlands, and then by the grouped arid-adapted desert faunas of the remaining Southwest. The Southern Montane and Sinaloan faunas are quite distinct, but the quadrat size employed results in considerable blurring

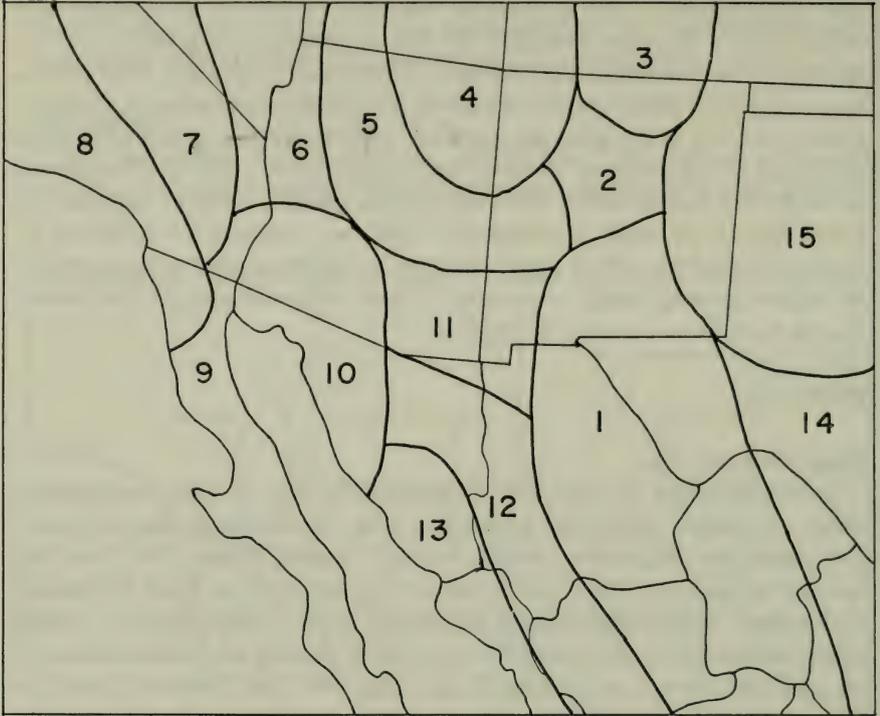


Fig. 2. Mammalian faunal provinces delineated by superimposing geographic range boundaries. Heavy lines coincide with concentrations of range terminations. Open areas contain fewer range terminations and are more homogenous in species composition. (1) Mapimian; (2) San Matean; (3) Coloradan; (4) Uintian; (5) Navajonian; (6) Kaibabian; (7) Mohavian; (8) San Bernardinoian; (9) Bajan; (10) Sonoran; (11) Yaquinian; (12) Madrean; (13) Sinaloan; (14) Tamaulipan; (15) Balconian.

of their boundaries with each other. Thus we are really dealing with four major mammalian fauna regions: (1) Northern Boreal or Coloradan; (2) Southern Montane (Durangan + Yaquinian); (3) Tropical or Sinaloan; (4) Grassland and Desert. Our concern here is with region 4.

Southwestern grasslands and deserts are divided by cluster analysis into an eastern and a western region. The two meet along the Continental Divide of northwestern New Mexico and along the grassland-desert transition south and west of the Mogollon Rim in Arizona. We may further limit our present attention to the eastern desert-grassland sector. We find that it consists of several recognizable subdivisions, to which the names Kansan, Balconian, Lower Mapimian, Mapimian, and Upper Mapimian may be applied. The Balconian province is more closely allied to the Kansan by distance but is closer to lower Mapimian in correlation analyses. In either analysis it is quite clear that a Mapimian

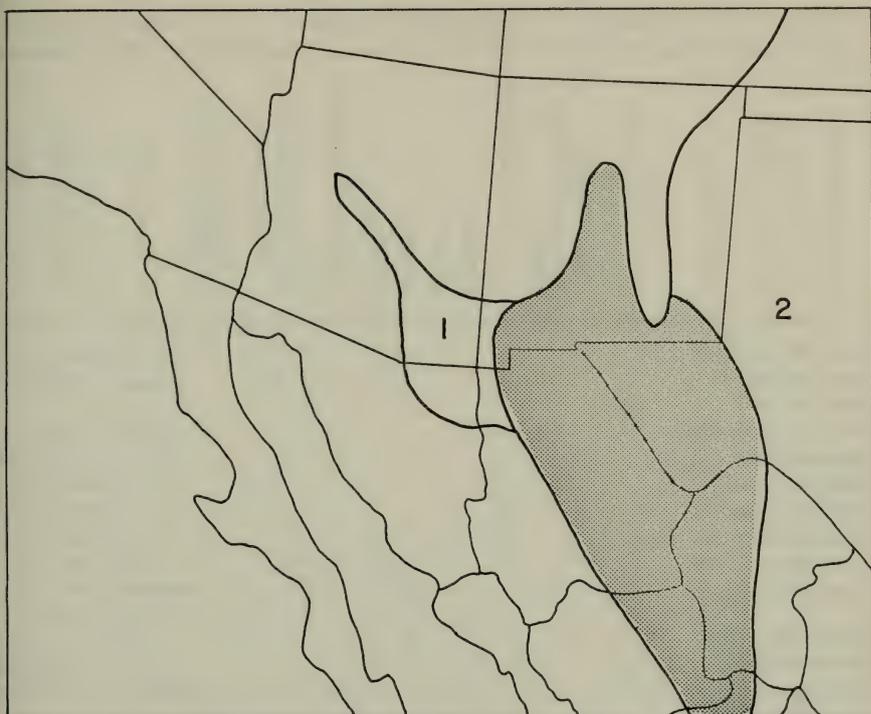


Fig. 3. Area occupied by Chihuahuan Desert mammal fauna as discussed in this report (stippled region). Closely related faunal assemblages which are part of the eastern arid-adapted fauna are, first, the upper Mapimian (1), and, second, the combined Balconian and Tamaulipan (2).

province exists, and that it is centered over the arid Bolson de Mapimi area in Chihuahua. By moving phenon lines leftward on the phenograms, and thus creating more and more inclusive provinces, we may add to the basic Mapimian of the distance analysis first the Lower, then the Upper Mapimian, and finally the Balconian and Kansan units. Where should we stop in our search for a natural faunal unit which profitably may be discussed as a "Chihuahuan Desert Mammal Fauna?" The Mapimian and Lower Mapimian of distance analysis closely coincide with the homogenous area revealed by superimposed range boundaries, and also with some previous definitions of Chihuahuan Desert based on, for example, the co-occurrence of *Larrea* and *Flourensia*; and we may thus logically defend our restriction of "Chihuahuan" to this region. Of course, the boundaries of the Chihuahuan fauna are only approximated by our quadrats, and we have attempted to make them coincide with the natural physiographic boundaries which do exist, as shown in Fig. 3.

TABLE 1. Habitat and status of Chihuahuan Desert mammals.

| | Desert | Grassland | Riparian | Woodland (oak, juniper) | Forest (long needled pine or higher) | Widespread, common, in its habitat | Local, uncommon | Status in area uncertain or marginal | Rare or endangered |
|----------------------------------|--------|-----------|----------|-------------------------|--------------------------------------|------------------------------------|-----------------|--------------------------------------|--------------------|
| <i>Didelphis virginiana</i> | | | | | | | | X | |
| <i>Sorex saussurei</i> | | | | | X | | | | X |
| <i>Sorex milleri</i> | | | | | X | | | | X |
| <i>Notiosorex crawfordi</i> | X | X | | X | | | X | | |
| <i>Scalopus montanus</i> | | | | | X | | | | X |
| <i>Scalopus aquaticus</i> | | | | | | | | X | |
| <i>Mormoops megalophylla</i> | | | | | | | | X | |
| <i>Choeronycteris mexicana</i> | | | | | | | | X | |
| <i>Leptonycteris nivalis</i> | | | | | | | | X | |
| <i>Myotis lucifugus</i> | | | X | | | | | | X |
| <i>Myotis yumanensis</i> | | | X | | | | | | X |
| <i>Myotis velifer</i> | | X | X | | | | | | X |
| <i>Myotis auriculus</i> | | | | X | X | | X | | |
| <i>Myotis thysanodes</i> | | X | | X | | X | | | |
| <i>Myotis volans</i> | | | | X | X | X | | | |
| <i>Myotis californicus</i> | X | X | | X | X | X | | | |
| <i>Myotis leibii</i> | X | X | | X | X | X | | | |
| <i>Lasionycteris noctivagans</i> | | | | | X | | | X | |
| <i>Pipistrellus hesperus</i> | X | X | | X | | X | | | |
| <i>Eptesicus fuscus</i> | | | | X | X | X | | | |
| <i>Lasiurus borealis</i> | | | X | | | | X | | |
| <i>Lasiurus cinereus</i> | | | | | X | | | X | |
| <i>Euderma maculatum</i> | | | | X | X | | | X | |
| <i>Plecotus townsendii</i> | X | X | | X | X | | | | X |
| <i>Antrozous pallidus</i> | X | X | X | X | | X | | | |
| <i>Tadarida brasiliensis</i> | X | X | X | X | X | X | | | X |
| <i>Tadarida femorosacca</i> | X | | | | | | | X | |
| <i>Tadarida macrotis</i> | X | X | | X | | | | X | |
| <i>Eumops perotis</i> | X | | | | | | | X | |
| <i>Dasyurus novemcinctus</i> | | X | X | X | | | | X | |
| <i>Lepus californicus</i> | X | X | | | | X | | | |
| <i>Lepus callotis</i> | | X | | X | | | X | | X |
| <i>Sylvilagus auduboni</i> | X | X | X | X | | X | | | |
| <i>Sylvilagus floridanus</i> | | | | X | X | | X | | X |
| <i>Cynomys ludovicianus</i> | | X | | | | | | | X |
| <i>Cynomys mexicanus</i> | | X | | | | | X | | X |
| <i>Spermophilus mexicanus</i> | | X | | | | | X | | X |
| <i>Spermophilus spilosoma</i> | X | X | | | | X | | | |

TABLE 1. (Continued)

| | Desert | Grassland | Riparian | Woodland (oak, juniper) | Forest (long needled pine or higher) | Widespread, common, in its habitat | Local, uncommon | Status in area uncertain or marginal | Rare or endangered |
|---|--------|-----------|----------|-------------------------|--------------------------------------|------------------------------------|-----------------|--------------------------------------|--------------------|
| <i>Spermophilus variegatus</i> | X | X | X | X | | X | | | |
| <i>Spermophilus leucurus</i> | X | X | | X | | | | X | |
| <i>Spermophilus interpres</i> | X | X | | X | | X | | | |
| <i>Eutamias cinereicollis</i> | | | | X | X | | X | X | |
| <i>Eutamias dorsalis</i> | | | | X | X | | X | | X |
| <i>Eutamias canipes</i> | | | | X | X | | X | | X |
| <i>Thomomys bottae</i> | X | X | X | X | X | X | | | |
| <i>Geomys arenarius</i> | | X | X | | | X | | | |
| <i>Pappogeomys castanops</i> | X | X | | | | X | | | |
| <i>Perognathus flavescens</i> (incl. <i>apache</i>) | X | X | | | | X | | | |
| <i>Perognathus flavus</i> | X | X | | | | X | | | |
| <i>Perognathus penicillatus</i> | X | X | | | | X | | | |
| <i>Perognathus hispidus</i> | | X | | | | | X | X | |
| <i>Perognathus intermedius</i> | X | | | | | X | | | |
| <i>Perognathus nelsoni</i> | X | | | | | X | | | |
| <i>Dipodomys ordii</i> | X | X | | | | X | | | |
| <i>Dipodomys merriami</i> | X | X | | | | X | | | |
| <i>Dipodomys nelsoni</i> | X | | | | | X | | | |
| <i>Dipodomys spectabilis</i> | X | X | | | | X | | | |
| <i>Castor canadensis</i> | | | X | | | | X | | X |
| <i>Reithrodontomys montanus</i> | X | | | | | | X | X | |
| <i>Reithrodontomys megalotis</i> | X | X | X | X | | X | | | |
| <i>Reithrodontomys fulvescens</i> | | X | | | | X | | | |
| <i>Peromyscus eremicus</i> | X | X | | | | X | | | |
| <i>Peromyscus maniculatus</i> | X | X | | | | X | | | |
| <i>Peromyscus leucopus</i> | | X | X | | | X | | | |
| <i>Peromyscus boylei</i> | | | | X | X | X | | | |
| <i>Peromyscus pectoralis</i> | X | X | | | | X | | | |
| <i>Peromyscus polius</i> | | | | | | | X | X | |
| <i>Peromyscus truei</i> | | | | X | X | | X | X | |
| <i>Peromyscus difficilis</i> | | | | X | X | | X | X | |
| <i>Baiomys taylori</i> | | X | | | | | X | X | |
| <i>Onychomys leucogaster</i> | X | X | | | | X | | | |
| <i>Onychomys torridus</i> | X | | | | | X | | | |
| <i>Sigmodon hispidus</i> | X | X | | | | X | | | |
| <i>Sigmodon fulviventor</i> | | X | | | | X | | | |

TABLE 1. (Continued)

| | Desert | Grassland | Riparian | Woodland (oak, juniper) | Forest (long needled pine or higher) | Widespread, common, in its habitat | Local, uncommon | Status in area uncertain or marginal | Rare or endangered |
|---------------------------------|--------|-----------|----------|-------------------------|--------------------------------------|------------------------------------|-----------------|--------------------------------------|--------------------|
| <i>Sigmodon ochrognathus</i> | | X | | X | | | X | | X |
| <i>Neotoma micropus</i> | X | X | | | | X | | | |
| <i>Neotoma albigula</i> | X | X | X | X | | X | | | |
| <i>Neotoma goldmani</i> | X | | | | | | X | | |
| <i>Neotoma mexicana</i> | | | | X | X | | X | | |
| <i>Microtus pennsylvanicus</i> | | X | X | | | | | | X |
| <i>Microtus mexicanus</i> | | | | X | X | | | | X |
| <i>Ondatra zibethicus</i> | | | X | | | | | X | |
| <i>Zapus princeps</i> | | | X | | | | | | X |
| <i>Erethizon dorsatum</i> | | X | | X | X | | | X | |
| <i>Canis lupus</i> | | X | | X | X | | | | X |
| <i>Canis latrans</i> | X | X | X | X | X | X | | | |
| <i>Vulpes macrotis</i> | X | X | | | | | X | | |
| <i>Urocyon cinereoargenteus</i> | X | X | X | X | X | X | | | |
| <i>Bassariscus astutus</i> | X | X | X | X | X | | X | | |
| <i>Procyon lotor</i> | X | X | X | X | X | | X | | |
| <i>Mustela frenata</i> | | | | | | | | X | |
| <i>Taxidea taxus</i> | X | X | | | | X | | | |
| <i>Mephitis mephitis</i> | X | X | X | X | X | X | | | |
| <i>Mephitis macroura</i> | X | X | X | | | | X | | |
| <i>Spilogale putorius</i> | X | X | X | X | | | X | | |
| <i>Conepatus mesoleucus</i> | X | X | X | X | | | X | | |
| <i>Ursus americanus</i> | | | | X | X | | | | X |
| <i>Ursus arctos</i> | | | | | | | | | X |
| <i>Felis concolor</i> | | | | X | X | | | | X |
| <i>Lynx rufus</i> | X | X | X | X | X | | X | | |
| <i>Tayassu tajacu</i> | X | X | X | X | | | | X | |
| <i>Cervus canadensis</i> | | | | | | | | X | |
| <i>Olocoileus hemionus</i> | X | X | | X | | | X | | |
| <i>Odocoileus virginianus</i> | | | | X | X | | X | | |
| <i>Antilocapra americana</i> | X | X | | | | | | | X |
| <i>Ovis canadensis</i> | | | | | | | X | | X |

Species whose ranges surround or are in contact with the desert but do not extend into it or occur relictually on desert mountain ranges are not included. Based primarily on Anderson (1972), Baker (1956), Davis (1966), and Findley et al. (1975).

The fauna of the region thus defined is listed in Table 1. There we have categorized the species which occur within the northern Chihuahuan Desert as we define it according to major altitudinally

determined plant communities. Those species listed as occurring in grassland and desert are properly considered to comprise the Chihuahuan Desert Mammal Fauna. Symbols indicating our estimation of the status of each species are also included. Selected kinds are discussed below.

DISCUSSION

Montane Species in the Desert

The desert surrounds many small mountain ranges which are occupied by relict populations of organisms which survive because of the cooler and more mesic habitats provided by the mountains. Mountain refugia in our area include: the Organs, Guadalupe, Davis, and Chisos in the United States; the Carmen, Encantada, Burro, Pino, San Marcos, Guadalupe, Parras, and Encarnacion ranges in Coahuila; and the Nido, Almagre, Mojada, and Hechiceros ranges in Chihuahua.

A few montane species have received notice because of their presumed endangered status. *Ovis canadensis* is now rare or absent from most of its former range in the northern Chihuahuan Desert because of hunting pressure and perhaps competition from domestic goats and sheep. At a few places bighorn sheep have been reintroduced with some degree of success, as on the San Andres and Big Hatchets in New Mexico and in the Black Gap area of Trans-Pecos, Texas.

The grizzly (*Ursus arctos*), while not originally confined to mountains, found its last redoubt in the Sierra del Nido of Chihuahua, where a few survived into the 1960s. Koford (1969) concluded that they are now extinct there.

Although Mexican voles (*Microtus mexicanus*) occur on all the higher mountains surrounding the Chihuahuan Desert, the population on the Texas Guadalupe has received special attention because of its presumed taxonomic distinctiveness (*M. m. guadalupensis*) and because of its presumed endangered status. However, there is little evidence (Findley and Jones 1962) that the Guadalupe population is meaningfully different from other populations in the southwestern United States, and the extent of habitat available for it in the Guadalupe is marginal at best.

That other montane species occurred in the Chihuahuan Desert area and are now absent is attested by the work of Smartt (1972) who reviewed the presence of *M. longicaudus* in southern New Mexico. It is probably correct to say that all organisms whose ranges in the Chihuahuan Desert area are limited to long-needled pine forest or higher are threatened because these habitats are fragile, limited, and heavily exploited by man. Furthermore, populations living on islands of whatever sort are highly subject to chance extinction (MacArthur and Wilson 1967). The mammalian faunas of most boreal islands in the

Southwestern deserts were already depauperate when first studied, probably because of this island-extinction effect, coupled with a virtual lack of immigration to the boreal islands (Brown 1971). All organisms on all montane islands in the Chihuahuan and other deserts are distinctive in an evolutionary sense in that they have been isolated since late Pluvial time and have accumulated distinctive sets of alleles. In our judgment all elements of all isolated montane biotas in the desert should be regarded as biologically unique and threatened. Some mammals which fall into this category are: *Sorex milleri*, *Scalopus montanus*, *Sylvilagus floridanus*, *Eutamias dorsalis*, *Eutamias canipes*, *Sigmodon ochrognathus*, *Microtus mexicanus*, *Ursus arctos*, *Felis concolor*, *Odocoileus virginianus*, and *Ovis canadensis*.

Grassland Species

The grassland habitat, like the montane woodlands and forests, tends to become insular in the drier parts of the Chihuahuan Desert. Moreover, decades of overgrazing as well as farming attempts in some areas have greatly reduced the extent of viable grassland in our area. On the bajadas bordering the Rio Grande in southern New Mexico, for example, grass was once cut and baled for hay where now the soil is greatly diminished and creosote bush is dominant (Dittmer 1951). Grassland has waned because of overuse by man, but a historical trend from mid to short grasses and then to shrub desert, taking place over the last 10,000 years, is well documented. Thus man has probably given the grasslands the nudge that pushed them to extinction in many parts of the present desert.

With the waning of grasslands many mammals have become rare, relictual, or extinct. A wet grassland mammal whose history is well documented in this respect is *Microtus pennsylvanicus*, which in late Pluvial times was widespread in the southern plains and northern Chihuahuan Desert. At the turn of the century, it was still found in *refugia* in western New Mexico, and now appears limited, in our area, to a strip of riparian grassland 150 m \times 3 km in size, 4.8 km (3 miles) southeast of Galeana, Chihuahua (Anderson 1972). Smartt (1972) reported the former occurrence of *Microtus ochrogaster* in the Little Hatched Mountains in Hidalgo County, New Mexico, and Harris et al. (1972) reported the grassland shrew (*Cryptotis parva*) from the same area. Clearly, a substantial grassland fauna has disappeared from our region in relatively recent time. Black-tailed prairie dogs (*Cynomys ludovicianus*) were widespread in the New Mexican and Texan sectors of the desert, and are now nearly extinct in the former area (Findley et al. 1975) and greatly reduced in the latter (Davis 1966). The Mexican species *C. mexicanus* undoubtedly represents a relict of a former, more southern distribution of *C. ludovicianus* or its ancestor. Bison were extirpated early from their former limited range in the Chihuahuan Desert, and

pronghorns (*Antilocapra*) are greatly reduced, especially in the northern Mexican section of the desert. Additionally, there are several small grassland species which are rare and local and may be considered threatened. Threatened, endangered, or extirpated grassland species are *Lepus callotis*, *Cynomys ludovicianus*, *Cynomys mexicanus*, *Reithrodontomys montanus*, *Baiomys taylori*, *Sigmodon fulviventer*, *Microtus pennsylvanicus*, *Odocoileus hemionus*, *Antilocapra americana*, and *Bison bison*.

Riparian Species

Beaver and muskrat occur sporadically along the Rio Grande, Rio Conchas, and Pecos rivers. Muskrats are seemingly less common, there being no records for Coahuila, for example, where beaver were to be found at the time of Baker's study (Baker 1956). The western jumping mouse (*Zapus princeps*) has been recorded along the Rio Grande in Socorro and Bernalillo counties, New Mexico (Findley et al. 1975) but has not been taken there since the 1930s and may be extinct as a riparian component of the desert. Our southernmost record of the mink (*Mustela vison*) in New Mexico is from the Rio Grande in Socorro County, also technically within the desert, but this species has probably not been an important riparian species in Chihuahuan Desert within historic time.

Bats

Until definitive studies on the role of pesticides in the population dynamics of insectivorous bats are completed, we must regard all of them as threatened. Disquieting evidence of decline in all temperate zone insectivorous bat populations is at hand (Jones 1966). Species which roost in caves are endangered additionally because of widespread cave vandalism. In the Chihuahuan desert area the following species are especially vulnerable because they are cavernicolous, feed in agricultural areas, or occupy endangered riparian habitats: *Mormoops megalophylla*, *Myotis lucifugus*, *Myotis yumanensis*, *Myotis velifer*, *Myotis thysanodes*, *Myotis leibii*, *Myotis californicus*, *Plecotus townsendii*, and *Tadarida brasiliensis*.

Desert Species

Desert species of mammals are those which are primarily adapted for life in arid regions. Groups which predominate in this category are geomyids and heteromyids together with assorted muroids and a few sciurids, lagomorphs, carnivores, and bats. Evidence concerning change of status of the members of this assemblage during historic time is scanty, but not altogether lacking.

The three genera of pocket gophers tend to sort themselves out on the basis of what seems to be increased tolerance of xeric conditions. *Thomomys* is chiefly montane, though it persists in suitable enclaves in

desert areas. In the heart of the Chihuahuan Desert it is relictual in its distribution as though it were formerly more widespread, perhaps in more mesic times. *Geomys* is primarily a grassland genus, occurring in only a small area of the Chihuahuan Desert. In the northern Rio Grande Valley, *Thomomys bottae* continuously occupies the riparian alluvium until *Geomys arenarius* is encountered, and then *T. bottae* becomes patchy in its distribution. *Pappogeomys* is a true desert genus; where it occurs with *Geomys* in the plains, it occupies the xeric interfluves while *Geomys* preempts the friable, moister, arroyo soils. In northeastern New Mexico where three genera occur, this set of habitat relationships is maintained (Best 1973). *Pappogeomys* once occurred as far north as the northern Rio Grande Valley (A. H. Harris pers. comm.). Now it is very rare in the Albuquerque area and in much of the lower Rio Grande Valley in New Mexico.

The fragmentations of the range of *Thomomys* in the Chihuahuan heartland, together with the withdrawal of *Pappogeomys* from its northern limits, suggest increasingly mesic conditions in the north and increasingly xeric ones in the south, or perhaps decreasing plant cover in the latter area because of human activity. Heteromyids offer less clear-cut evidence on this question. Gennaro (1968) has provided detailed data on distributions of selected species at their northern peripheries in New Mexico. *Dipodomys merriami* is rare and patchy in the upper Rio Grande Valley, as are *Perognathus intermedius* and *Onychomys torridus*. Perhaps these three low desert forms were more widespread northerly and have since contracted as has *Pappogeomys*. Certainly the relictual stands of creosote in Bernalillo County, New Mexico, lend credence to this notion.

With one exception, other desert species seem widespread and common throughout the Chihuahuan Desert area. The exception is the hog-nosed skunk (*Conepatus mesoleucas*). This carnivore once occurred as far north as Albuquerque, having been taken there in 1902 by Barber, but now is known no further north than Socorro, some 112 km (70 miles) to the south. Many low desert species seem to benefit from land misuse because the results often simulate increased aridity in reducing plant cover and creating shrub desert conditions.

In summary, there is some evidence suggesting that Chihuahuan forms are retreating from the northern limits of the desert, but in the main the desert-adapted segment of the Chihuahuan fauna seems to be faring better than the other groups considered previously, and may even benefit slightly from the present regimen of overuse.

SUMMARY

The Chihuahuan Desert mammal fauna consists of a large number of species which are widespread and common. In the main these are arid-

adapted taxa living in arid lowland and foothill habitats. Such desert species suffer little or may even increase their ranges as a result of human activity. To the extent that they are restricted to higher, more mesic habitats, Chihuahuan mammals tend to survive more precariously. Larger carnivores and ungulates of all habitats tend to be threatened if not extinct. Habitat change as a result of grazing and farming and uncontrolled hunting in some areas are the principal problems. However, many habitats in the Chihuahuan Desert were fragile at best even in prehistoric time and were able to sustain little human use, and late Pleistocene and archaeological evidence suggests that diminution of the Chihuahuan fauna has been going on for thousands of years.

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Mammals of the Southern Chihuahuan Desert: An Inventory

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The southern limits of the Chihuahuan Desert are not readily delimited. Because of this, an inventory of the kinds of mammals of this geographic area in the Republic of Mexico can, at best, be only an estimate. In compiling the list of mammalian taxa, I have relied on numerous sources to initially set the boundaries of the Chihuahuan Desert. Particularly useful were Shreve (1936, 1937), Brand (1937), Dice (1943), Jaeger (1957), and McGinnies et al. (1968). Distributional patterns of mammals were obtained chiefly from Hall and Kelson (1959), Dalquest (1953), Baker (1956), Baker and Greer (1962), and Anderson (1972). A wide variety of sources provided additional information. Notable was the habitat information provided in Leopold (1950, 1959).

A total of seven orders of mammals is represented by species known to occur within the southern area of the Chihuahuan Desert, as I have interpreted it. In terms of diversity, this is fewer than the number of orders (11) in the tropical portion of the Nearctic and the same as in the Great Plains (Hoffman and Jones 1970). Fewer families (20) are in the southern Chihuahuan Desert than in the tropical region of the Nearctic (39), yet familial diversity in the Chihuahuan Desert exceeds that of the Boreal Region of the Nearctic by seven families. However, no families of mammals in the southern Chihuahuan Desert are found only there. The diversity in genera is not great, with only 55. This slightly exceeds the number (53) found in the Boreal Region of the Nearctic, and is considerably less than in the tropics (165). The restrictions of the arid environment are reflected by the number of species in the southern Chihuahuan Desert; a total of 101 species probably occurs in the desert south of the international boundary. This is approximately 46 species fewer than found in the Boreal Region and is considerably less than in the Central American tropics (circa 407). Although it is difficult to enumerate and evaluate the diversity within the species, as many as 167 named subspecies may occur in this desert (see Table 1).

TABLE 1. Checklist of mammals of the southern Chihuahuan Desert (? = questionable occurrence).

| | |
|--------------------------------|-----------------------------------|
| ORDER MARSUPIALIA | FAMILY MOLOSSIDAE |
| FAMILY DIDELPHIDAE | <i>Tadarida brasiliensis</i> |
| <i>Didelphis virginiana</i> | <i>T. b. mexicana</i> |
| <i>D. v. texensis</i> | <i>Tadarida femorosacca</i> |
| <i>D. v. californica</i> | <i>Tadarida macrotis</i> |
| ORDER INSECTIVORA | <i>Eumops perotis</i> |
| FAMILY SORICIDAE | <i>E. p. californicus</i> |
| <i>Sorex saussurei</i> | <i>Molossus molossus</i> |
| <i>Notiosorex crawfordi</i> | <i>M. m. aztecus</i> |
| ORDER CHIROPTERA | ORDER LAGOMORPHA |
| FAMILY PHYLLOSTOMATIDAE | FAMILY LEPORIDAE |
| <i>Choeronycteris mexicana</i> | <i>Sylvilagus floridanus</i> |
| <i>Leptonycteris nivalis</i> | <i>S. f. nelsoni</i> |
| <i>L. n. longala</i> | <i>S. f. orizabae</i> |
| <i>Diphylla ecaudata</i> | <i>Sylvilagus audubonii</i> |
| <i>Desmodus rotundus</i> | <i>S. a. minor</i> |
| FAMILY VESPERTILIONIDAE | <i>S. a. parvulus</i> |
| <i>Myotis lucifugus</i> | <i>Lepus californicus</i> |
| <i>M. l. occultus</i> | <i>L. c. texianus</i> |
| <i>Myotis yumanensis</i> | <i>L. c. asellus</i> |
| <i>M. y. yumanensis</i> | <i>Lepus callotis</i> |
| <i>Myotis velifer</i> | <i>L. c. callotis</i> |
| <i>M. v. velifer</i> | <i>L. c. gaillardi</i> |
| <i>Myotis evotis</i> | ORDER RODENTIA |
| <i>M. e. auricularis</i> | FAMILY SCIURIDAE |
| <i>Myotis thysanodes</i> | <i>Eutamias dorsalis</i> |
| <i>M. t. thysanodes</i> | <i>E. d. dorsalis</i> (?) |
| <i>Myotis volans</i> | <i>E. d. nidoensis</i> |
| <i>M. v. interior</i> | <i>Ammospermophilus interpres</i> |
| <i>Myotis californicus</i> | <i>Spermophilus mexicanus</i> |
| <i>M. c. californicus</i> | <i>S. m. parvidens</i> |
| <i>Myotis leibii</i> | <i>Spermophilus spilosoma</i> |
| <i>M. l. melanorhinus</i> | <i>S. s. ammophilus</i> |
| <i>Pipistrellus hesperus</i> | <i>S. s. canescens</i> |
| <i>P. h. australis</i> | <i>S. s. marjenuatus</i> |
| <i>P. h. maximus</i> | <i>S. s. pallescens</i> |
| <i>Eptesicus fuscus</i> | <i>S. s. spilosoma</i> |
| <i>E. f. pallidus</i> | <i>Spermophilus variegatus</i> |
| <i>Lasiurus borealis</i> | <i>S. v. couchii</i> |
| <i>L. b. borealis</i> | <i>S. v. grammurus</i> |
| <i>Lasiurus cinereus</i> | <i>S. v. rupestris</i> |
| <i>L. c. cinereus</i> | <i>S. v. variegatus</i> (?) |
| <i>Lasiurus ega</i> | <i>Cynomys ludovicianus</i> |
| <i>L. e. xanthinus</i> | <i>C. l. arizonensis</i> |
| <i>Plecotus townsendii</i> | <i>Cynomys mexicanus</i> |
| <i>P. t. pallescens</i> | FAMILY GEOMYIDAE |
| <i>P. t. australis</i> | <i>Thomomys bottae</i> |
| <i>Antrozous pallidus</i> | <i>T. b. toltecus</i> |
| <i>A. p. pallidus</i> | <i>T. b. nelsoni</i> (?) |

TABLE 1. (Continued)

ORDER RODENTIA (Continued)

*Thomomys umbrinus**T. u. camargensis**T. u. goldmani**T. u. humilis**T. u. juntae**T. u. nelsoni**T. u. newmani**T. u. retractus**T. u. villai**T. u. zacatecae**Geomys arenarius**G. a. arenarius**Pappogeomys castanops**P. c. clarkii**P. c. consitus**P. c. excelsus**P. c. goldmani**P. c. subnubulis**P. c. sordidulus*

FAMILY HETEROMYIDAE

*Perognathus flavus**P. f. flavus**P. f. gilvus**P. f. medius**P. f. pallescens**Perognathus apache**P. a. apache**Perognathus hispidus**P. h. paradoxus**P. h. zacatecae**Perognathus penicillatus**P. p. eremicus**Perognathus intermedius**P. i. intermedius**Perognathus nelsoni**P. n. canescens**P. n. nelsoni**Dipodomys ordii**D. o. extractus**D. o. idoneus**D. o. obscurus**D. o. ordii**Dipodomys spectabilis**D. s. cratodon**D. s. spectabilis**D. s. zygomaticus**Dipodomys nelsoni**Dipodomys merriami**D. m. ambiguus**D. m. atronassus**D. m. olivaceus**Liomys irroratus**L. i. alleni*

FAMILY CRICETIDAE

*Reithrodontomys montanus**R. m. montanus**Reithrodontomys megalotis**R. m. megalotis**Reithrodontomys fulvescens**R. f. canus**R. f. griseoflavus**Peromyscus eremicus**P. e. alcorni**P. e. anthonyi**P. e. phaeus**Peromyscus maniculatus**P. m. blandus**Peromyscus leucopus**P. l. arizonae**P. l. tornillo**Peromyscus boylii**P. b. ambiguus**P. b. rowleyi**Peromyscus pectoralis**P. p. laceianus**P. p. pectoralis**Peromyscus truei**P. t. erasmus**P. t. gentilis**Peromyscus difficilis**P. d. difficilis**Peromyscus polius**Peromyscus melanophrys**P. m. coahuilensis**P. m. consobrinus**P. m. xenurus**Baiomys taylori**B. t. ater (?)**B. t. paulus**Onychomys leucogaster**O. l. albescens**Onychomys torridus**O. t. canus**O. t. torridus**Sigmodon hispidus**S. h. berlandieri**Sigmodon ochrognathus**S. o. madreensis**S. o. montanus*

TABLE 1. (Continued)

| | |
|---------------------------------|------------------------------|
| ORDER RODENTIA (Continued) | <i>P. l. hernandezii</i> |
| <i>S. o. ochrognathus</i> | <i>P. l. mexicanus</i> |
| <i>Sigmodon fulviventris</i> | <i>Nasua narica</i> (?) |
| <i>S. f. minimus</i> | <i>N. n. molaris</i> |
| <i>Neotoma albigula</i> | FAMILY MUSTELIDAE |
| <i>N. a. leucodon</i> | <i>Mustela frenata</i> |
| <i>N. a. melanura</i> | <i>M. f. frenata</i> |
| <i>N. a. robusta</i> | <i>M. f. neomexicanus</i> |
| <i>Neotoma micropus</i> | <i>Taxidea taxus</i> |
| <i>N. m. canescens</i> | <i>T. t. berlandieri</i> |
| <i>Neotoma goldmani</i> | <i>Spilogale putorius</i> |
| <i>Neotoma mexicana</i> | <i>S. p. leucoparia</i> |
| <i>N. m. inornata</i> | <i>Mephitis mephitis</i> |
| <i>N. m. mexicana</i> | <i>M. m. estor</i> |
| <i>N. m. navus</i> | <i>M. m. varians</i> |
| <i>N. m. tenuicauda</i> | <i>Mephitis macroura</i> |
| <i>Microtus mexicanus</i> | <i>M. m. macroura</i> |
| <i>M. m. madrensis</i> (?) | <i>M. m. milleri</i> |
| <i>Microtus pennsylvanicus</i> | <i>Conepatus mesoleucus</i> |
| <i>M. p. chihahuensis</i> | <i>C. m. mearnsi</i> |
| FAMILY ERETHIZONTIDAE | <i>C. m. venaticus</i> (?) |
| <i>Erethizon dorsatum</i> | FAMILY FELIDAE |
| <i>E. d. couesi</i> | <i>Felis concolor</i> |
| ORDER CARNIVORA | <i>F. c. azteca</i> |
| FAMILY CANIDAE | <i>F. c. stanleyana</i> |
| <i>Canis latrans</i> | <i>Lynx rufus</i> |
| <i>C. l. impavidus</i> | <i>L. r. baileyi</i> |
| <i>C. l. mearnsi</i> | <i>L. r. escuinapae</i> |
| <i>C. l. texensis</i> | ORDER ARTIODACTYLA |
| <i>Canis lupus</i> | FAMILY TAYASSUIDAE |
| <i>C. l. baileyi</i> | <i>Dictyoyles tajacu</i> |
| <i>Vulpes macrotis</i> | <i>D. t. angulatus</i> |
| <i>V. m. neomexicana</i> | FAMILY CERVIDAE |
| <i>V. m. zinseri</i> | <i>Odocoileus hemionus</i> |
| <i>Urocyon cinereoargenteus</i> | <i>O. h. crooki</i> |
| <i>U. c. nigrirostris</i> | <i>Odocoileus virginiana</i> |
| <i>U. c. scotti</i> | <i>O. v. carminus</i> |
| FAMILY URSIDAE | <i>O. v. couesi</i> |
| <i>Ursus americanus</i> | <i>O. v. texana</i> |
| <i>U. a. amblyceps</i> | <i>O. v. miquihuanensis</i> |
| <i>U. a. eremicus</i> | FAMILY ANTILOCAPRIDAE |
| <i>U. a. machetes</i> | <i>Antilocapra americana</i> |
| <i>Ursus arctos</i> (?) | <i>A. a. mexicana</i> |
| FAMILY PROCYONIDAE | FAMILY BOVIDAE |
| <i>Bassariscus astutus</i> | <i>Bison bison</i> |
| <i>B. a. astutus</i> | <i>B. b. bison</i> |
| <i>B. a. flavus</i> | <i>Ovis canadensis</i> |
| <i>Procyon lotor</i> | <i>O. c. mexicana</i> |
| <i>P. l. fuscipes</i> | |

The largest number of genera and species occurring in the southern Chihuahuan Desert are in the orders Chiroptera, Rodentia, and Carnivora. There are 24 species in 13 genera of bats, while 47 species of 19 different genera of rodents are found. The carnivores are represented by 17 species in 15 genera. The diversity in the chiropterans is not as great as in Texas where 33 species are known to occur (Packard and Mollhagen 1971). The ecological limitations and thus local geographical restrictions placed on the bats by the desert are quite severe. Certain species are restricted to the ecotonal areas of the desert, only foraging over the various desert habitats for short periods. Distribution of playas, artesian springs, intermittent streams, and man-made water tanks are extremely important to the existence of many of the bats in the Chihuahuan Desert.

Rodents are the most successful group of mammals in the southern Chihuahuan Desert in terms of faunal diversity and perhaps also in numbers. The composition of the rodent fauna suggests it has effectively radiated into most available habitat types and occupational roles. The rather surprising number of genera and species of carnivores likely reflects the rather close association of this group to the considerable niche diversity of the rodents. The carnivores, being opportunists,

TABLE 2. Mammals of the southern Chihuahuan Desert listed by suspected faunal affinities.

| | |
|---------------------------------|----------------------------------|
| DECIDUOUS FOREST SPECIES (5) | <i>Canis lupus</i> |
| <i>Didelphis virginiana</i> | <i>Ursus americanus</i> |
| <i>Lasiurus borealis</i> | <i>Ursus arctos</i> |
| <i>Sylvilagus floridanus</i> | <i>Procyon lotor</i> |
| <i>Peromyscus leucopus</i> | <i>Mustela frenata</i> |
| <i>Urocyon cinereoargenteus</i> | <i>Taxidea taxus</i> |
| BOREAL OR MONTANE SPECIES (5) | <i>Mephitis mephitis</i> |
| <i>Myotis evotis</i> | <i>Felis concolor</i> |
| <i>Myotis volans</i> | <i>Lynx rufus</i> |
| <i>Plecotus townsendii</i> | <i>Odocoileus hemionus</i> |
| <i>Microtus pennsylvanicus</i> | <i>Odocoileus virginianus</i> |
| <i>Ovis canadensis</i> | <i>Antilocapra americana</i> |
| GREAT BASIN OR SOUTHERN | <i>Bison bison</i> |
| MONTANE (4) | SOUTHERN SPECIES – TROPICAL (13) |
| <i>Thomomys bottae</i> | <i>Choeronycteris mexicana</i> |
| <i>Thomomys umbrinus</i> | <i>Leptonycteris nivalis</i> |
| <i>Peromyscus truei</i> | <i>Desmodus rotundus</i> |
| <i>Spilogale putorius</i> | <i>Diphylla ecaudata</i> |
| WIDESPREAD SPECIES (18) | <i>Lasiurus ega</i> |
| <i>Myotis lucifugus</i> | <i>Tadarida brasiliensis</i> |
| <i>Eptesicus fuscus</i> | <i>Tadarida femorosacca</i> |
| <i>Lasiurus cinereus</i> | <i>Tadarida macrotis</i> |
| <i>Peromyscus maniculatus</i> | <i>Eumops perotis</i> |
| <i>Canis latrans</i> | <i>Molossus molossus</i> |

TABLE 2. (Continued)

| | |
|-----------------------------------|----------------------------------|
| SOUTHERN SPECIES – TROPICAL (13) | |
| (Continued) | |
| <i>Liomys irroratus</i> | <i>Spermophilus mexicanus</i> |
| <i>Reithrodontomys fulvescens</i> | <i>Spermophilus pilosoma</i> |
| <i>Baiomys taylori</i> | <i>Spermophilus variegatus</i> |
| <i>Sigmodon hispidus</i> | <i>Pappogeomys castanops</i> |
| | <i>Perognathus flavus</i> |
| | <i>Perognathus apache</i> |
| | <i>Perognathus penicillatus</i> |
| | <i>Perognathus intermedius</i> |
| | <i>Perognathus nelsoni</i> |
| STEPPE SPECIES (4) | <i>Dipodomys spectabilis</i> |
| <i>Cynomys ludovicianus</i> | <i>Dipodomys nelsoni</i> |
| <i>Perognathus hispidus</i> | <i>Dipodomys merriami</i> |
| <i>Dipodomys ordii</i> | <i>Dipodomys merriami</i> |
| <i>Reithrodontomys montanus</i> | <i>Reithrodontomys megalotis</i> |
| SOUTHWESTERN MONTANE (10) | <i>Peromyscus eremicus</i> |
| <i>Sorex saussurei</i> | <i>Peromyscus pectoralis</i> |
| <i>Myotis californicus</i> | <i>Peromyscus melanophrys</i> |
| <i>Pipistrellus hesperus</i> | <i>Onychomys leucogaster</i> |
| <i>Eutamias dorsalis</i> | <i>Onychomys torridus</i> |
| <i>Peromyscus boylii</i> | <i>Sigmodon fulviventer</i> |
| <i>Peromyscus difficilis</i> | <i>Neotoma albigula</i> |
| <i>Sigmodon ochrognathus</i> | <i>Neotoma micropus</i> |
| <i>Neotoma mexicana</i> | <i>Vulpes macrotis</i> |
| <i>Microtus mexicana</i> | <i>Bassariscus astutus</i> |
| <i>Erethizon dorsatum</i> | <i>Nasua narica</i> |
| SOUTHWESTERN (36) | <i>Mephitis macroura</i> |
| <i>Notiosorex crawfordii</i> | <i>Conepatus mesoleucus</i> |
| <i>Myotis yumanensis</i> | <i>Dicotyles tajacu</i> |
| <i>Myotis velifex</i> | SOUTHWESTERN-CHIHUAHUAN (5) |
| <i>Myotis leibii</i> | <i>Lepus callotis</i> |
| <i>Myotis thysanodes</i> | <i>Cynomys mexicanus</i> |
| <i>Antrozous pallidus</i> | <i>Geomys arenarius</i> |
| <i>Sylvilagus audubonii</i> | <i>Peromyscus polius</i> |
| <i>Lepus californicus</i> | <i>Neotoma goldmani</i> |
| <i>Ammospermophilus interpres</i> | |

doubtlessly have capitalized on the numbers and kinds of rodents and the local abundance of lagomorphs.

The faunal affinities of the mammals of the southern Chihuahuan Desert are somewhat complex, and in many ways somewhat similar to certain of the affinities seen in the grasslands of North America (Hoffman and Jones 1970). The mammalian fauna seems divisible into nine different sources (Table 2). The largest number of species, 36, is southwestern in origin as compared to only 9 species of southwestern origin in the northern central Great Plains (where 115 species are known). In addition, 10 species occurring in the desert seem to have their affinities with what I have termed the southwestern montane (although these could be placed in the southwestern group). Widespread species (or vicariants) whose faunal affinities are difficult

to ascertain are 18 in number in the desert compared to 27 in the Great Plains. There are 13 southern-oriented (or tropical) species in the desert as compared to only 3 on the central Great Plains. The proximity of the southern Chihuahuan Desert to tropical areas and warmer prevailing temperatures probably accounts for this infusion of species. Only five species seem endemic to the Chihuahuan Desert proper (Table 2). The remaining species are rather evenly divided in their faunal affinities. Five species are deciduous forest types, four are steppe species, five are boreal or montane, and four are Great Basin or southern montane (in the peripheral zones of the "Basin"). Whereas the great bulk of the species on the central Great Plains are derived from boreal or montane, steppe, and deciduous forest regions, those in the southern Chihuahuan Desert are southwest or southern in their origins. Certain species and subspecies as well as introduced kinds (Table 3) are not grouped into this analysis.

TABLE 3. Additional species or subspecies of the southern Chihuahuan mammalian fauna.

| | |
|--|--|
| SOME PERIPHERAL SPECIES OR SUBSPECIES | <i>Reithrodontomys megalotis zacatecae</i> |
| <i>Plecotus mexicanus</i> | <i>Peromyscus maniculatus rufinus</i> |
| <i>Lepus californicus eremicus</i> | <i>Onychomys torridus ater</i> |
| <i>Perognathus flavus fuscus</i> | <i>Urocyon cinereoargenteus madrensis</i> |
| <i>Dipodomys ordii pullus</i> | <i>Dicotyles tajacu sonoriensis</i> |
| <i>Castor canadensis mexicanus</i> | INTRODUCED SPECIES |
| <i>Oryzomys couesi</i> | <i>Mus musculus</i> |
| <i>Ondatra zibethica</i> | <i>Rattus rattus</i> |

The species analysis of southern Chihuahuan Desert mammals closely approximates the species density contour of Simpson (1964) for that general area in question. Sharp faunal breaks in contour densities occur to the east and west of the Chihuahuan Desert. To the east, fewer species occur, whereas to the east and south, many more species are found. Likely, this reflects the greater diversity of niches in the southern and western areas or those that are available are more fully occupied. The Chihuahuan Desert may act as a barrier to the dispersal of many more mesic-adapted mammalian taxa to the south, east, and northeast.

Diversity in the cricetines and heteromyids rodents is greatest in the Chihuahuan Desert of the nonvolant taxa. Burt (1958) pointed out that soil types likely restrict the heteromyids to the arid and semiarid southwest. Both of these taxa have seemingly capitalized on a combination of physiological and trophic adaptations to occupy a wide diversity of niches.

I have divided the mammalian fauna of the southern Chihuahuan Desert into nine different trophic categories (Table 4) and six different

TABLE 4. Mammals of the southern Chihuahuan Desert separated into trophic categories.

OMNIVORES (3)

Didelphis virginiana
Ursus americanus
Ursus arctos

INSECTIVORES (23)

Sorex saussurei
Notiosorex crawfordi
Choeronycteris mexicana
Leptonycteris nivalis
Myotis yumanensis
Myotis lucifugus
Myotis velifer
Myotis evotis
Myotis thysanodes
Myotis volans
Myotis californicus
Myotis leibii
Pipistrellus hesperus
Eptesicus fuscus
Lasiurus borealis
Lasiurus cinereus
Lasiurus ega
Plecotus townsendii
Antrozous pallidus
Tadarida brasiliensis
Tadarida femorosacca
Tadarida macrotis
Eumops perotis
Molossus mollosus

INSECTIVORE-HERBIVORES (2)

Onychomys leucogaster
Onychomys torridus

HERBIVORE-INSECTIVORES (11)

Peromyscus eremicus
Peromyscus maniculatus
Peromyscus leucopus
Peromyscus boylii
Peromyscus pectoralis
Peromyscus truei
Peromyscus difficilis
Peromyscus polius
Peromyscus melanophrys
Baiomys taylori
Erethizon dorsatum

HERBIVORE-GRANIVORES (12)

Thomomys bottae
Geomys arenarius
Pappogeomys castanops
Reithrodontomys montanus

Reithrodontomys megalotis
Reithrodontomys fulvescens
Neotoma albigula
Neotoma micropus
Neotoma goldmani
Neotoma mexicana
Dicotyles tajacu

HERBIVORES (16)

Cynomys ludovicianus
Cynomys mexicanus
Sylvilagus floridanus
Sylvilagus audubonii
Lepus californicus
Sigmodon hispidus
Sigmodon ochrognathus
Sigmodon fulviventris
Microtus mexicanus
Microtus pennsylvanicus
Odocoileus hemionus
Odocoileus virginiana
Antilocapra americana
Bison bison
Ovis canadensis

GRANIVORE-HERBIVORES
(SOME SPECIES SEASONALLY
INSECTIVOROUS) (16)

Eutamias dorsalis
Ammospermophilus interpres
Spermophilus mexicanus
Spermophilus spilosoma
Spermophilus variegatus
Perognathus flavus
Perognathus apache
Perognathus hispidus
Perognathus penicillatus
Perognathus intermedius
Perognathus nelsoni
Dipodomys ordii
Dipodomys spectabilis
Dipodomys nelsoni
Dipodomys merriami
Liomys irroratus

CARNIVORES (15)

Canis latrans
Canis lupus
Vulpes macrotis
Urocyon cinereoargenteus
Bassariscus astutus
Procyon lotor

TABLE 4. (Continued)

| | |
|---------------------------|-----------------------------|
| CARNIVORES | <i>Mephitis macroura</i> |
| (15) (Continued) | <i>Conepatus mesoleucus</i> |
| <i>Nasua narica</i> | <i>Felis concolor</i> |
| <i>Mustela frenata</i> | <i>Lynx rufus</i> |
| <i>Tadidea taxus</i> | SANGUIVORES (2) |
| <i>Spilogale putorius</i> | <i>Desmodus rotundus</i> |
| <i>Mephitis mephitis</i> | <i>Diphylla ecaudata</i> |

habitat types (Table 5). There are 23 insectivorous types (mostly bats) and 57 species that combine herbivory with some other trophic combination such as granivory or insectivory. Probably more than three species employ omnivory at various stages in their life history, and shifts in food strategies make it difficult to categorize many species. Nevertheless, the divisions I have made are based largely on results of food-habit patterns revealed in my 4-year study of the mammals in the Chihuahuan Desert and closely associated areas. In addition, I have relied on the literature to estimate the food niche of many species. Where a combination such as insectivore-herbivore is indicated, it means the species is insectivorous for a greater portion of the calendar year than it is an herbivore. It is interesting to note that the herbivore-insectivore niche is composed chiefly of sciurid and heteromyid rodents. Much of this concentration into similar food niches may result from the degree of vertical stratification of the fauna and/or habitat differences.

The division of the Chihuahuan Desert mammalian fauna into eight habitat types is based on the floristic divisions made by Rowell (1967). In certain areas these divisions are not wholly applicable, whereas those employed by Wauer (1971) might prove more useful. The habitat type with greatest mammalian diversity is the desert grassland. This results from the large number of rodent species that are found in it. Many of the species are not restricted to a single habitat type and occur in several habitats, particularly when these are adjacent. This accounts for the high degree of mammalian diversity in such habitat types as the grasslands, yucca-juniper savannah, oak forest, and creosote bush-tar-bush desert scrub. There is a high degree of association of mammalian species, habitat types, and faunal affinities. Thus it is not surprising that many of the desert grassland species (for example) have southwestern faunal affinities.

The current status (rare or endangered) of many species of mammals of the southern Chihuahuan Desert is relatively unknown. Certain species, such as the Mexican prairie dog (*Cynomys mexicanus*), grizzly bear (*Ursus arctos*), wolf (*Canis lupus*), and desert mountain sheep (*Ovis canadensis*), are unquestionably endangered. In fact, the latter three

TABLE 5. Some associations of southern Chihuahuan Desert mammals with habitat types (no attempt is made to group species of bats).

| | |
|--|-----------------------------------|
| 1. CREOSOTE BUSH –TARBUSH DESERT SCRUB (23) | <i>Cynomys mexicanus</i> |
| <i>Notiosorex crawfordi</i> | <i>Thomomys bottae</i> |
| <i>Sylvilagus audubonii</i> | <i>Pappogeomys castanops</i> |
| <i>Lepus californicus</i> | <i>Perognathus flavus</i> |
| <i>Ammospermophilus interpres</i> | <i>Perognathus apache</i> |
| <i>Spermophilus mexicanus</i> | <i>Perognathus hispidus</i> |
| <i>Thomomys bottae</i> (?) | <i>Perognathus penicillatus</i> |
| <i>Geomys arenarius</i> | <i>Dipodomys ordii</i> |
| <i>Perognathus flavus</i> | <i>Dipodomys spectabilis</i> |
| <i>Perognathus penicillatus</i> | <i>Dipodomys nelsoni</i> |
| <i>Perognathus intermedius</i> | <i>Liomys irroratus</i> |
| <i>Dipodomys spectabilis</i> | <i>Reithrodontomys montanus</i> |
| <i>Dipodomys merriami</i> | <i>Reithrodontomys megalotis</i> |
| <i>Peromyscus eremicus</i> | <i>Reithrodontomys fulvescens</i> |
| <i>Peromyscus maniculatus</i> | <i>Peromyscus maniculatus</i> |
| <i>Onychomys torridus</i> | <i>Baiomys taylori</i> |
| <i>Neotoma micropus</i> (?) | <i>Onychomys leucogaster</i> |
| <i>Neotoma goldmani</i> | <i>Sigmodon hispidus</i> |
| <i>Canis latrans</i> | <i>Sigmodon fulviventer</i> |
| <i>Vulpes macrotis</i> | <i>Neotoma micropus</i> |
| <i>Mephitis mephitis</i> | <i>Microtus pennsylvanicus</i> |
| <i>Lynx rufus</i> | <i>Canis latrans</i> |
| <i>Odocoileus hemionus</i> | <i>Vulpes macrotis</i> |
| <i>Ovis canadensis</i> (?) | <i>Mustela frenata</i> |
| | <i>Taxidea taxus</i> |
| 2. SOTOL – LECHUGIULLA (15) | <i>Mephitis mephitis</i> |
| <i>Sylvilagus audubonii</i> | <i>Mephitis macroura</i> |
| <i>Ammospermophilus interpres</i> | <i>Conepatus mesoleucus</i> |
| <i>Spermophilus variegatus</i> | <i>Felis concolor</i> (?) |
| <i>Perognathus flavus</i> | <i>Lynx rufus</i> |
| <i>Perognathus penicillatus</i> | <i>Antilocapra americana</i> |
| <i>Perognathus nelsoni</i> | <i>Bison bison</i> |
| <i>Reithrodontomys megalotis</i> | |
| <i>Peromyscus maniculatus</i> | 4. YUC CA – JUNIPER SAVANNAH (24) |
| <i>Peromyscus boylii</i> | <i>Notiosorex crawfordi</i> |
| <i>Peromyscus pectoralis</i> | <i>Spermophilus variegatus</i> |
| <i>Peromyscus melanophrys</i> | <i>Perognathus nelsoni</i> |
| <i>Neotoma albigula</i> | <i>Reithrodontomys megalotis</i> |
| <i>Canis latrans</i> | <i>Reithrodontomys fulvescens</i> |
| <i>Bassariscus astutus</i> | <i>Peromyscus boylii</i> |
| <i>Spilogale putorius</i> | <i>Peromyscus pectoralis</i> |
| 3. DESERT GRASSLAND (39) | <i>Peromyscus truei</i> |
| <i>Notiosorex crawfordi</i> | <i>Peromyscus difficilis</i> |
| <i>Sylvilagus audubonii</i> | <i>Peromyscus melanophrys</i> |
| <i>Lepus californicus</i> | <i>Sigmodon ochrognathus</i> |
| <i>Lepus callotis</i> | <i>Neotoma albigula</i> |
| <i>Spermophilus mexicanus</i> | <i>Neotoma mexicana</i> |
| <i>Spermophilus spilosoma</i> | <i>Microtus mexicanus</i> |
| <i>Cynomys ludovicianus</i> | <i>Erethizon dorsatum</i> |
| | <i>Urocyon cinereoargenteus</i> |

TABLE 5. (Continued)

| | |
|---|---|
| 4. YUCCA – JUNIPER SAVANNAH (24) (Continued) | |
| <i>Bassariscus astutus</i> | <i>Neotoma mexicanus</i> |
| <i>Procyon lotor</i> (?) | <i>Urocyon cinereoargenteus</i> |
| <i>Spilogale putorius</i> | <i>Ursus americanus</i> |
| <i>Mephitis mephitis</i> | <i>Bassariscus astutus</i> |
| <i>Conepatus mesoleucus</i> | <i>Procyon lotor</i> |
| <i>Felis concolor</i> | <i>Spilogale putorius</i> |
| <i>Lynx rufus</i> | <i>Mephitis mephitis</i> |
| <i>Odocoileus hemionus</i> | <i>Conepatus mesoleucus</i> |
| 5. PINON PINE – JUNIPER (20) | <i>Felis concolor</i> (?) |
| <i>Eutamias dorsalis</i> | <i>Odocoileus hemionus</i> |
| <i>Thomomys bottae</i> | 7. PONDEROSA PINE – DOUGLAS FIR – ARIZONA CYPRESS (15) |
| <i>Peromyscus maniculatus</i> | <i>Sorex saussurei</i> |
| <i>Peromyscus boylii</i> | <i>Eutamias dorsalis</i> |
| <i>Peromyscus truei</i> | <i>Thomomys umbrinus</i> |
| <i>Peromyscus difficilis</i> | <i>Peromyscus maniculatus</i> |
| <i>Peromyscus polius</i> | <i>Peromyscus truei</i> |
| <i>Sigmodon ochrognathus</i> | <i>Peromyscus difficilis</i> |
| <i>Neotoma mexicana</i> | <i>Neotoma mexicana</i> |
| <i>Microtus mexicanus</i> | <i>Microtus mexicanus</i> |
| <i>Erethizon dorsatum</i> | <i>Erethizon dorsatum</i> |
| <i>Canis latrans</i> | <i>Ursus americanus</i> |
| <i>Urocyon cinereoargenteus</i> | <i>Ursus arctos</i> (?) |
| <i>Ursus americanus</i> | <i>Mephitis mephitis</i> |
| <i>Ursus arctos</i> (?) | <i>Conepatus mesoleucus</i> (?) |
| <i>Bassariscus astutus</i> | <i>Felis concolor</i> |
| <i>Spilogale putorius</i> | <i>Odocoileus hemionus</i> |
| <i>Felis concolor</i> | 8. STREAM RIPARIAN (17) |
| <i>Lynx rufus</i> | <i>Didelphis virginiana</i> |
| <i>Odocoileus hemionus</i> | <i>Sylvilagus floridanus</i> |
| 6. OAK FOREST (23) | <i>Spermophilus variegatus</i> |
| <i>Sylvilagus audubonii</i> | <i>Thomomys bottae</i> |
| <i>Spermophilus mexicanus</i> | <i>Geomys arenarius</i> |
| <i>Spermophilus variegatus</i> | <i>Pappogeomys castanops</i> |
| <i>Thomomys umbrinus</i> | <i>Reithrodontomys fulvescens</i> |
| <i>Perognathus nelsoni</i> | <i>Peromyscus leucopus</i> |
| <i>Reithrodontomys megalotis</i> | <i>Sigmodon hispidus</i> |
| <i>Reithrodontomys fulvescens</i> | <i>Neotoma micropus</i> |
| <i>Peromyscus leucopus</i> | <i>Canis latrans</i> |
| <i>Peromyscus boylii</i> | <i>Urocyon cinereoargenteus</i> |
| <i>Peromyscus pectoralis</i> | <i>Procyon lotor</i> |
| <i>Peromyscus truei</i> | <i>Nasua narica</i> |
| <i>Sigmodon hispidus</i> | <i>Mephitis mephitis</i> |
| <i>Sigmodon ochrognathus</i> | <i>Dicotyles tajacu</i> |
| | <i>Odocoileus virginiana</i> |

species may well be extirpated in the Chihuahuan Desert. Additional rare or status unknown species are: *Diphylla ecaudata*; *Tadarida macrotis*; *Ammospermophilus interpres*; *Geomys arenarius*; *Peromyscus*

polius; *Neotoma goldmani*; *Microtus mexicanus*; *Microtus pennsylvanicus*; *Vulpes macrotis*; and *Felis concolor*. Not included in the checklist of mammals of the southern Chihuahuan Desert are *Myotis planiceps* (which probably occurs rarely in the southernmost portions of the desert), and the jaguar (*Felis onca*) which may roam over parts of the desert occasionally. Both of these species are rare. Certain of the above-listed species may be abundant but in a restricted habitat (such as *Microtus pennsylvanicus*, Bradley and Cockrum 1968). Thus destruction of such a restricted habitat could result in extirpation. It is quite urgent that additional information on the status of the populations of Chihuahuan Desert mammals be gathered.

Additional zoogeographical studies following the methods of Hagmeier (1966), Peters (1968), and Rotramel (1973) could be employed most profitably in any future analysis of Chihuahuan Desert mammals.

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Major Game Mammals and Their Habitats in the Chihuahuan Desert Region

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I will begin this paper with the general description of the area in North America as given by Victor Stevenson (1973:26-27). The Chihuahuan Desert is included within this area.

Before the coming of Europeans, he says, the great mid-continental prairies and high plains formed a seemingly endless landscape of waving grass, bordered only by earth and sky. This grassland sea extended from the edge of the deciduous forests of what is now Pennsylvania and Ohio to the Rocky Mountains, and from the Mackenzie River in Canada southward to the Gulf of Mexico. Other similar grasslands existed in the arid climate of northern New Mexico, Arizona, and southwestern Texas, and extended into Mexico far southward to the Mexican states of Queretaro and Hidalgo.

The dominant large mammals, bison and pronghorn that contributed so much to the physiognomy of the prairies by their presence, were hunted almost to extinction in the 19th century. Both are now protected, and the pronghorn has made a phenomenal recovery (Stevenson 1973:26) in the United States but not in Mexico. In Mexico the bison is gone now, and even the pronghorn is on the verge of extinction.

What is the status of other big game mammals in the Mexican part of the Chihuahuan Desert? Leaving aside the case of the "berrendos" which I will discuss later, I will refer to the following species characteristic of the landscape of the Chihuahuan Desert.

Order CARNIVORA— Carnivores, Coyotes, Wolves, Foxes

The coyote (*Canis latrans*) is the most frequently seen, or heard, carnivore in the country, mainly in the desert areas of northern Mexico. The coyote is one of the species that has benefited and increased as a

result of human settlement. The introduction of domestic animals provided a source of food. Livestock carrion, live sheep, calves, colts, as well as chickens and pigs have become standard items of the coyote's diet. Coyotes are subject to intense hunting. Hunting with firearms, trapping, poisoning, and even horse chasing and lassoing them on foot have not decreased their numbers. North of Tamaulipas there is a peculiar contest every year in which the successful hunters receive trophies and the people's applause.

On the other hand, the gray wolf (*Canis lupus*), once abundant in the deserts north of Mexico, has been more sensitive to human hunting. It is now present only in very restricted areas north of Chihuahua. The improper use of sodium fluoroacetate has been fatal to this species. From a biological viewpoint, wolves are rather interesting mammals and efforts should be made to protect them and establish areas in which they do not interfere with human interests.

The gray fox (*Urocyon cinereoargenteus*) is the most numerous and widely distributed carnivore. It is not uncommon in the Chihuahuan Desert, but it is certainly more abundant in south and southeast Mexico. This animal has shown an ability to adapt to many induced environmental changes. It is hunted in semitropical and tropical areas for its fur and because it is considered obnoxious to human interests.

Family URSIDAE—Bears

Black Bear—*Ursus americanus*. Leopold (1959:411) indicated that it is surprising that the black bears of Mexico have maintained themselves so well in the face of ceaseless hunting and persecution. Scouts, cattlemen, lumbermen, or others that happen to be in the area where these animals still exist consider it improper not to shoot them when encountered, regardless of season, age, sex, or legal protection. In the recent past, the number has decreased, especially in the Sierra del Nido, west of the city of Chihuahua, where during 1956-62 I saw them frequently. In the vicinity of Santa Clara and on the slopes of the Sierra Huachinera, southwest of Casas Grandes, there are fewer bears. The population of black bears in the Sierra del Carmen has also decreased.

Grizzly Bear—*Ursus horribilis*. It is quite a while since there were grizzlies in Baja, both in the south and near the Mexico-American border. Many episodes in history have passed since Dr. Kennerly, one of the naturalists of the U.S. and Mexican Boundary Survey, described the on-slaught of a group of these magnificent plantigrades near Los Nogales.

This species has now disappeared from the Sierra del Nido. The last stand was a small group of 20 individuals that I personally saw during 1956-62. At the end of 1973, by poisoning with sodium fluoroacetate, eight specimens were killed. The poison was used illegally by cattlemen and by its use the last representatives of this species in the Sierra del

Nido disappeared. At the end of 1971, the Oficina General de Fauna Silvestre (Mexican Wildlife Office) surveyed the status of these mammals. They found tracks clear enough to conclude that there were at least 10 bears, some of them adults. But the poisoning of the eight specimens in November and December 1973 signaled the extinction of these animals in Chihuahua.

I was unable to convince the cattlemen to maintain this remnant of grizzlies, and it was not possible to establish a sanctuary to protect them.

Leopold (1959) stated that in 1957, he examined the skin of a magnificent male grizzly killed by Isaías García in Cañon Madera on the east slope of Sierra del Nido on 24 October 1955. On 4 October 1957, García killed a female grizzly in the same area. Filomeno Barrios, owner of Rancho Providencia, shot a yearling grizzly in the same area.

In 1962 I saw another grizzly exhibited in the streets of Chihuahua on an automobile by several "senoritas." It had also been shot in the Sierra del Nido. A survey in the same area by Aurelio Malaga Alba and myself estimated the remaining number at 20.

Puma or Mountain Lion—*Felis concolor*

This animal is very seldom seen now. It used to be abundant in the Sierra del Gavilán, in the northwest of Chihuahua. Its number has decreased notably.

Family CERVIDAE—Deer

The deer family was represented originally in Mexico by four species. In the Chihuahuan Desert region, the wapiti or elk that occurred along the extreme northern border was exterminated at an early date. The elk of New Mexico, Arizona, and northern Mexico was named *Cervus merriami*. It is well known that the wapiti disappeared in the early 1900s, but Mearns cites one record of two bulls seen on San José Mountain in northeastern Sonora. There is no evidence to suggest that the native elk ever penetrated far into the Sierra Madre or into other areas of the Chihuahuan Desert region.

Interest in the elk in Mexico has been renewed from time to time during efforts to introduce the northern form (*Cervus canadensis*) into Coahuila. A group of Mexican hunters, during 1971 and 1972, through the Office of the Mexican Wildlife Service, was interested in introducing 60 specimens from northern Colorado; this is one example of several with the same purpose.

Whether elk ever will become acclimated in Mexico is doubtful. As things stand now, the species must be considered a potential rather than an actual member of the game fauna of Mexico (Leopold 1959:502).

Mule deer—*Odocoileus hemionus*. The mule deer had a range

throughout Baja California and the desert ranges of Sonora and the Central Highlands as far as Northern San Luis Potosí and Southwestern Tamaulipas. At the present time it has suffered from the heavy pressure of hunting and land usage. Its numbers and distribution have been reduced.

Where ranch owners have established protective measures, the number has been maintained in accordance with the carrying capacity of the area. Unfortunately, this practice on ranches in Mexico is not common and few hunters accept the restrictions. Despite protective laws, mule deer in Mexico are hunted the year round and this never-ending persecution has contributed materially to their scarcity.

White-tailed Deer—*Odocoileus virginianus*. This animal occurs throughout the country, except in Baja California. It is rather persistent and perhaps is the best example of a mammal that has withstood the pressures of natural predators and man. In pre-Columbus times it was hunted intensely. The Mayas used ingenious traps to catch these deer. In other parts of the country it has also served to fulfill the basic needs of man and the atavism in man that is masked as hunting activity, whether hunting for food or sport hunting. The Mexican state of Yucatán is known, rather poetically, as the "Land of the Pheasant and the Deer," but presently there are neither.

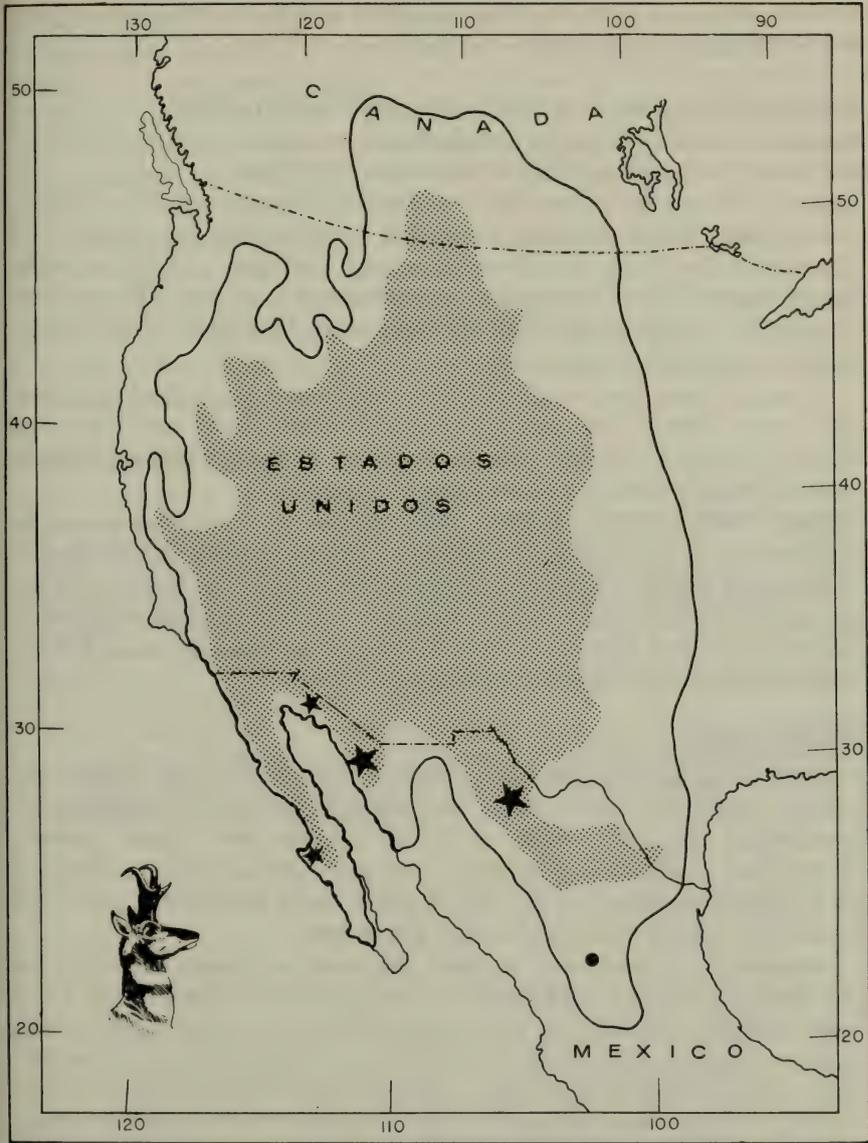
It is not an exaggeration to say that in the whole Mexican Chihuahuan Desert there is not a deer population larger in number than the number of deer in Texas. An increase in numbers could be attained by giving them effective protection. As in the case of the Bura, the number increases very rapidly under protection.

Family ANTILOCAPRIDAE—Pronghorn antelope

This family consists of a single species, the berrendo or *Antilocapra americana*. It is endemic to the New World. The pronghorn occurred originally throughout the plains and deserts of North America far south to the vicinity of Tehuacán Puebla, Mexico (Alvarez 1964:14) on the Mexican plains, the antelope originally occurred in abundance. In 1540 a great hunt was held in honor of the first Spanish Viceroy, Don Antonio de Mendoza, in a place known up to the present time as "El Cazadero" for this reason.

In 1925, according to Nelson (1925), the Mexican population of pronghorn was estimated at 2395 animals, distributed as follows: Coahuila, 600; Chihuahua, 700; Sonora, 595; and Baja California, 500. In 1945, I saw a group of 15 animals in the vicinity of the railroad station in Saltillo City. Now the species is extremely endangered.

The scattered areas that still support some antelope are few (see map 1). In 1971, a group of 51 specimens was moved from New Mexico to



Map showing the distribution of the pronghorn (*Antilocapra americana*) in North America: Heavy line, at the arrival of the Europeans; stippled area, in 1924; stars, localities in Mexico where at the present small groups occur formed by a few specimens each; black dot, reintroduction of 50 individuals in 1971 in a ranch near the City of San Luis Potosí.

San Luis Potosí. The transportation of these animals by airplane was a success but, for a different reason, the number was reduced in the winter of 1972. The farmers showed interest in protecting them, but

diseases and coyotes made their adaptation a slow process. This species tends to disappear in Mexico.

Family BOVIDAE—Bighorn sheep, bison, and related animals

Bison—*Bison bison*. The original Mexican fauna included two members of the family Bovidae—bighorn and bison, or cíbola (*Bison bison*). Apparently, the species did not follow the grasslands very deeply into Mexican territory. Edward Palmer stated that "according to the testimony of old people, the Bison was abundant around Monclova and Parras when first settlers reached these points, probably half a century after the conquest. For some years they killed large numbers for food, but soon they ceased to appear" (Leopold 1959).

In recent times some cattle ranchers tried to introduce the bison from the United States. The last effort was in 1955, when the owner of Rancho Palomas in Chihuahua had several of a small group of these animals illegally shot by hunters from Mexico City.

Bighorn Sheep—*Ovis canadensis*. This species had a former range in northern Mexico from Baja California to Coahuila. Now only scattered remnants of bighorns remain in northwestern Sonora and there are none in the Chihuahuan Desert region of Mexico. The only substantial populations are in Baja California. This situation is a consequence of habitat deterioration in the Chihuahuan Desert. t00

CONCLUSION

Land usage has established a cattle-raising activity that necessarily competes with the wildlife. Also, as a result of the growth in the human population, new town roads and even airstrips have been created. Timber and candelilla exploitation in northern Mexico have contributed to the impoverishment of our major game fauna despite the legal protection the species have received for a long time.

Attempts have been made to treat this fauna as a useful resource, on the basis of a rational exploitation and adequate management, but it has been difficult to attain this end because there is not sufficiently strong public opinion to support the corresponding authorities to promote projects of protection of the fauna. Lacking an attitude of respect toward animals, it would be necessary to put a warden next to each potential hunter. The Mexican peasant believes that he can get immediate benefits from the animals and does not regard them as a source of income through their recreative value. Land ownership, on the other hand, is the strongest obstacle to managing these faunistic resources properly.

The distribution production and agricultural resources was classified in 1960 as follows: 50.3% of the total number of land lots (1,240,000) were units of infrasubsistence, with an annual income of less than \$80,

hardly enough to support a family and accounting for only 4.2% of the total production; 33.8% were subfamilial units with a production of less than \$400 and contributing 17.1% to the total; 12.6% were family units with production of 24.4%; 2.8% were multifamily with 22% of the total production, and 0.5% were multifamily (large) with 32.3% of the total production, and yields close to 400,000 pesos by land lot (Reyes Osorio et al. 1974; Dies 1974).

Seeing the above data, is it possible to forget the primary needs and contemplate only the recreative ones?

This, in part, explains the decline in the population of our major game fauna, which we must try to save, with the cooperation of everyone, for it is time to understand that wildlife belongs to humanity and not only to the countries where it occurs.

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Factors Governing the Distribution of Mammals in the Chihuahuan Desert Region

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To anyone examining the records of occurrence of any animal, it is immediately obvious that distribution is not unidimensional; rather, it occupies both time and space. Further, the distribution of an animal is seldom determined by a single factor, but rather by the interaction of numerous factors. As Burt (1938) has pointed out, the "factors that control mammalian distribution in space and time must be looked for in the various components that go to make up the environment. The factors vary in degree of importance, and it is, therefore, difficult . . . always to pick out those which are critical for a given species." To determine the factors that govern the extent of a species geographic range, information must be accumulated concerning the evolutionary history of the species, their reaction to physiographic and climatic barriers, their adaptiveness and innate responses to the environment, and their ability to cope with competitors (Baker 1968).

The purpose of this report is to assess those factors which govern the distribution of mammals within the Chihuahuan Desert region. As Andrewartha and Birch (1954) have pointed out, distribution may be considered as a facet of abundance, and distribution and abundance may be said to be reverse sides of the same coin. Thus the factors that affect the distribution of a species may also affect its abundance. I will consider here, because of the limitations of the available data, only the range of species based on the criteria of presence or absence. I shall not be concerned with the pattern of arrangement (abundance) of the organisms within the zone of occupation. The basic data are from the distribution of each species living within the Chihuahuan Desert region as given by Hall and Kelson (1959) and from the accounts of mammals of the states of Texas (Bailey 1905; Davis 1966), New Mexico (Bailey 1913; 1931), and the Mexican states of Coahuila (Baker 1956), Chihuahua

(Anderson 1972), Durango (Baker and Greer 1962), and San Luis Potosí (Dalquest 1953). Recent taxonomic and ecological studies have been incorporated to update the aforementioned publications.

THE CHIHUAHUAN DESERT REGION

The Chihuahuan Desert region, as defined by Milstead (1960), lies in the area bounded by the 99th and 108th meridians and the 21st and 33rd parallels (Fig. 1). As outlined in Fig. 1, it includes the Chihuahuan

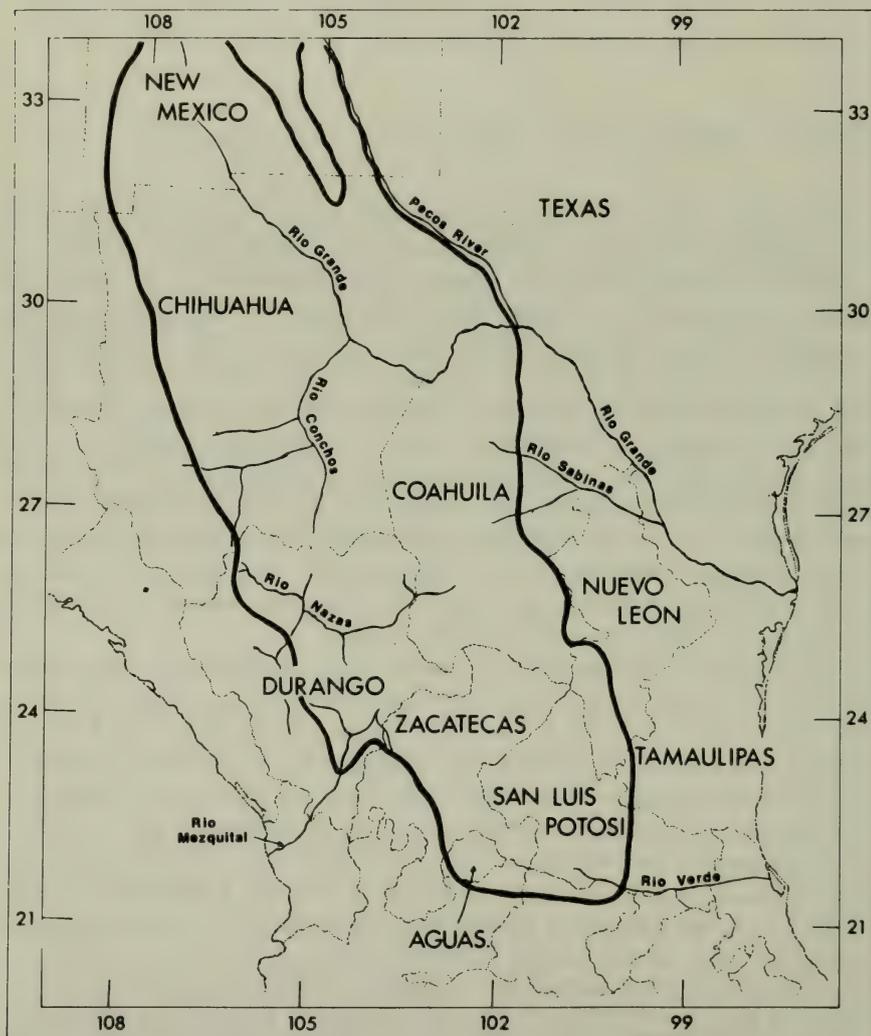


Fig. 1. The Chihuahuan Desert region.

Biotic Province of Blair (1940, 1950) and Dice (1943) plus the Chihuahuan-Zacatecas Province of Goldman and Moore (1945). Politically, the area would include parts of southern New Mexico, all of Texas west of the Pecos River (except for the Guadalupe Mountains), the eastern half of Chihuahua, the western portion of Coahuila and parts of Durango, Zacatecas, Nuevo Leon, San Luis Potosí, Aguascalientes, and Tamaulipas. My concept of the "desert" includes not only the desierto or true desert plains but also the pastizal or grasslands and the chaparral or desert shrub habitats. This is permissible, in my opinion, because, as I will bring out later, almost all of the mammals that occupy the desert also occur in the mesquite-grassland areas. Also included are the scattered boreo-montane plant communities isolated on the tops of many of the higher mountains within the northern portions of the desert.

Eight orders, 24 families, 60 genera, and approximately 119 species of mammals live within the confines of the Chihuahuan Desert region (Table 1).

TABLE 1. Distribution of 119 species in the Chihuahuan Desert region by vegetative zones.

| | Desert | Mesquite- Grassland | Montane | Riparian |
|---|--------|------------------------|---------|----------|
| <i>Didelphis virginiana</i> | | | | X |
| <i>Sorex milleri</i> | | | X | |
| <i>Sorex saussurei</i> | | | X | |
| <i>Notiosorex crawfordi</i> | X | | | |
| <i>Scalopus aquaticus</i> | | | ? | |
| <i>Scalopus montanus</i> | | | X | |
| <i>Choeronycteris mexicana</i> | X | X | | |
| <i>Leptonycteris nivalis</i> | X | X | X | |
| <i>Mormoops megalophylla</i> | X | X | | |
| <i>Myotis auriculus</i> | | X | X | |
| <i>Myotis californicus</i> | X | X | | |
| <i>Myotis leibii</i> | | X | | |
| <i>Myotis lucifugus</i> | | | X | |
| <i>Myotis thysanodes</i> | X | X | X | |
| <i>Myotis velifer</i> ¹ | X | X | | |
| <i>Myotis volans</i> | | | X | |
| <i>Myotis yumanensis</i> | X | X | | |
| <i>Myotis planiceps</i> | | | X | |
| <i>Lasionycteris noctivagans</i> | | | X | X |
| <i>Pipistrellus hesperus</i> ¹ | X | X | | |
| <i>Eptesicus fuscus</i> | | X | X | |
| <i>Lasiurus borealis</i> | | | X | X |
| <i>Lasiurus cinereus</i> | | X | ? | X |
| <i>Lasiurus ega</i> | X | X | | X |
| <i>Nycticeius humeralis</i> | | | | X |
| <i>Euderma maculatum</i> | X | X | | |
| <i>Plecotus phyllotis</i> | | | X | |

TABLE 1. (Continued)

| | Desert | Mesquite- Grassland | Montane | Riparian |
|---|--------|------------------------|---------|----------|
| <i>Plecotus townsendii</i> | X | X | | |
| <i>Antrozous pallidus</i> ¹ | X | X | | |
| <i>Tadarida mexicana</i> ¹ | X | X | | |
| <i>Tadarida femorosacca</i> | X | X | | |
| <i>Tadarida macrotis</i> | | | X | |
| <i>Eumops perotis</i> | X | | | |
| <i>Sylvilagus audubonii</i> ¹ | X | X | | |
| <i>Sylvilagus floridanus</i> | | X | X | X |
| <i>Lepus callotis</i> | | X | | |
| <i>Lepus californicus</i> ¹ | X | X | | |
| <i>Eutamias dorsalis</i> | | | X | |
| <i>Eutamias bulleri</i> | | | X | |
| <i>Ammospermophilus interpres</i> | X | | | |
| <i>Spermophilus mexicanus</i> | X | X | | |
| <i>Spermophilus spilosoma</i> | X | X | | |
| <i>Spermophilus variegatus</i> ¹ | X | X | X | |
| <i>Cynomys ludovicianus</i> | | X | | |
| <i>Cynomys mexicanus</i> | | X | | |
| <i>Sciurus alleni</i> | | X | | |
| <i>Sciurus nayaritensis</i> | | X | X | |
| <i>Sciurus niger</i> | | | | X |
| <i>Sciurus oculatus</i> | | | X | |
| <i>Thomomys bottae</i> | | X | X | |
| <i>Thomomys umbrinus</i> | X | X | X | |
| <i>Geomys arenarius</i> | X | | | |
| <i>Pappogeomys castanops</i> ¹ | X | X | | |
| <i>Perognathus merriami</i> | X | | | |
| <i>Perognathus flavus</i> ¹ | X | X | | |
| <i>Perognathus apache</i> | X | X | | |
| <i>Perognathus hispidus</i> | | X | | |
| <i>Perognathus intermedius</i> | X | X | | |
| <i>Perognathus penicillatus</i> | X | | | |
| <i>Perognathus nelsoni</i> | X | X | | |
| <i>Dipodomys merriami</i> ¹ | X | | | |
| <i>Dipodomys nelsoni</i> | X | | | |
| <i>Dipodomys ordii</i> | X | X | | |
| <i>Dipodomys ornatus</i> | | X | | |
| <i>Dipodomys spectabilis</i> | | X | | |
| <i>Liomys irroratus</i> | | X | | |
| <i>Castor canadensis</i> | | | | X |
| <i>Oryzomys couesii</i> | | | | X |
| <i>Reithrodontomys fulvescens</i> | X | X | | |
| <i>Reithrodontomys megalotis</i> | | X | | |
| <i>Reithrodontomys montanus</i> | | X | | |
| <i>Peromyscus boylii</i> | | X | X | |
| <i>Peromyscus difficilis</i> | | | X | |
| <i>Peromyscus eremicus</i> ¹ | X | X | | |

TABLE 1. (Continued)

| | Desert | Mesquite- Grassland | Montane | Riparian |
|--|--------|------------------------|---------|----------|
| <i>Peromyscus leucopus</i> | | X | | X |
| <i>Peromyscus maniculatus</i> ¹ | X | X | | |
| <i>Peromyscus melanophrys</i> | X | X | | |
| <i>Peromyscus pectoralis</i> ¹ | X | X | | |
| <i>Peromyscus polius</i> | | X | X | |
| <i>Peromyscus truei</i> | | X | X | |
| <i>Baiomys taylori</i> | | X | | |
| <i>Onychomys leucogaster</i> | X | X | | |
| <i>Onychomys torridus</i> | X | X | | |
| <i>Sigmodon fulviventris</i> | | X | | |
| <i>Sigmodon hispidus</i> ¹ | X | X | | |
| <i>Sigmodon leucotis</i> | | X | X | |
| <i>Sigmodon ochrognathus</i> | | X | X | |
| <i>Neotoma albigula</i> ¹ | X | X | | |
| <i>Neotoma goldmani</i> | X | | | |
| <i>Neotoma mexicana</i> | | | X | |
| <i>Neotoma micropus</i> | X | X | | |
| <i>Microtus pennsylvanicus</i> | | X | | |
| <i>Ondatra zibethicus</i> | | | | X |
| <i>Erethizon dorsatum</i> | | | X | |
| <i>Canis latrans</i> ¹ | X | X | X | X |
| <i>Canis lupus</i> | | | X | |
| <i>Vulpes macrotis</i> | X | | | |
| <i>Urocyon cinereoargenteus</i> ¹ | | X | X | |
| <i>Ursus americanus</i> | | X | X | |
| <i>Ursus arctos</i> | | X | X | |
| <i>Bassariscus astutus</i> ¹ | X | X | X | X |
| <i>Procyon lotor</i> | | | | X |
| <i>Nasua narica</i> | | | X | X |
| <i>Mustela nigripes</i> | | X | | |
| <i>Mustela frenata</i> | | X | | |
| <i>Taxidea taxus</i> ¹ | | X | X | |
| <i>Spilogale gracilis</i> ¹ | X | X | | |
| <i>Mephitis mephitis</i> | | X | X | |
| <i>Mephitis macroura</i> | | X | X | |
| <i>Conepatus mesoleucus</i> ¹ | X | X | X | |
| <i>Felis concolor</i> ¹ | | X | X | X |
| <i>Felis pardalis</i> | | | X | |
| <i>Lynx rufus</i> ¹ | | X | X | |
| <i>Tayassu tajacu</i> | X | X | | |
| <i>Odocoileus hemionus</i> | X | | | |
| <i>Odocoileus virginianus</i> ¹ | | X | X | |
| <i>Antilocapra americana</i> | | X | | |
| <i>Bison bison</i> | | X | | |
| <i>Ovis canadensis</i> | | X | X | |

¹Indicates species that occur throughout the entire Chihuahuan Desert region.

PHYSIOGRAPHIC BARRIERS INFLUENCING MAMMALIAN DISTRIBUTION

All mammals, as Hall (1946) and others have pointed out, reproduce geometrically and their tendency, as the population grows, is to push outwardly in search of new living spaces. The ability of a population to expand into new areas depends on its innate dispersal ability, on the

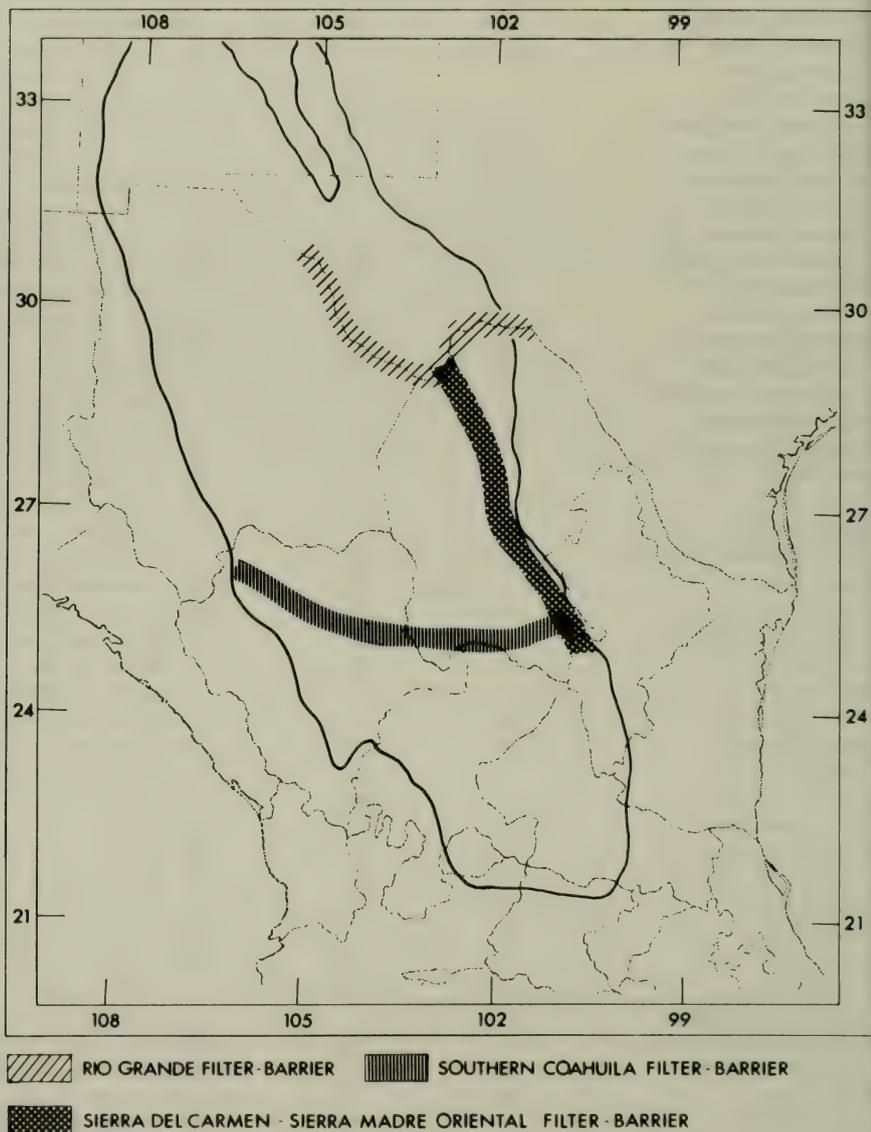


Fig. 2. Major filter barriers in the Chihuahuan Desert.

breadth of environmental conditions it can tolerate, and on the presence of barriers (Vaughn 1972). Barriers may be ecological, with environmental conditions under which a species cannot survive, or more simply physical, such as bodies of water, cliffs or mountains, or rough lava formations (Vaughn 1972). Barriers usually act as filters in that they keep some mammals from occupying all habitats suitable to them but allow others to pass and occupy such areas. Three important filter barriers to the dispersal of mammals in the Chihuahuan Desert may be recognized (Fig. 2). These are: (1) the Sierra del Carmen-Sierra Madre Oriental Axis Filter-Barrier; (2) the Rio Grande Filter Barrier; and (3) the Southern Coahuila-Rio Nazas Filter Barrier. Mammals of the same species that live on either side of these filter barriers often are isolated from each other and differ in morphology to the extent that they are classified as different subspecies.

Sierra del Carmen-Sierra Madre Oriental Axis Filter Barrier

Supposedly at one time, the eastern escarpment of the Cordillera was a continuous mountain chain which separated the Gulf Coastal Plain from the Mesa del Norte; however, subsequent erosion and other geological processes produced gaps and low passes in the escarpment which restricted montane mammals to isolated highlands and produced environments allowing some lowland species to pass from east to west and in the opposite direction (Baker 1956). Most of the faunal interchange across this barrier has been from the west to east with the result that today the eastern foothills of the Sierra del Carmen, Seranias del Burro, and other eastern mountains possess a fauna and flora more characteristic of the Chihuahuan Desert Shrub than of the Tamaulipan Thorn Shrub. Some Chihuahuan Desert mammals which occur east of the montane axis include:

Perognathus nelsoni
P. penicillatus
Dipodomys merriami

Peromyscus eremicus
Neotoma albigula

For other species, the escarpment of the Cordillera has served as a barrier. Small mammals characteristic of the Chihuahuan Desert Shrub, which are not found east of the montane axis, include:

Spermophilus spilosoma
Ammospermophilus interpres
Dipodomys nelsoni

Reithrodontomys megalotis
Peromyscus maniculatus
Neotoma goldmani

At least three small mammals (*Sylvilagus audubonii*, *Lepus californicus*, and *Pappogeomys castanops*) have distinct subspecies on either side of the montane axis.

There has been little westward movement of small mammals from the Tamaulipan Thorn Shrub to the deserts of northwestern Coahuila. However, several Coastal Plain species (including *Spermophilus mexicanus*, *Perognathus hispidus*, *Peromyscus leucopus*, and *Onychomys leucogaster*) occupy typical Chihuahuan Desert Shrub habitat where it is found east of the montane axis (Baker 1956).

Rio Grande Filter Barrier

The Rio Grande, which forms the southern boundary of Texas, is a stream large enough to prevent the dispersal southward of several kinds of land mammals in the northern portion of the Chihuahuan Desert. Conversely, it prevents the dispersal northward of mammals that occur in Mexico. An estimate of the river's effectiveness as a barrier to dispersal can be made in two principal ways. One is to note which species range as far as the river without crossing over to the other side. The second way is to note, within a species which has populations on the two sides, how much if any morphological dissimilarity there is between animals on opposite sides. From this kind of information, it is clear that the headwaters of the Rio Grande are not and have not been a major barrier to the dispersal of mammals. Lower down, in the region of the Big Bend, the Rio Grande is wider and deeper and flows in a permanent channel, a steep-walled canyon. For mammals adapted to live in the desert, this part of the river is an effective barrier to the interchange of individuals between populations of the two sides. In its lower reaches, the river is shallow and its banks are low and do not prevent the passage of mammals.

Two species which illustrate the influence of the Rio Grande on mammalian distribution are the prairie dog (*Cynomys ludovicianus*) and the gray woodrat (*Neotoma micropus*). Both of these species are known from desert areas in Trans-Pecos Texas and northern Chihuahua. However, neither species occurs in the desert areas immediately south of the river in western Coahuila and northeastern Chihuahua. The Mexican ground squirrel (*Spermophilus mexicanus*) is common in the desert areas of Trans-Pecos Texas but is not known from desert areas in northwestern Coahuila and Chihuahua. Lower down, where the river is shallower and its banks are lower, this species has invaded areas of suitable habitat in northeastern Coahuila. The northern distributional limits of at least one mammal correlates with the river. *Dipodomys nelsoni* lives near the Rio Grande in northwestern Coahuila but is unreported from almost identical habitat in Texas, less than 12.9 km (8 miles) to the north (Baker 1956). Several species which occur on both sides of the river have a population on one side of the river so morphologically different from the population on the other side that subspecific status has been accorded each of the geographic variants.

Along this part of the river there is no direct intergradation between the subspecies on the two sides. Mammals which fall within this category are:

| | |
|------------------------------|------------------------------|
| <i>Sylvilagus floridanus</i> | <i>Pappogeomys castanops</i> |
| <i>Thomomys bottae</i> | <i>Dipodomys ordii</i> |

The Southern Coahuila-Rio Nazas Filter Barrier ²

The most conspicuous break in mammalian distribution in the Chihuahuan Desert seems to occur in the vicinity of latitude 25°N (Baker 1956; Baker and Greer 1962). This line separates somewhat the more arid northern desert country (Mesa del Norte) from the humid southern area (Mesa Central). In southern Coahuila this barrier is formed by a series of mountains running east and west, including the Sierra de Parras and Sierra Guadalupe. The passage of many mammals is for the most part blocked by the high escarpment of these mountains. In Durango this barrier is formed by the Rio Nazas. This prominent stream has cut a deep and dissected valley from its headwaters in the Sierra Madre Occidental eastward across the central part of Durango where it joins with the southern Coahuila filter barrier (Baker and Greer 1962).

The southern distributional limits of eight species within the Chihuahuan Desert region correlate almost exactly with latitude 25°N (Fig. 3). These include:

| | |
|-----------------------------------|---------------------------------|
| <i>Eumops perotis</i> | <i>Reithrodontomys montanus</i> |
| <i>Ammospermophilus interpres</i> | <i>Mephitis mephitis</i> |
| <i>Perognathus merriami</i> | <i>Odocoileus hemionus</i> |
| <i>Sigmodon ochrognathus</i> | <i>Bison bison</i> |

The northern distributional limits of four species are reached at latitude 25°N (Fig. 4). These include:

| | |
|--|-------------------------------|
| <i>Sorex saussurei</i> | <i>Peromyscus melanophrys</i> |
| <i>Dipodomys ornatus (= phillipsi)</i> | <i>Sigmodon leucotis</i> |

Ten species occur both north and south of latitude 25°N and have well differentiated subspecies on either side of this line. These include:

| | |
|------------------------------|-----------------------------------|
| <i>Sylvilagus auduboni</i> | <i>P. flavus</i> |
| <i>S. floridanus</i> | <i>P. nelsoni</i> |
| <i>Lepus callotis</i> | <i>Dipodomys ordii</i> |
| <i>Pappogeomys castanops</i> | <i>D. spectabilis</i> |
| <i>Perognathus hispidus</i> | <i>Reithrodontomys fulvescens</i> |

²Since this paper was finished, Petersen (1976, *Southwest. Nat.* 20(4): 495-502) has analyzed in detail the Rio Nazas as a factor in mammalian distribution.

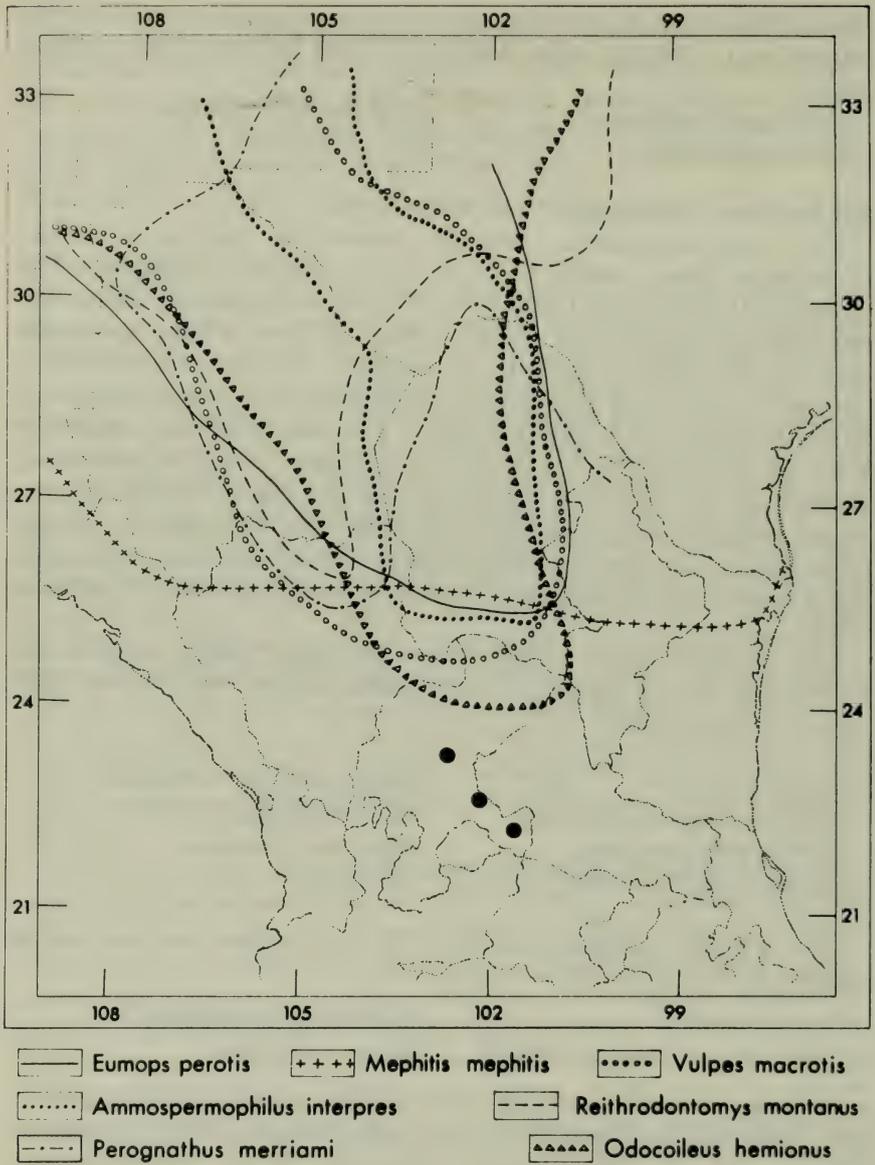


Fig. 3. Southern limits of distribution of seven species of mammals in the Chihuahuan Desert. Since the preparation of this map, three records of *Vulpes macrotis* from Zacatecas (indicated by dots) have come to my attention, indicating the distribution of this species does not stop at latitude 25°N.

Physiographic Barriers of Minor Importance

In addition to the major physiographic barriers, there are minor barriers which influence the local distribution of mammals in the Chihua-

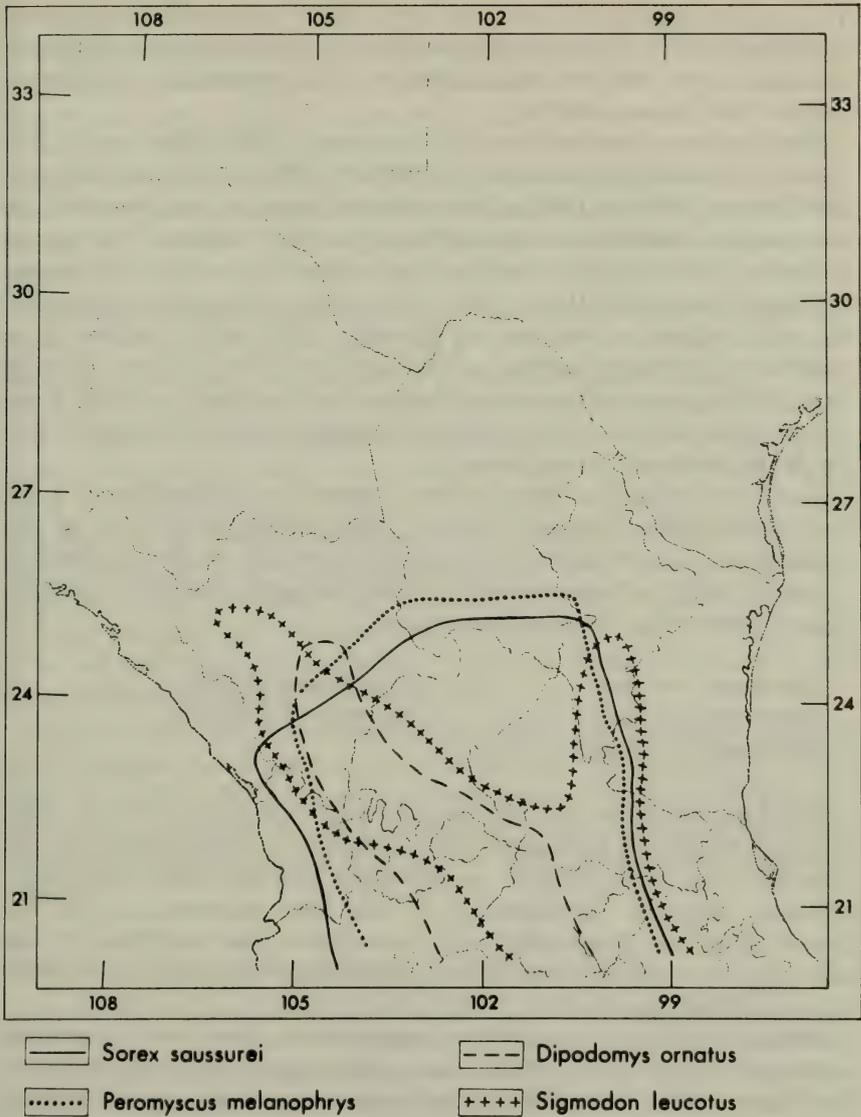


Fig. 4. Northern limits of distribution of four species of mammals in the Chihuahuan Desert.

huan Desert region. In this category, I would include: (1) lava fields; (2) bolsons; and (3) medianos or sand dunes.

Lava Fields. Two extensive lava fields, the Guadiana lava field in Durango and the lava fields of the Tularosa Basin in New Mexico, occur near the fringes of the Chihuahuan Desert. A third, smaller lava field, known as the Kenzin lava beds, occurs in southwestern New Mexico.

The primary influence of the lava flows on the mammalian populations inhabiting them is in providing a means for the selective regulation of dark coat color but they also influence local mammalian distribution (Baker 1960; Benson 1933).

The Guadiana lava field is of Recent origin (within the past 10,000 years) and covers approximately 2330 km² (900 miles²) in south-central Durango (Baker 1960). The main influence of the lava field on mammalian distribution is in increasing suitable habitats for species preferring rocky habitat situations and restricting habitats for species that prefer finer soils (Baker 1960). The lava flow has added considerable rocky habitat to the area. As a result, rock-dwelling rodents have much more extensive habitat on the lava field than is found in most parts of the surrounding areas. Dark-colored rodents, notably *Peromyscus pectoralis* and *Spermophilus variegatus*, seem to be highly successful in this limited environment.

The lava flow has produced no new habitat for soil-dwellers as it has for rock-dwellers. Instead, the lava flow covered over much of the available soil and reduced considerably this habitat in the lava field as compared with surrounding areas. Mammals preferring finer soils adjacent to but not on the lava field include:

| | |
|------------------------------|-----------------------------|
| <i>Dipodomys merriami</i> | <i>Onychomys torridus</i> |
| <i>Perognathus flavus</i> | <i>Sigmodon fulviventer</i> |
| <i>Pappogeomys castanops</i> | |

The Tularosa Basin lava beds and the Kenzin lava beds of New Mexico have influenced mammalian distribution in a similar fashion to the Guadiana lava field; that is, by increasing suitable habitat for rock-dwelling mammals. Furthermore, at least three mammals in the Tularosa Basin have geographic races restricted to the lava flows. These are: *Neotoma albigula melas*, *Perognathus intermedius ater*, and *Peromyscus difficilis griseus*.

Bolsons. A bolson is an enclosed depression or basin without exterior drainage (Thayer 1916). Bolsos occur throughout the desert plains of the Mesa del Norte and are normally quite arid, although during the rainy portions of the year some basins will have standing water or lagunas in their lower parts. Due to the lack of external drainage, their soils usually have a higher than normal alkaline level (Muller 1947). The most extensive bolson on the Mesa del Norte is the Bolson de Mapimi located in south-central Chihuahua and adjacent areas in Coahuila and Durango. This is not just a single bolson but rather a complex of several depressions interspersed with enclosed mountains (Shreve 1942).

The mere presence of bolsos seems to have little direct influence on mammalian distribution. Most of the mountainous areas surrounding the

basins have passes low enough to permit the passage of mammals from one basin to another. There are no species that are strictly confined to bolsons although Nelson's kangaroo rat (*Dipodomys nelsoni*) and Goldman's wood rat (*Neotoma goldmani*) are, for the most part, confined to interior basins in Chihuahua, Coahuila, and Durango (Baker 1963). Local differences of vegetation and soils resulting from the formation of bolsons may actually limit the local distribution of many mammalian species.

Medanos. Medanos or sand dunes are not common in the Chihuahuan Desert. The most extensive dunes, most of which are unstable and active, are located near Samalayuca in northern Chihuahua and the White Sands in the Tularosa Basin of New Mexico. The Samalayuca dunes are the only place in Mexico where the apache pocket mouse (*Perognathus apache*) is known to occur. Three rodents also have pale races which occur only on these dunes. These are: *Onychomys leucogaster albescens*, *Spermophilus spilosoma ammophilus*, and *Dipodomys ordii extractus*. The White Sands are dunes of gypsum and quartz sands. Twenty species of mammals live on the dunes (see Benson 1933, for a complete list) and, of these, two have pale subspecies which are found only on the sands. These are the desert pocket gopher (*Geomys arenarius brevirostris*) and the apache pocket mouse (*P. apache gypsi*).

Areas where stable, less extensive sand dunes are common include El Paso (especially northeast and southeast of the city), east of Torreon in Coahuila, and the El Oro region of Coahuila and Chihuahua. There are no mammals endemic to these places but for several kinds, including *Pappogeomys castanops* and *D. ordii*, the sand dunes provide optimum habitat.

Mammals Occurring Throughout the Chihuahuan Desert

As is true in all major biotic communities, there are some species in the Chihuahuan Desert that are tolerant of a wide range of environmental conditions or have specialized requirements that are met in several biotypes. Physiographic barriers appear to have had little influence on the distribution of these species. There are 24 such eurytopic taxa in the Chihuahuan Desert (Table 1). Among these, carnivores and especially rodents are well represented. Examples among the small, terrestrial rodents that fall in this category are the plateau pocket gopher (*Pappogeomys castanops*), Merriam's kangaroo rat (*Dipodomys merriami*), the cactus mouse (*Peromyscus eremicus*), and the white-throated wood rat (*Neotoma albigula*). The coyote, gray fox, ringtailed cat, spotted skunk, mountain lion, and bobcat are exemplary carnivores in this regard. Four bats and two lagomorphs are in this category, but the white-tailed deer is the only ungulate occurring throughout the area.

VEGETATION, PLANT-MAMMAL RELATIONSHIPS, AND PLEISTOCENE CLIMATIC INFLUENCES

Vegetation

There is considerable vegetational variability within the Chihuahuan Desert region. Many different names and classifications for the major vegetative zones within the area are available. In this report, I have chosen to emphasize only the grossly distinctive types of vegetation of which there are three (adapted from Leopold 1950): desert, mesquite-grassland, and the montane pine-oak forest (Fig. 5). A fourth vegetation type, which is important for many mammals, is the park-like stands of willow (*Salix*), cottonwood (*Populus*), and cypress (*Taxodium*) which occur as riparian growth along permanent water courses in the desert.

Plant-Mammal Relationships

The distribution of many mammals is correlated with the variety and abundance of vegetation which, in turn, depend largely on physiographic and climatic factors. Vegetation is important as a factor influencing mammalian distribution chiefly because the plants furnish shelter and food. The distribution of each mammal in the Chihuahuan Desert with respect to the major vegetation zones is given in Table 1. Of the 119 mammals living in the desert, 52 (44%) actually participate in the desert scrub ecosystem, but, of these, only 11 (21%) are restricted to the desert vegetation zone. The other 41 also occur in one of the other vegetation zones.

The place of most rapid faunal change is between the montane forest and the desert. There is little appreciable change between the grassland and desert vegetative zones. With only a few exceptions, most mammals that occur in the desert also occur in the grasslands and vice versa. The grassland is seen as an area of broad faunal transition rather than an area of distinctness equivalent to that of the forest and desert.

Montane plant communities are scattered throughout the Chihuahuan Desert on the tops of the higher mountain ranges. For mammals inhabiting these communities, the intervening desert constitutes a formidable barrier. The isolated and scattered occurrence of mountainous regions in the desert has resulted in an island-type distribution for the mammals living there. Conversely, for desert mammals the cooler and moister climates of higher altitudes serve as a barrier to their dispersal. Desert species are not often completely isolated, however, because, at lower elevations in the mountains, erosion and other geological processes have produced passes (with desert vegetation) which provide avenues for dispersal of desert mammals.

Different kinds of mammals vary in their responses to vegetation changes. Carnivores and bats (except for the genus *Myotis*) seem less

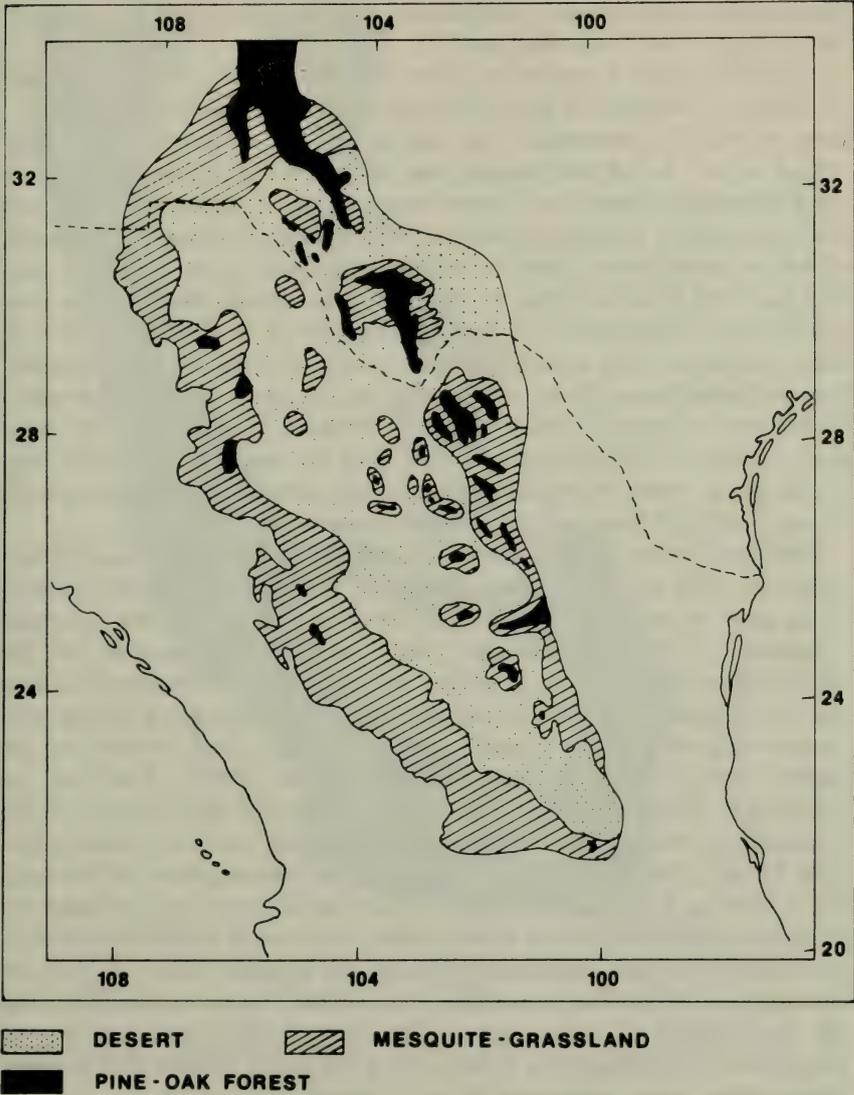


Fig. 5. Major vegetation zones of the Chihuahuan Desert region (adapted from Leopold 1950).

sensitive to vegetational influences than other mammals living in the Chihuahuan Desert. The distribution of rodents, in particular, is heavily influenced by vegetation. Most rodents are directly dependent on plants for food, cover, and home sites (Hooper 1949). Many species depend on a particular floral aggregation, in which both the kind of plant and the growth form of the vegetation are important. A modification in the

distribution of the floral aggregation is followed by a similar change in the occurrence of the rodent kind.

Another aspect of vegetation, other than the type of plant that occurs in an area, is the spacing and size of the plants and the resulting "cover" they provide for mammals. The role in the life of animals played by "plant cover" is not well known, but all species of *Reithrodontomys* in the Chihuahuan Desert are almost always found in places with high and thick vegetation. Similarly, the eastern cottontail (*Sylvilagus floridanus*), which occupies brushy habitats in pine-oak areas, is not known to venture far from brush or other protective cover. While these factors may not in and of themselves be determining factors in the distribution of these mammals, they undoubtedly have an influence on local distribution and abundance. Heavy plant cover, on the other hand, seems not to be favored by most of the heteromyid rodents. For example, the silky pocket mouse (*Perognathus flavus*) lives on sandy desert soils and avoids areas where vegetation is dense; the animal prefers open places where clumps of plant growth are widely scattered.

The distribution of a few kinds of mammals in the Chihuahuan Desert coincides with the occurrence of riparian and heavily wooded habitats along permanent streams that drain the area (Table 1). The opossum (*Didelphis virginiana*) infringes into the eastern segments of the Chihuahuan Desert where it occurs along permanent streams (such as the Rio Grande) and in some irrigated areas. This species is confined to narrow strips of riparian vegetation and seemingly rarely moves into the nearby desert plains or arid foothills (Baker 1956). The rice rat (*Oryzomys couesi peragrus*) is a tropical species that occurs in the Chihuahuan Desert only at a single locality along the Rio Verde in San Luis Potosí (Dalquest 1953). Several species characteristic of the eastern deciduous forests of the United States barely enter the northeastern portions of the Chihuahuan Desert where they occur in riparian habitats or in heavily wooded regions associated with streams. These include the evening bat (*Nycticeius humeralis*), the red bat (*Lasiurus borealis*), and the fox squirrel (*Sciurus niger*). The raccoon (*Procyon lotor*) occurs throughout the Chihuahuan Desert along the major streams and in other places where some permanent water is present.

Pleistocene Climatic Changes

For montane mammals, late Pleistocene climatic changes and concomitant changes in the environment have had a direct effect upon the process of speciation and the patterns of distribution of living species. These climatic changes took place during the time of the last glacial advance (Wisconsin) in the northern part of the continent and continued into the post-Wisconsin period. The Wisconsin glacial period in the Chihuahuan Desert region was marked by a shift to cool, moist climates



Fig. 6. Routes by which montane mammals may have reached the Chihuahuan Desert region.

that supported more mesic environments. The dominant vegetation was a boreal forest of pine, spruce, and fir.

During the Wisconsin period, montane mammals may have reached the Chihuahuan Desert either by way of: (1) a northern route, along the eastern escarpment of the Rocky Mountains in New Mexico and Texas; (2) a trans-plateau route, through mountains across the Mesa del Norte from Durango; or (3) a southern route, along the Sierra Madre Oriental (Fig. 6).

Mammals found on mountains north of latitude 26°N are most closely related to mammals living on mountains to the northwest in New Mexico and other parts of the western United States (Baker 1956). Mammals that fit this category include:

| | |
|---------------------------------------|--|
| <i>Myotis volans</i> | <i>Peromyscus boylii rowleyi</i> |
| <i>M. auriculus</i> | <i>P. difficilis nasutus</i> |
| <i>M. lucifugus</i> | <i>Sigmodon ochrognathus</i> |
| <i>Sylvilagus floridanus robustus</i> | <i>Neotoma mexicana inornata</i> |
| <i>S. floridanus nelsoni</i> | <i>Erethizon dorsatum</i> |
| <i>Eutamias dorsalis</i> | <i>Odocoileus virginianus carminis</i> |

Montane mammals occurring south of latitude 26°N are most closely related either to mammals to the west on the mountains of Durango and Zacatecas or to mammals to the south on the mountains of Nuevo Leon, Tamaulipas, Veracruz, and Hidalgo (Baker 1956). Mammals in this category and having close affinities with those on mountains to the west are:

| | |
|-------------------------|-------------------------------|
| <i>Sciurus alleni</i> | <i>Peromyscus truei</i> |
| <i>Eutamias bulleri</i> | <i>Neotoma mexicana navus</i> |

Mammals in this category and having close affinities with those on mountains to the south are:

| | |
|---------------------------------------|--|
| <i>Sorex saussurei</i> | <i>Peromyscus difficilis petricola</i> |
| <i>Sylvilagus floridanus orizabae</i> | <i>Odocoileus virginianus</i> |
| <i>Reithrodontomys megalotis</i> | <i>miquihuanensis</i> |
| <i>saturatus</i> | |

Evidence that many northern species extended their ranges southward into northern Mexico during the Wisconsin pluvial cycle is provided by the current distribution of relict species in the area (Russell 1969). *Sorex milleri*, a living monotypic species endemic to higher elevations in the Sierra del Carmens of north-central Coahuila and the Sierra Madre Oriental in southeastern Coahuila, is a close relative of *S. cinereus*. Findley (1955) postulated that the southern segment of *S. cinereus*, which expanded southward during the Wisconsin pluvial stage, became isolated in post-Wisconsin time and gave rise to *S. milleri*. The post-Wisconsin shift to aridity resulted in the present disjunct distribution of *S. milleri*. Two other species, *Scalopus montanus* and *Cynomys mexicanus*, have restricted ranges in northeastern Mexico and both species are geographic isolates, separated from the main range of their nearest relatives to the north and northeast (Baker 1956). These isolated populations reached the sites of their present occurrence by range extensions

of the main body of their respective genera when environmental conditions were more mesic than now in the intervening areas (Russell 1969). Both populations were left in isolation by the extirpation of the connecting populations with the post-pluvial trend to aridity.

The disjunct distributional patterns in northern Mexico of *Eutamias dorsalis*, *Neotoma mexicana*, and *Sigmodon ochrognathus* furnish additional information as to the effects of the post-Wisconsin shift to xeric conditions in the lowlands (Russell 1969). All of the aforementioned species are presently restricted to pockets of favorable habitat found at higher elevations in the isolated mountains of the region. Undoubtedly, each of these species enjoyed a more widespread and continuous distribution across the intervening lowlands during the more mesic pluvial stage (Russell 1969).

Montane species were not the only mammals affected by Pleistocene climatic changes. For many desert species, the cooling climate decreased available habitat and fragmented the species into isolated populations, restricted to small desert refugia. Russell (1969) has provided an excellent analysis of the influence of climatic changes on a desert species, the plateau pocket gopher (*Pappogeomys castanops*). According to Russell (1969), the cool, moist Wisconsin climates were unfavorable to *P. castanops* and, as northern boreal vegetation gradually replaced the xerophytic lowland species, *P. castanops* was forced out of most of the areas where it occurred previously and into desert *refugia* (Fig. 7A). There were three main *refugia* which were probably located in the rain shadow of higher mountains where drier environments prevailed (Fig. 7B). *Refugia* A and B were in the rain shadow of the Sierra Madre Oriental; *refugium* A was located to the south of the east-west oriented Sierra Guadalupe-Sierra Parras ranges, and *refugium* B was located to the north of the same escarpment. A third *refugium* (C) probably occurred on the low coastal plain somewhere east of the Sierras. During the period of isolation, these three disjunct populations evolved as separate systems; however, the period of isolation was not long enough for complete reproductive isolation to develop and the trend toward speciation was incomplete. As arid conditions returned at the close of the Wisconsin, *Pappogeomys* dispersed northward again and contact was reestablished between the isolated populations (Fig. 7C). However, interbreeding was restricted between the descendants of certain Pleistocene isolates and intergradation was minimal. Reproductive isolation was especially well developed between Wisconsin populations A and B, and a broad area of sympatry was developed in northeastern Durango and northern Zacatecas (Fig. 7D).

It is feasible that during the Wisconsin other desert species underwent evolutionary histories similar to that of *P. castanops*, which may account for their present distributional and variational patterns.



Fig. 7. Influences of Pleistocene climatic changes on the distribution of *Pappogeomys castanops*. (10A). Possible pattern of distribution of *P. castanops* in the early Wisconsin. (10B). Possible disjunct pattern of distribution of major populations (A-C) of *P. castanops* during the time of pluvial maximum in the Wisconsin. (10C and D). Possible patterns of emigration and gene flow from the three major refugia in the early stages of post-Wisconsin time (all maps taken from Russell 1969).

SUBSTRATES AND EDAPHIC INFLUENCES

Cover and the resulting shelter it provides is an important environmental feature for many mammals. These shelters may be of various

types. In the desert, they may be grouped as shelters in soils, those in and under rocks, and those built in plants. Plant shelters have been considered earlier. The number and kinds of shelters in soils and those in and under rocks are determined to a large extent by edaphic factors which have considerable influence on the geographic distribution of mammals in the Chihuahuan Desert.

Stones, boulders, and rocks are abundant in the Chihuahuan Desert and they are essential environmental features for several mammals such as:

| | |
|-----------------------------------|----------------------------|
| <i>Spilogale gracilis</i> | <i>Perognathus nelsoni</i> |
| <i>Bassariscus astutus</i> | <i>Neotoma mexicana</i> |
| <i>Spermophilus variegatus</i> | <i>N. goldmani</i> |
| <i>Ammospermophilus interpres</i> | |

The presence of rocky cliffs containing cracks and crevices may be positive distributional factors for certain bats (such as *Eumops perotis*, *Tadarida macrotis*, and *Pipistrellus hesperus*) which use these places as roosting sites.

Other kinds of mammals do not respond solely to the presence or absence of rocks, but rather to a combination of rocky situations and some other biotic factor such as vegetation. Bighorn sheep (*Ovis canadensis*) are inhabitants of rough, rocky, mountainous terrain in Trans-Pecos Texas and Coahuila. The mere presence of bluffs and cliffs, however, does not necessarily constitute good mountain sheep range (Davis and Taylor 1939). The vegetation must be of a particular type. Bighorn sheep apparently prefer areas where they have an unobstructed view of the terrain; that is, where low, shrubby, xerophytic vegetation predominates (Davis and Taylor 1939).

Type of soil may be presumed to influence mammalian distribution in a number of ways. As mentioned earlier, many mammals burrow into the soil and construct nests for shelter. For these species, soil type and the texture of the soil are of importance in determining local abundance and occurrence. Soils also affect the distribution of plants which furnish homes as well as emergency shelter, food, and moisture to desert-dwelling mammals.

Muller (1947) recognized four soil types in Coahuila and these may be used in a general way for the entire Chihuahuan Desert. There are stony, immature soils (gravelly soils), light desert soils and alkaline desert soils (fine soils), and dark loamy soils. Stony, immature soils blanket many areas, especially the foothills of the desert ranges. Light desert soils are widespread on the Mesa del Norte. Alkaline soils are present in the undrained basins and result from extreme aridity. Dark loamy soils, characteristic of more humid situations, are generally con-

fined to the higher mountains. Hard surfaces are prevalent throughout the Chihuahuan Desert. Limestone is abundant as are deposits of gypsum and soils heavily impregnated with it. These soils of limestone derivation support primarily desert shrub vegetation. Outcrops of granite are uncommon at elevations occupied by the desert and these igneous soils support primarily grassland vegetation.

Mammals living in the Chihuahuan Desert vary greatly in their tolerances to different types of soil. Some species, such as the coyote (*Canis latrans*), seem to tolerate all kinds of soil. However, those mammals which habitually live underground are more or less limited according to their digging ability in relation to the soil texture. Four kinds of pocket gophers (*Thomomys bottae*, *T. umbrinus*, *Pappogeomys castanops*, and *Geomys arenarius*) occur in the Chihuahuan Desert and their distribution is primarily controlled by soil conditions. *Thomomys* is extremely adaptable as regards habitat. They occur in soils ranging from loose sands to hard, often clayey soils and in vegetative zones grading from dry desert to montane meadows. Unlike *Thomomys*, *Pappogeomys* is partial to deep, sandy or silty soils that are relatively free from rocks. As a result, *Pappogeomys* often is partially isolated in small populations where suitable habitat is surrounded on one or more sides by thin, rocky soils of uplands and mountains (Baker 1956). *Geomys arenarius* occurs only in southern New Mexico and adjacent places in Texas and Chihuahua. This gopher seems to prefer sandy river bottom habitats and cannot tolerate clayey or gravelly soils. For the most part, the three genera are mutually exclusive in their distribution. However, in some places (such as western Texas), they occur in the same general area. Under such conditions, *Thomomys* usually occupy the shallower, rocky soils in the mountains, *Geomys* lives in the deep sands along the rivers, and *Pappogeomys* utilizes the areas in between (Davis 1966).

Perhaps the most striking examples of mammalian preferences for specific types of substrate in the Chihuahuan Desert are to be found among the heteromyid rodents. In most desert localities no single species of heteromyid rodent occurs on all types of substrate, and some species are tightly restricted to a single type of soil. An excellent analysis of the influences of substrates on local distribution and abundance of three species of pocket mice (*Perognathus merriami*, *P. penicillatus*, and *P. nelsoni*) was conducted by Porter (1962) in the Big Bend Region of Texas. He showed that pocket mice were not restricted to any specific textural types of soil, although some soil types were preferred to others (Fig. 8). The desert pocket mouse (*P. penicillatus*) preferred deep loams and sandy loams and was rarely found on shallow, rocky, sandy, and sandy clay loams. Nelson's pocket mouse (*P. nelsoni*) reached its peak of abundance on shallow soils made up of sandy loams and loams. *Perognathus merriami* attained its maximum abundance on deep soils

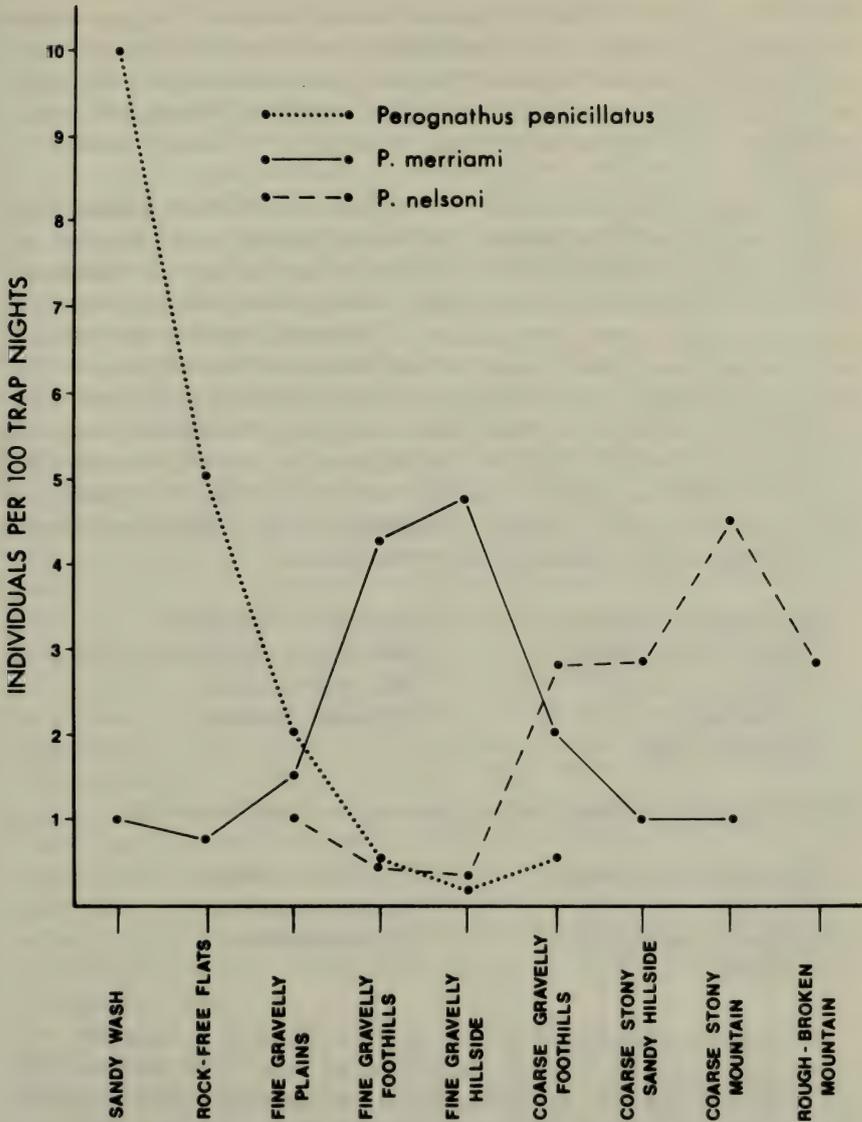


Fig. 8. Average number (individuals per 100 trap nights) of three species of *Perognathus* captured on nine habitat types in the Big Bend area (taken from Porter 1962).

containing clays (sandy clay loams) and was uncommon on soils preferred by the other two species of pocket mice. Size and abundance of rocks present in the soil appeared to be the most significant factors controlling the distribution and abundance of pocket mice (Porter 1962). The desert pocket mouse preferred deep, rock-free soils (less

than 5% gravel). Nelson's pocket mouse attained its maximum abundance on shallow soils containing more than 70% gravel, large rocks, and boulders. Merriam's pocket mouse was found most commonly on desert erosion pavement soils containing at least 50% rocks, by weight, very few of which were as large as 7.6 cm (3 inches) in diameter.

Fine, sandy soils are common throughout much of the Chihuahuan Desert where they often mantle the coarser, gravelly or rocky soils occurring on the foothills of desert mountain ranges. In such situations, soil type often is the important factor in determining which species will occur in a given area. Some species of mammals burrow into the soil while others make their homes in rock fissures or beneath stones. The sand-dwellers might have difficulty in hopping through rock piles where there is little or no soil between the closely packed boulders and, conversely, rock-dwellers would be out of place on a sand dune. For the mammals inhabiting sandy soils, the thin, rocky soils of uplands and mountains constitute a barrier. Mammals in the Chihuahuan Desert which commonly live in sandy, deep soils include:

| | |
|-------------------------------|-------------------------------|
| <i>Spermophilus spilosoma</i> | <i>Onychomys leucogaster</i> |
| <i>Cynomys ludovicianus</i> | <i>Peromyscus maniculatus</i> |
| <i>Perognathus flavus</i> | <i>Neotoma micropus</i> |
| <i>P. penicillatus</i> | <i>Sigmodon hispidus</i> |
| <i>Dipodomys ordii</i> | |

Mammals which seem to prefer rocky or gravelly soils include:

| | |
|--------------------------------|---------------------------|
| <i>Perognathus intermedius</i> | <i>Onychomys torridus</i> |
| <i>P. nelsoni</i> | <i>Sigmodon leucotis</i> |
| <i>Dipodomys spectabilis</i> | <i>S. ochrognathus</i> |
| <i>D. nelsoni</i> | |

A few kinds of mammals are tolerant of both sandy and gravelly soils. *Peromyscus eremicus*, for example, prefers rocky soils but will also occur on sandy and clay soils. Where clay soils predominate, this is usually the only species of *Peromyscus* present (Baker 1956). *Dipodomys merriami* lives on desert flats and in sandy areas but is equally abundant in coarser soils and rocky situations (Baker 1956). The ability of this species to survive in most xeric situations has probably accounted for its wide distribution within the Chihuahuan Desert.

CLIMATE (MOISTURE AND TEMPERATURE)

Moisture, in the form of precipitation, affects the distribution of mammals indirectly through regulation of the number and size of streams

and lakes, regulation of amount of soil-moisture, and regulation of the kind of flora. Temperature is influential chiefly as it affects the vegetation of an area. Different slope exposures with slightly different temperatures might shelter different mammal species as a result of different vegetation cover (Burt 1938). Since, within the Chihuahuan Desert, there is a wide annual fluctuation in temperatures and precipitation, one might suspect that climate could have a direct effect on the geographic distribution of some mammals. However, in comparing distributions of mammals occurring in the desert with temperature and rainfall patterns, I have not been able to ascertain any direct influence of climate upon the distribution of most mammals.

Several authors (Nelson and Goldman 1934; Davis 1940a, b; Baker 1953) have suggested that *Pappogeomys* is replacing *Thomomys* in parts of Mexico and western Texas as a result of changing climatic conditions. Reichman and Baker (1972) studied the distributional relationships of *Pappogeomys* and *Thomomys* from 1968 to 1970 in a zone of sympatry along Limpia Creek in the Davis Mountains. From early 1969 until April 1970, the Davis Mountains received little or no rain, and Limpia Creek did not flow regularly. As the area became drier, *Thomomys*, which once occurred from near the stream bed to the foot of the rocky bluffs lining the canyon, moved closer to the stream and *Pappogeomys* spread into the vacated areas. Reichman and Baker (1972) attributed the recession of the range of *Thomomys* and the subsequent advance of *Pappogeomys* in part to the decrease in amount and change in patterns of precipitation in the Davis Mountains. As precipitation decreased, soil moisture also should have decreased and *Pappogeomys*, being adapted to drier soil, would be favored. Furthermore, as the Davis Mountains became drier, xerophytic plants probably became commoner, which would have favored *Pappogeomys*. The results of Reichman and Baker's analysis on a smaller scale may explain some of the larger scale changes in distribution between these two genera of pocket gophers in the Chihuahuan Desert.

SURFACE WATER

Many desert mammals (such as kangaroo rats and pocket mice) can live their entire lives without procuring a drink of free water. They simply derive their water by metabolic means or from succulent vegetation. For other mammals, however, surface water is necessary for survival in the desert and, thus, may act as a positive distributional factor. Fresh-water streams and rivers are essential to the existence of several mammals in the Chihuahuan Desert. The beaver (*Castor canadensis*) and the muskrat (*Ondatra zibethicus*) occur in the desert only along the Rio Grande and Rio Pecos and their tributaries. These mammals must have access to a stream for the building of safety retreats. The racoon

(*Procyon lotor*) occurs adjacent to most of the major streams and lagunas in the desert where the animal procures much of its food along the water's edge. Almost all bats require drinking water and many species, especially in arid regions, congregate along streams and pools where water is available. The scattered occurrence of these watering places in the desert could influence the local distribution of bats.

Other mammals for which surface water may play a role in their distribution include:

Urocyon cinereoargenteus

Nasua narica

Felis pardalis

Tayassu tajacu

Odocoileus virginianus

FOOD

Food is undoubtedly often a limiting factor in the distribution of mammals. However, most mammals when living in the proper type of plant association are able to find a few species of plants upon which they may feed. There are few instances in the Chihuahuan Desert where mammals seem limited by availability of food. If the preferred food items are not available, most species are capable of shifting to alternative food sources. Two mammals in which availability of a particular food item may influence distribution are the desert fox (*Vulpes macrotis*) and the black-footed ferret (*Mustela nigripes*). The desert fox generally lives in the open desert where its presence and relative numbers are pretty much controlled, under natural conditions, by the presence and abundance of nocturnally active rodents (Davis 1966). The range of the desert fox coincides closely with that of large kangaroo rats which are favored food items of these foxes (Fig. 9). The black-footed ferret, now extinct in the Chihuahuan Desert, probably once occurred throughout Trans-Pecos Texas where it lived in close association with the prairie dog upon which it preyed.

INTERSPECIFIC COMPETITION

Competition between closely related species could affect habitat selection of mammals, especially in areas where the related forms occur sympatrically. Under strenuous conditions of interspecific competition, one species could completely exclude the other from a particular environment. Thus, interspecific competition is a factor that could influence local distributional patterns of mammals. However, at the present time, little is known of the effects of competition on mammalian distribution within the Chihuahuan Desert.

One group of mammals living in the Chihuahuan Desert for which interspecific competition almost certainly plays an important role in determining patterns of distribution is the pocket gopher. According to

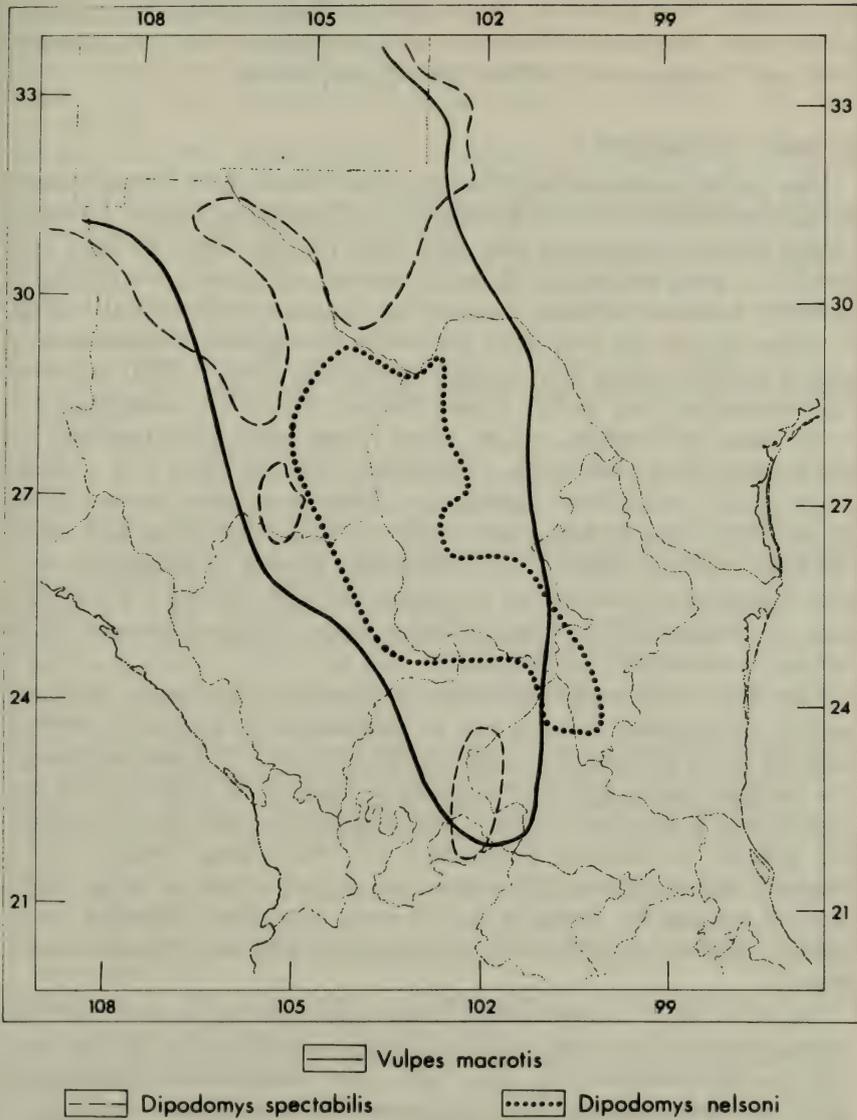


Fig. 9. Distribution of the desert fox (*Vulpes macrotis*) with respect to the distribution of two species of large kangaroo rats (*Dipodomys spectabilis*, *D. nelsoni*).

Russell (1968), interspecific competition in conjunction with edaphic factors is more effective in determining the pattern of distribution of *Pappogeomys castanops* than are climate, topography, or vegetation. It has often been noted that where the ranges of *Pappogeomys* and *Thomomys* meet, the populations do not become sympatric but tend to exclude

one another from particular environments (Russell 1968; Davis 1966). Under such conditions, *Thomomys* usually prefers rocky and gravelly soils, and *Pappogeomys* is limited to deep, sandy soils.

HUMAN ACTIVITIES

Man and his associated activities must also take a place among factors influencing mammalian distribution in the Chihuahuan Desert. Environmental changes associated with man have proved both beneficial and harmful to other mammals. Of the detrimental influences, overgrazing is probably the most serious. Overgrazing has destroyed optimal habitat for some species and may have altered the ecological interrelationships among certain species. For example, Baker and Greer (1962) reported that white-sided jack rabbits (*Lepus callotis*) have been diminishing for many years in Durango and in many places have been replaced by black-tailed jack rabbits (*L. californicus*). White-sided jack rabbits prefer grassy areas where grazing by domestic animals has not been severe. According to Baker and Greer (1962), overgrazing and other ranching activities, which have altered plant growth on grasslands, may have improved the habitat for *L. californicus* and reduced it for *L. callotis*. Anderson (1972) expected that a similar situation between these two species existed in Chihuahua.

Man kills other mammals both for food and recreation. Without proper management, hunting can be detrimental to a species and this appears to be the case for some mammals in the Chihuahuan Desert. For example, the mule deer (*Odocoileus hemionus*), in Coahuila and San Luis Potosí, is in danger of being exterminated because the population has become so reduced in numbers by overhunting (Baker 1956). Similarly, the black bear (*Ursus americanus*) population is being slowly reduced because the animal is shot at every opportunity. Hunting black bear is a popular sport for both Mexicans and hunters from the United States.

Not all of man's activities have been detrimental to mammals and in some cases man has even improved habitat conditions for certain species. For approximately the past 1000 years, Indians have constructed rock fences throughout the Chihuahuan Desert. These fences are favored home sites for many rodents (for example, *Spermophilus variegatus* and *Peromyscus pectoralis*), and, where they are positioned next to overgrazed fields, they often provide the only suitable habitat for rock-dwelling species.

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Reproductive Strategies in Desert Rodents

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Desert environments typically are considered relatively harsh, requiring adaptations to extremes of temperature and precipitation, and highly variable, thus offering populations few predictable parameters to depend upon. Rodent populations have solved successfully the problem of extremes through various behavioral and physiological strategies. Nocturnality, denning, and burrowing provide protection from temperature and humidity extremes. Water requirements have been solved by kidney modifications which make best use of metabolic water (heteromyids), or behaviorally through use of succulent vegetation (*Neotoma*), or insectivory/omnivory (*Spermophilus*, *Onychomys*).

The nature of the harshness of desert environments seems well understood, and elaboration of various physiological and behavioral alternatives has proceeded at a reasonable pace (e.g., Bartholomew and Cade 1957; Chew and Butterworth 1964; Eisenberg 1963; Schmidt-Nielsen 1964). It is important to note that researchers have drawn this information from a biological level of organization that concentrates on individual animals.

Obtaining information on population-level parameters is more difficult, as evidenced by the relative lack of detailed demographic studies on desert rodents. Our purpose is to review appropriate vital statistics pertaining to desert rodent populations. We will query some of these data through a simulation model and, finally, will discuss reproductive strategies in light of current ecological speculation. We have concentrated on Chihuahuan Desert rodents, but also have drawn freely from other North American deserts where necessary.

Evolving an effective demographic strategy in desert environments requires adaptations that allow a rodent population to take advantage of good conditions, as well as being able to sustain varying periods of resource shortage. It is the unpredictability of desert environments that

TABLE 1. Relative monthly variability for precipitation and temperature between a typical desert climate (Deming, New Mexico) and a strongly seasonal temperate climate (Lansing, Mich.). Data cover period from 1950 to 1973 (U.S. Weather Bureau 1950-73).

| Month | Precipitation | | | | | | Temperature | | | | | |
|-----------|---------------|------------------------------|-----------|------------------------------|-----------|------------------------------|-------------|------------------------------|-----------|------------------------------|-----------|------------------------------|
| | Deming | | | Lansing | | | Deming | | | Lansing | | |
| | Mean (Cm) | Coefficient of Variation (%) | Mean (Cm) | Coefficient of Variation (%) | Mean (Cm) | Coefficient of Variation (%) | Mean (°C) | Coefficient of Variation (%) | Mean (°C) | Coefficient of Variation (%) | Mean (°C) | Coefficient of Variation (%) |
| January | 1.02 | 99.33 | 4.46 | 48.78 | 5.24 | 34.88 | -5.28 | 45.10 | | | | |
| February | 1.02 | 133.48 | 4.25 | 57.07 | 7.36 | 26.19 | -4.33 | 47.10 | | | | |
| March | 0.91 | 143.86 | 5.55 | 37.74 | 10.67 | 14.94 | 0.28 | 770.99 | | | | |
| April | 0.48 | 174.91 | 7.54 | 32.44 | 14.89 | 9.51 | 7.83 | 23.39 | | | | |
| May | 0.27 | 188.02 | 6.74 | 52.19 | 19.75 | 5.74 | 13.83 | 13.43 | | | | |
| June | 0.72 | 132.58 | 8.95 | 46.28 | 25.07 | 4.80 | 19.43 | 7.67 | | | | |
| July | 5.30 | 52.44 | 7.71 | 52.88 | 27.06 | 3.75 | 21.38 | 6.06 | | | | |
| August | 4.82 | 60.35 | 7.38 | 36.14 | 25.67 | 3.75 | 20.62 | 6.91 | | | | |
| September | 2.75 | 136.05 | 6.59 | 62.17 | 22.49 | 4.74 | 16.53 | 6.89 | | | | |
| October | 1.73 | 102.62 | 5.33 | 63.21 | 16.53 | 7.82 | 10.90 | 19.50 | | | | |
| November | 0.81 | 141.55 | 6.06 | 44.11 | 9.65 | 14.98 | 3.47 | 55.55 | | | | |
| December | 1.28 | 115.39 | 5.36 | 54.18 | 5.42 | 28.96 | -2.70 | 80.50 | | | | |

populations must contend with rather than variability per se.

For example, temperature and precipitation records for Deming, New Mexico (northern Chihuahuan Desert), and Lansing, Michigan (strongly seasonal north temperate climate), indicate a pattern of variation and predictability. We expected the desert environment to be less seasonal and highly variable, and the north temperate region to be highly seasonal and less variable. Coefficients of variation for monthly means serve our example. For precipitation, the north temperate seasonal region is more variable 1 out of 12 months, and for temperature, more variable for all 12 months of the year (Table 1). Thus, desert environments, at the least, appear no more variable than strongly seasonal environments.

Biologically, however, such variation is relative. Populations faced with limiting thresholds must learn to track critical resources, while populations presented with an abundant resource may turn their attentions elsewhere. Understanding resource thresholds and evaluating resource predictability based on these thresholds are critical to understanding control of desert rodent populations.

Assuming a threshold level of at least 2.54 cm of precipitation in either September, October, or November as being critical for subsequent primary production (after Mojave Desert data of Beatley 1974), and thus critical for desert rodent populations (discussion and references below), the nature of the desert environment can be seen more clearly. The probability of a failure in primary production is 0.0031 in Lansing, Michigan, and 0.3023 in Deming, New Mexico. We expect the desert rodents to contend with this resource shortage about 3 out of 10 years, while their northern counterparts may in effect ignore this possibility. It is not simple variability that is important, but rather predictability regarding some threshold level (Fig. 1).

A summary of population statistics for 11 genera containing 29 species of Chihuahuan Desert rodents is given in Table 2. Some species were excluded because of lack of information. Numbered references cited in Table 2 (in parentheses) are given in Appendix I, which may be cross-referenced with the bibliography.

Information from Table 2 can be summarized as follows. Most species have been reported in breeding condition from 7-10 months of the year, a few may be found breeding during all 12 months. This condition reflects variation in when these rodents breed rather than the length of any given breeding season, which is probably much shorter. Most species have the capacity for multiple litters within a breeding season. Litter sizes average 2-5 with a range of 1-12. Densities are highly variable, and no general pattern is apparent. Annual probabilities of survival are usually low (10-15%). Body sizes are small to medium, being generally less than about 200 g. All are iteroparous.

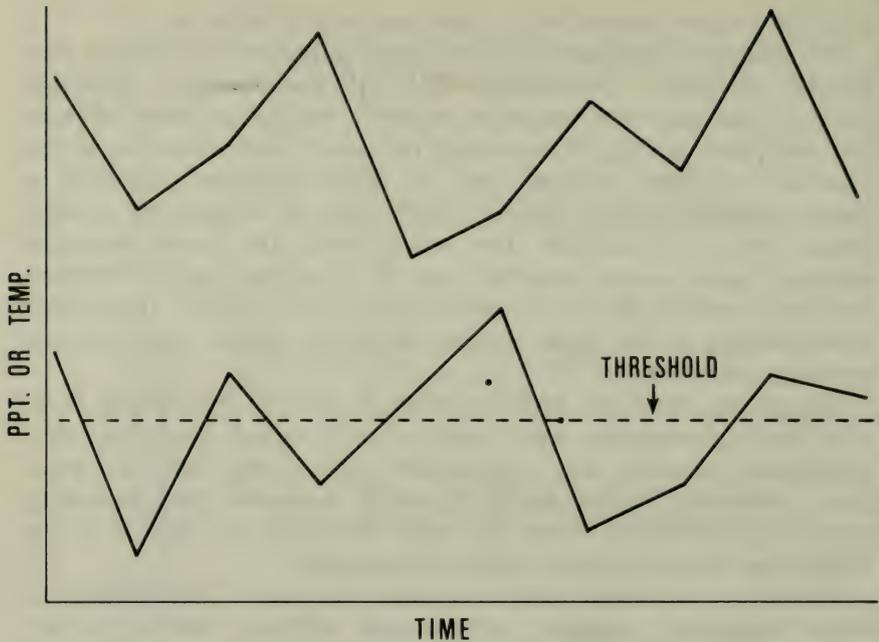


Fig. 1. Resource variability with super-abundance, and predictability with reference to a given threshold level. See text for discussion.

These factors can be combined into several fundamental demographic parameters. In order to explore reproductive and survival potentials in a typical desert rodent, we have posed the following questions: (1) How rapidly can a population respond to varying conditions (specifically, what are the effects of varying age-specific breeding structure, and breeding intensity)? (2) Given a pause in breeding, how long can the population wait before it becomes ecologically extinct? Computer simulations were utilized as an approach to these questions.

Simulations were conducted on a modified Leslie matrix model (Leslie 1945, 1948). Modifications utilized for these runs included variable age-specific breeding rates and a stochastic exchange between age classes. Only whole animals are allowed to proceed into the subsequent age class, thus runs with the same starting conditions produce slightly different results. Descriptions of these modifications must be published elsewhere (Tipton and Conley, unpubl. data). Survival and fertility data on *Perognathus formosus* were taken from French et al. (1974). These data are quite complete, and represent a typical desert rodent.

Survival rates for 1965 plot A were extrapolated to a maximum age of 4 years (from Fig. 11, French et al. 1974). Age-specific litter sizes were taken from Table 10 of French et al. (1974). Because of the absence of

sex-specific survival rates, we assumed a 1:1 sex ratio and included only females in the simulations. We utilized two breeding periods, each of 3-months duration (April-June and July-September). The two periods of nonreproductive activity were October-December and January-March. This pattern closely approximates actual reproductive patterns, and allowed us to include breeding young-of-the-year in several simulations. Females were allowed only one litter per breeding period, thus our estimates of maximum rates of increase are generally conservative. All simulations were initiated with a density of 50 animals structured to approximate a stable-age distribution. Simulations were run for 5-year durations with varying patterns of reproductive activity.

Among the various demographic changes that can affect reproductive output, changes in the percent of females in breeding condition and age at sexual maturity were considered. French et al. (1974) found a positive correlation between increasing litter size and increasing breeding rates; however, litter sizes were held constant over time because of the lack of sufficient age-specific litter data.

With increasingly favorable environmental conditions, a higher percentage of the population becomes reproductively active. Under the most favorable conditions, young-of-the-year, offspring from the first breeding period, also reproduce (French et al. 1974). The population response to these changing breeding rates is illustrated in Fig. 2. Four-fold population increases within one year are possible with 90% of the adults and no young reproducing, or with 50% of the adults and 50% of the young-of-the-year reproducing. Assuming that a high percentage of adults will be reproductively active under conditions when young reproduce, an instantaneous rate of increase of 0.97 can be obtained with 90% of the adults and young-of-the-year reproducing. It should be noted that higher population growth rates would result if litter sizes do increase with increasing breeding rates.

Instantaneous rates of increase reflect the ability of a population to respond to favorable conditions. With a reproductive pattern of one year breeding, one nonbreeding, and three breeding, we searched for effects of varying percent reproductive activity and young-of-the-year as a breeding component. With constant survival and fertility rates, terminal densities varied from 26,000 for the 90% breeding population to 427 for the 50% breeding population (excluding young-of-the-year). Rates of increase varied from 0.31 to 0.45. Allowing young-of-the-year to breed approximately doubles the instantaneous rate of increase in the 50% breeding simulation (Fig. 2).

The *Perognathus formosus* populations in the Nevada desert respond strongly to the absence of primary production at the beginning of the breeding season. During 2 of the 9 years these populations were studied, reproductive activity was essentially zero. Thus, the populations waited,

TABLE 2. Selected reproductive characteristics of Chihuahuan Desert rodent species.

| Species | Breeding Season Length ^a | Litters Per Year | Litter Size | |
|----------------------------------|-------------------------------------|-------------------------|--------------------------------------|--|
| | | | Mean | Range ^b |
| FAMILY SCIURIDAE | | | | |
| <i>Spermophilus pilosoma</i> | 6 | 2 | 5.6 | 3-9 |
| | (1) | (1,3) | (2,11) | (1,2,3,4,11) |
| <i>Spermophilus mexicanus</i> | 1.5 | | 6.3 | 5-10 |
| | (1,3,10) | | (1,2,10) | (1,2,10) |
| <i>Spermophilus variegatus</i> | 5 | 2 | 5.69 | 5-8 |
| | (1) | (1,3) | (2,11, 12,14) | (1,2,11, 12,13,14) |
| FAMILY GEOMYIDAE | | | | |
| <i>Thomomys bottae</i> | 10.6 | 1-3 | 4.58 | 1-16 |
| | (3,15,16, 17,18) | (16,18,22, 23,24) | (2,4,16,17, 18,19,20, 21,22,24) | (2,3,4,16, 17,18,19, 20,21,22) |
| FAMILY HETEROMYIDAE | | | | |
| <i>Perognathus flavus</i> | 8.0 | ≥ 2 | 4.0 | 2-6 |
| | (3,25) | (1,12) | (26,27) | (1,3,12, 26,27) |
| <i>Perognathus penicillatus</i> | 5.5 | ≥ 1 | 3.8 | 2-6 |
| | (3,28) | (28) | (2,27, 28,29) | (2,3,14, 27,28,29) |
| <i>Perognathus apachei</i> | | | | |
| <i>Perognathus nelsoni</i> | ≥ 5.0 | | 2.65 | 2-5 |
| | (2) | | (2,14) | (2,14) |
| <i>Perognathus merriami</i> | | | 4.0 | 4-4 |
| | | | (2) | (2,3) |
| <i>Dipodomys spectabilis</i> | 7.8 | 1-3 | 2.3 | 1-4 |
| | (1,3, 31,32) | (3,32) | (31,32) | (1,3, 31,32) |
| <i>Dipodomys merriami</i> | 7.3 | >2 | 2.49 | 1-5 |
| | (1,2,11,18, 28,33,34, 35,36,38) | (18,26,28, 33,35,37 38) | (11,14,18,26, 27,28,33,34, 35,36,38) | (1,2,3,11,14, 18,26,27,28, 33,34,35,36,38) |
| <i>Dipodomys ordii</i> | 6.8 | >1-2 | 3.16 | 1-6 |
| | (18,25, 42,43) | (12,18,30, 35,42,45) | (2,4,12, 18,26,35, 42,44,45) | (1,2,4,12, 18,26,35, 42,44,45) |
| <i>Dipodomys nelsoni</i> | | | 2.0 | 2-2 |
| | | | (14) | (14) |
| FAMILY CRICETIDAE | | | | |
| <i>Reithrodontomys megalotis</i> | 12.0 | >2-7 | 4.25 | 1-7 |
| | (3,47) | (48,49,50) | (3,11,18, 48,49) | (3,11,18, 48,49,50) |
| <i>Reithrodontomys montanus</i> | 12 | 5 | 2.93 | 2-5 |
| | (3) | (51) | (3,51) | (3,48,51) |

References are numbered (in parentheses), and correspond to citation list in Appendix I.

| Maximum Percentage Adult Females Breeding ^c | Age at Sexual Maturity | Density (Animals per Hectare) | | Annual Probability of Survival | Average Life Expectancy ^e |
|--|------------------------------|--|---------------|--------------------------------------|---|
| | | Mid-range ^d | Maximum | | |
| | | 1.98 (5,6,7, 8,9) | 12.68 (5) | | |
| 50% - 75% (16,17, 19,24) | 3 Mo. (16) | 26.26 (15,18,24) | 84.00 (24) | M = .42 F = .69 (62) | M _{e₆} = 7.6 Mo. F _{e₆} = 12.3 Mo. (24) |
| | | 1.83 (5,6,7,9) | 9.42 (5) | | |
| | | 1.12 (5,6,7, 29,30) | 3.62 (5) | | |
| | | .36 (6) | .36 (6) | | |
| | | 2.41 (5,6,8, 31,32) | 14.86 (5) | .14-.25 (31) | |
| 67% (30) | <2 Mo. (33) | 4.42 (5,6,7,8, 30,37,39, 40,41) | 18.29 (39) | .12-.19 (37) | e ₁ = 6.21- 6.88 Mo. (41) |
| 94% (30) | 2-3 Mo. (43,45) | 7.29 (5,6,8,9, 30,46) | 52.54 (5) | | |
| | >4 Mo. (49) | .93 (5,7) | 1.45 (5) | | |
| | 2 Mo. (3) | 9.66 (5,52) | 32.97 (5) | | |

TABLE 2 (Continued)

| Species | Breeding Season Length ^a | Litters Per Year | Litter Size | |
|-------------------------------|-------------------------------------|------------------|--|--|
| | | | Mean | Range ^b |
| <i>Peromyscus maniculatus</i> | 9.2 | ≥3-10.4 | 4.69 | 1-9 |
| | (1, 3, 15, 18, 53) | (15, 55, 58) | (2, 3, 11, 18, 53, 54, 55, 56, 57, 58) | (1, 2, 3, 4, 11, 13, 18, 53, 54, 55, 56, 57, 58) |
| <i>Peromyscus eremicus</i> | 9.5 | ≥2-7.3 | 2.86 | 1-5 |
| | (1, 2) | (1, 63) | (2, 3, 12, 18, 28, 54, 63) | (1, 2, 3, 12, 18, 28, 54, 63) |
| <i>Peromyscus boylii</i> | 6.0 | ≥2 | 3.95 | 2-6 |
| | (1, 15, 53) | (1, 12) | (2, 11, 14, 15, 18, 53) | (1, 2, 3, 11, 12, 13, 14, 15, 18, 53) |
| <i>Peromyscus nasutus</i> | 8.0 | | 3.75 | 3-6 |
| | (1, 3) | | (1, 2, 12) | (1, 2, 3, 12) |
| <i>Peromyscus difficilis</i> | >2 | ≥3 | 2.83 | 2-3 |
| | (1, 2, 14) | (13) | (13, 14) | (13, 14) |
| <i>Baiomys taylori</i> | 12 | ≥9 | 2.61 | 1-5 |
| | (3, 65) | (65) | (3, 65) | (3, 65) |
| <i>Baiomys musculus</i> | 12.0 | | 2.63 | 1-4 |
| | (3) | | (3, 13) | (3, 13) |
| <i>Onychomys leucogaster</i> | 6.4 | ≥2-5.1 | 4.00 | 1-6 |
| | (1, 3, 4, 25, 58, 66) | (12, 58, 68) | (18, 58) | (1, 4, 12, 18, 48, 50, 58, 67, 68) |
| <i>Onychomys torridus</i> | 7.2 | 2-3 | 3.73 | 2-6 |
| | (1, 3, 30, 66) | (1) | (1, 2, 11, 18, 34) | (1, 2, 3, 11, 12, 18, 34) |
| <i>Sigmodon hispidus</i> | 8.3 | >2 | 5.63 | 2-12 |
| | (3, 69, 70) | (1, 69) | (2, 9, 18, 48, 68, 69, 70, 71, 72, 73) | (1, 2, 9, 18, 48, 68, 69, 70, 71, 72, 73) |
| <i>Sigmodon fulviventer</i> | | | 3.50 | 3-4 |
| | | | (3) | (3) |
| <i>Neotoma albigula</i> | 9.8 | ≥2 | 1.87 | 1-4 |
| | (1, 2, 3, 25, 75, 76) | (1, 3, 12) | (2, 3, 11, 75, 76) | (2, 3, 11, 12, 75, 76) |
| <i>Neotoma micropus</i> | 6.3 | 1-5 | 2.25 | 1-4 |
| | (3, 4, 78) | (3, 4, 12, 78) | (2, 4, 78, 79) | (2, 3, 4, 12, 48, 78, 79) |
| FAMILY ERETHIZONTIDAE | | | | |
| <i>Erethizon dorsalis</i> | 1.7 | 1 | 1.02 | 1-2 |
| | (1, 3, 80) | (80) | (80) | (3, 18, 80) |

^aA mean breeding season length was calculated from all references in which breeding season was defined. Season length expressed in months.

^bRange was obtained from all references reviewed.

^cMaximum percentage adult females breeding constitutes the maximum percentage breeding during any given month or trapping interval.

TABLE 2. (Continued)

| Maximum Percentage Adult Females Breeding ^c | Age at Sexual Maturity | Density (Animals per Hectare) | | Annual Probability of Survival | Average Life Expectancy ^c |
|--|------------------------|---------------------------------------|--------------|--------------------------------|--|
| | | Mid-range ^d | Maximum | | |
| 83% - 89% | 34-49 Days | 12.56 (5, 6, 7, 9, 15, 46, 52) | 76.81 | .01 | 2.41-3.16 Months |
| (53, 57) | (53, 59) | 55.57, 60, 61) | (6) | (55) | (62) |
| | <1-3 Mo. | 1.76 | 3.3 | | |
| | (28, 59, 63) | (7) | (7) | | |
| 93% | 51 Days | 24.51 | 37.81 | | |
| (53) | (59) | (14, 15, 64) | (14, 15, 64) | | |
| | 44 Days | | | | |
| | (3) | | | | |
| | 90-160 Days | 3.88 (5, 6, 9, 30, 46, 52, 60, 61) | 10.00 | | |
| | (1, 58, 67) | .77 | 3.30 | | |
| | | (7, 30) | (7) | | |
| 32% - 86% | 40-50 Days | 30.60 (5, 9, 52, 70, 71, 73, 74) | 237.22 | .049 | 14.23 weeks |
| (9, 70, 73) | (1, 72) | | (71) | (81) | (81) |
| | | 37.66 | 39.51 | .032 | 9.75 Weeks |
| | | (81) | (81) | (81) | (81) |
| | 300 Days | 14.91 | 86.0 | | |
| | (75) | (5, 7, 8, 77) | (77) | | |
| 58% - 75% | 5-10 Mo. | 5.80 | 31.1 | .097-.288 | Me ₆ =5.6 Mo. Fe ₆ =7.6 Mo. |
| (78, 79) | (75, 78) | (5, 6, 78) | (78) | (78) | (78) |
| | 2-3 Yrs. | | | | |
| | (1, 80) | | | | |

^dDensity mid-ranges were calculated from each pertinent study, and an overall mean was calculated from these values. In references which failed to provide density ranges, average density values were used.

^cThe notation "e_n" denotes the life expectancy of animals at age n. In cases where e_n values were unavailable, average life expectancies for animals of trappable age are presented.

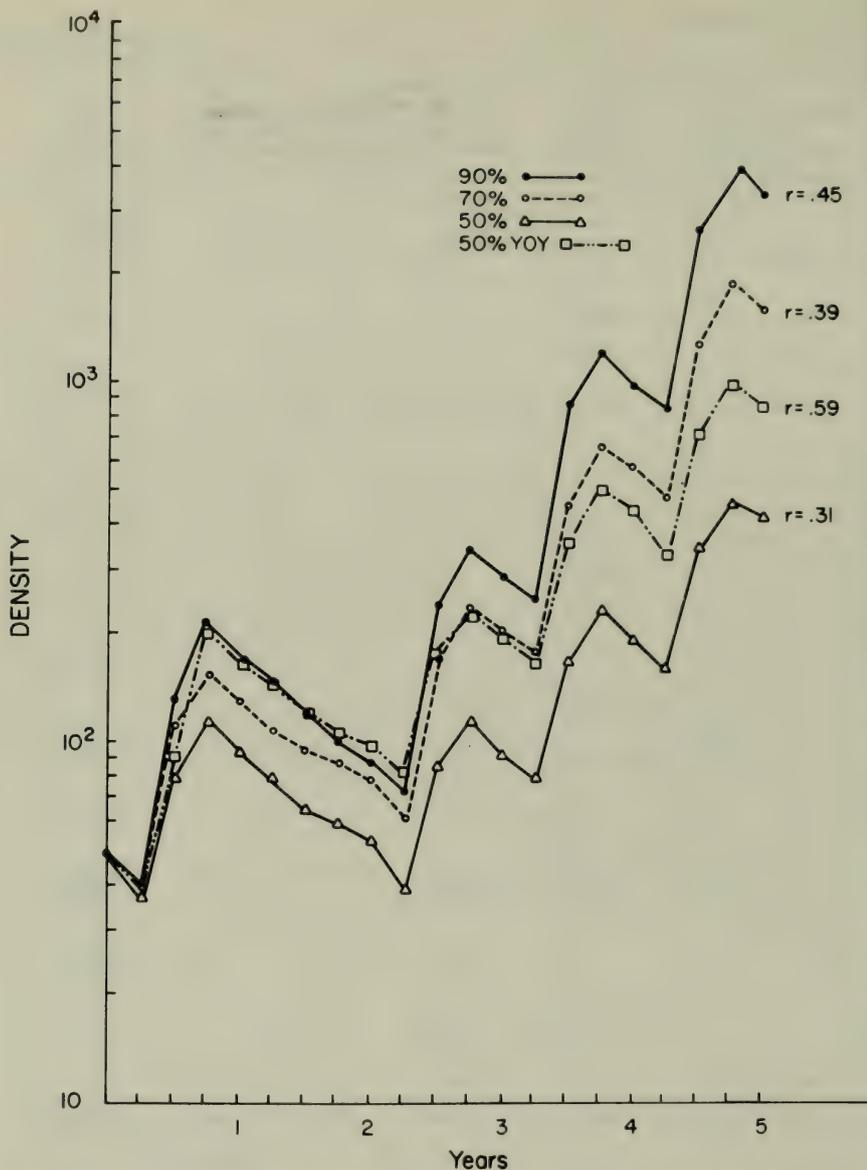


Fig. 2. Simulated population growth under varying schedules of age-specific percent breeding. Populations were allowed to breed normally for 1 year, followed by 1 year of no reproduction and 3 years of normal reproduction. Instantaneous rates of increase were taken from the second breeding period of the first year (the only period where young-of-the-year were reproductively active).

in effect, for better conditions. We have simulated these periods of non-reproduction in two ways, 50% breeding with various periods of non-reproduction, and 3 years nonreproduction with varying percent breed-

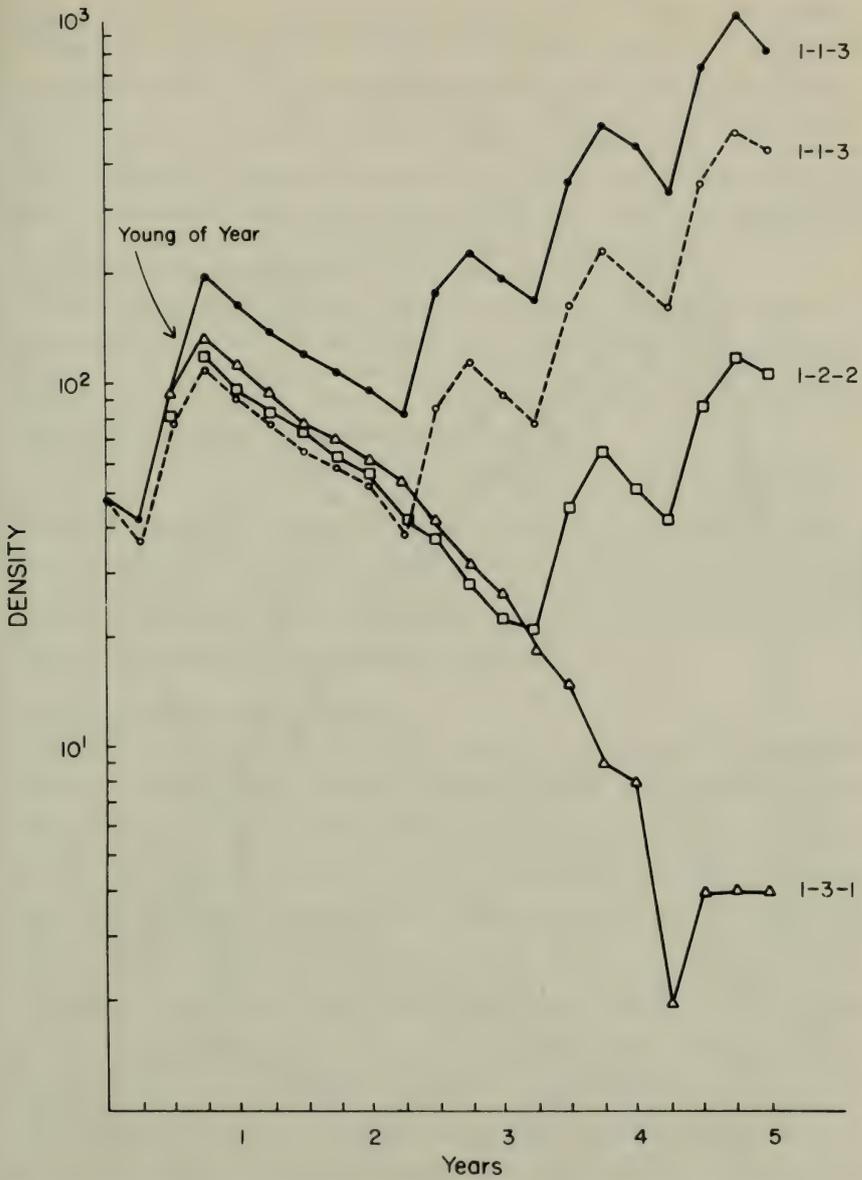


Fig. 3. Simulated population response to 50% age-specific breeding and varying lengths of no reproduction. Numerical sequence at ends of the density curves represent years of breeding-no breeding-breeding.

ing during the first and fifth year. Assuming a 50% age-specific breeding rate, we posed the question, "how long can the population afford to pause, and still remain ecologically viable?" We conducted four simu-

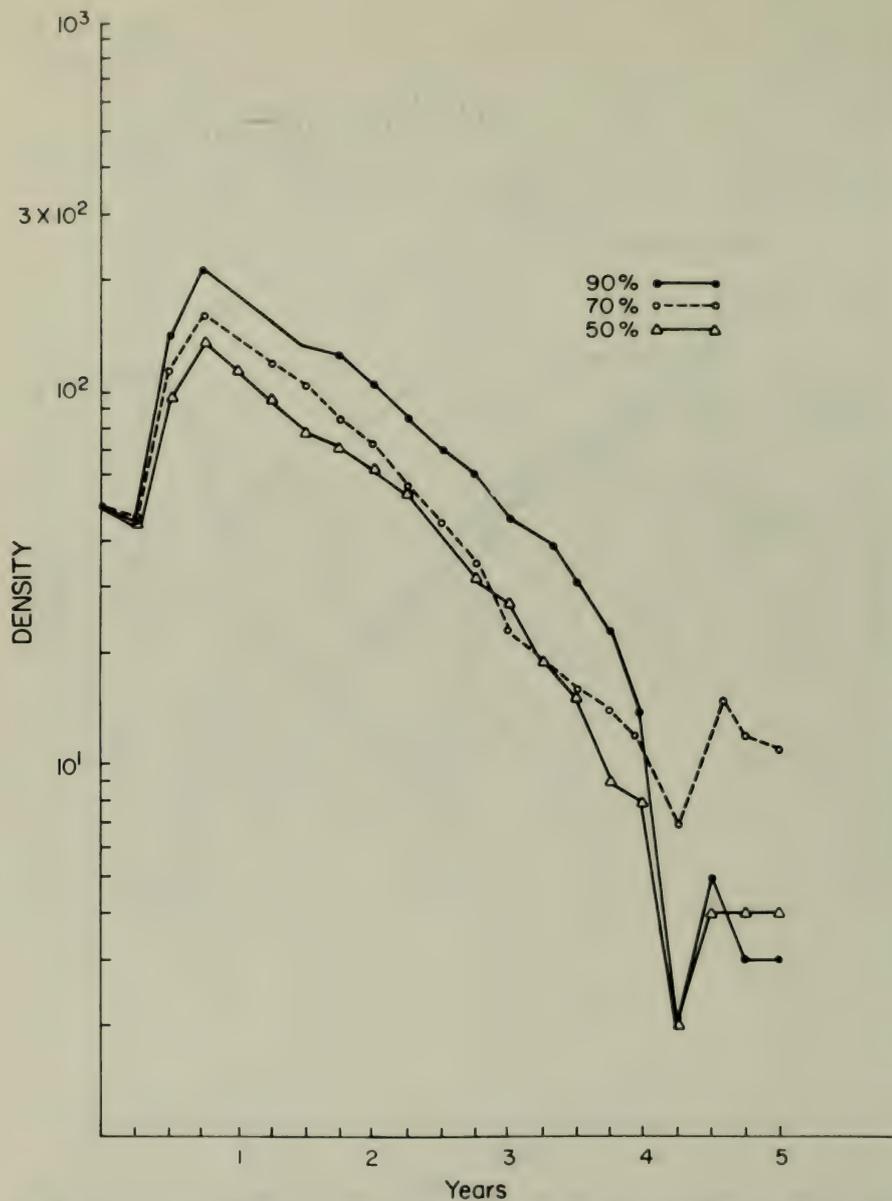


Fig. 4. Simulated population response to varying age-specific breeding intensity for a reproduction pattern of 1 year of breeding, 3 years of no breeding, 1 year of breeding.

lated patterns. All populations were allowed to breed normally for year one. Reproduction was then set to zero for periods of 1, 2, and 3 years. Reproduction was then allowed to resume for the duration of the 5-year

period (Fig. 3). Terminal population densities varied from a maximum of 1027 to a minimum of 1. Thus, even under extreme conditions of reproductive failure in 3 successive years, the population tends to retain the ability to respond. Even though some populations could persist up to 3 years with no reproduction, low terminal densities increase the probability of random extinction. Several of our simulated populations went extinct subsequent to a 3-year pause, with 50% and 70% age-specific breeding rates (Fig. 4). A favorable year, with young-of-the-year breeding, greatly enhances probability of population survival.

These population estimates are conservative because we used constant survival rates during the periods of nonreproduction. Survival rates appear to increase during adverse periods because of reduced surface activity, i.e., torpor, etc. (French et al. 1966, 1967), which would increase the probability of population survival.

The effect of including young-of-the-year in the breeding structure produces the most dramatic results, but it is evident that age-specific percent breeding and young-of-the-year breeding are positively correlated (French et al. 1974). Results of these simulations indicate that this theoretical desert population is capable of explosive growth rates under favorable conditions and can withstand prolonged periods of little or no reproductive activity under adverse conditions.

REPRODUCTIVE STRATEGIES

Recent ecological literature has discussed apparent correlations between demographic strategies and environmental variability. It has been argued that in strongly seasonal and/or unpredictable environments, natural selection tends to favor such characteristics as high maximum rate of natural increase, early reproduction, semelparity, small body size, and short lifespan, while in relatively constant environments, selection favors lower maximum rate of natural increase, delayed reproduction, iteroparity, large body size, and long lifespan (see MacArthur and Wilson 1967; Slobodkin and Sanders 1969; Pianka 1970, 1972; Hairston et al. 1970; Gadgil and Bossert 1970; Roughgarden 1971; Gadgil and Solbrig 1972; MacArthur 1972). Using the terminology of MacArthur and Wilson (1967), those characteristics which lead to high productivity and which are associated with seasonal or unpredictable environments are said to result from "r-selection"; while characteristics which lead to ecological efficiency and which tend to be associated with stable environments are said to be "K-selected".

Pianka (1970) emphasized the relative nature of r- and K-selection and visualized an r-K continuum. Several recent workers have attempted to determine relative positions of certain taxa along this continuum by examining the r- and K-selection correlates of closely related biotypes and species (Gadgil and Solbrig 1972; Randolph 1973; Fleming

1974). Fleming (1974) studied two species of heteromyid rodents and concluded that the species which inhabited a more seasonal environment was relatively more *r*-selected than its counterpart from a more constant environment.

Since *r*-selection is generally thought to occur in seasonal and/or unpredictable environments and since the Chihuahuan Desert is unpredictable relative to rodent resource thresholds, we would predict that the Chihuahuan rodents should be relatively *r*-selected. However, French et al. (1973) plotted survival rates and reproductive capacities of several small mammal taxonomic-demographic groups and noted that sciurid-type, heteromyid-type, and fossorial-type rodents appeared to be relatively *K*-selected, while microtine-type and murid-type rodents seemed to be *r*-selected. According to French's classification, 15 of the Chihuahuan Desert rodent species are members of *K*-selected groups, while only 2 species are members of *r*-selected groups. Therefore, on the basis of these general taxonomic-demographic groups, the predominance of relatively *K*-selected species in the unpredictable desert environment seems to contradict a basic tenet of the *r*- and *K*-selection concept.

In the general manner of previous workers, we have attempted to determine the relative positions of Chihuahuan Desert rodent genera along an *r*-*K* continuum by examining characteristics of these genera (Table 3). The only characteristics used in our rankings were those for which numerical data or estimates could be obtained, and our results are limited by this restriction. Furthermore, our rankings represent a compilation of information obtained from a wide variety of sources, and the comparative use of such diverse data is probably questionable. The four characteristics used in our ranking system were all weighted equally. It may be, however, that certain correlates are more closely associated with resource allocation than others, in which case a weighting scheme would have been more appropriate. Finally, our rankings were limited by the reliance upon *r*- and *K*-selection correlates, which provide only indirect measures of relative *r*-*K* continuum positions. The crucial evidence needed for *r*- and *K*-selection presumably involves the determination of the proportion of an organism's total resources which is allocated to reproductive activities (Gadgil and Solbrig 1972). Such data were not available for the desert rodent genera. Because of these numerous limitations, we consider such rankings as in Table 3 to be, at best, highly questionable.

We generally feel that it is more important to emphasize the dynamic nature of the demographic characteristics of desert-dwelling rodents than to speculate about their relative positions on the *r*-*K* continuum. As previously mentioned, the *r*- and *K*-selection hypothesis leads to the expectation of desert inhabitants being relatively *r*-selected, while, ac-

TABLE 3. Comparison of predicted "r" and "K" correlates with characteristics^a of Chihuahuan desert rodent genera.

| Genus | Variability in population size ^b | Relative competition level ^c | Age of sexual maturity (females) ^d | Relative body size ^e | Relative position on r-K continuum ^f |
|--|---|---|---|---------------------------------|---|
| Predicted K-selected species (Pianka 1970) | Fairly constant | Usually keen | Delayed | Large | 1.00 |
| Predicted r-selected species (Pianka 1970) | Variable | Variable often lax | Early | Small | 3.00 |
| <i>Neotoma</i> | 3.42x (1) | 2 | 10.0 Mo. (1) | 1 | 1.25 |
| <i>Spermophilus</i> | 1.50x (1) | 3 | 12.0 Mo. (1) | 1 | 1.50 |
| <i>Thomomys</i> | 2.00x (1) | 2 | 3.0 Mo. (2) | 1 | 1.50 |
| <i>Erethizon</i> | | 3 | 30.0 Mo. (1) | 1 | 1.66 |
| <i>Dipodomys</i> | 8.27x (2) | 1 | 2.0 Mo. (3) | 1 | 1.75 |
| <i>Onychomys</i> | 9.86x (2) | 3 | 4.0 Mo. (2) | 2 | 2.25 |
| <i>Reithrodontomys</i> | 4.57x (2) | 2 | 3.0 Mo. (2) | 3 | 2.25 |
| <i>Perognathus</i> | 30.00x (3) | 1 | 2.5 Mo. (2) | 3 | 2.25 |
| <i>Sigmodon</i> | 5.50x (2) | 3 | 1.5 Mo. (3) | 1 | 2.25 |
| <i>Baiomys</i> | | 1 | 1.5 Mo. (3) | 3 | 2.33 |
| <i>Peromyscus</i> | 15.71x (3) | 2 | 1.5 Mo. (3) | 2 | 2.50 |

^aIncluded are those characteristics listed in Table 1 of Pianka (1970) which are variable among Chihuahuan rodent genera and for which relative values could be obtained.

^bThe largest fold increase from minimum to maximum density reported in any study. The r-K continuum rankings are shown in parentheses, 1 = $\leq 4.00x$; 2 = $> 4.00x$ but $< 10.00x$, and 3 = $> 10.00x$.

^cThe ranking 1 indicates a relatively high level of competition; 2, an intermediate level; and 3, a low level of competition.

^dThe r-K continuum rankings are shown in parentheses, 1 = ≥ 10.0 ; 2 = > 2.0 but < 10.0 ; and 3 = ≤ 2.0 .

^eThe ranking 1 indicates a relatively large animal; 2, and animal of intermediate size; and 3, a small animal.

^fValues were obtained by summing the rankings for each genus and dividing this sum by the number of characteristics.

According to the taxonomic-demographic group classification of French et al. (1973), K-selected species actually predominate in the Chihuahuan Desert. Contrary to both the prediction and its apparent alternative, however, it appears that the r- and K-selection correlates of many Chihuahuan rodents are temporally dynamic, and that these animals are relative r-strategists at certain times and K-strategists at others.

Rainfall levels and the resultant presence or absence of primary production appear to influence the dynamic nature of the demographic

parameters of desert rodents. Numerous workers have suggested that desert rodent reproductive success is directly related to precipitation and primary production (Reynolds and Haskell 1949; Reynolds 1958, 1960; McCulloch and Inglis 1961; McCulloch 1962; Chew and Butterworth 1964; Beatley 1969; French et al. 1974). French et al. (1974) noted that in years of good plant production *Perognathus formosus* populations exhibited high prevalence of pregnancy, large litter sizes, high population growth rates, and increased reproduction by young-of-the-year. Years of poor plant production, however, can result in the complete inhibition of reproduction in desert rodents (French et al. 1967, 1974). Plant estrogens (Pinter and Negus 1965), plant gonadotropins (Bodenheimer and Sulman 1946), and dietary water (Beatley 1969; Bradley and Mauer 1971) have been suggested as substances which trigger rodent reproductive activity, but regardless of the physiological mechanism involved, desert rodent reproduction does seem to be related directly to plant production.

Mean lifespans and survival rates of desert rodents also appear to be correlated with rainfall and plant production (French et al. 1966, 1967). In this case, however, the relationship is inverse, with greater longevity occurring during periods of environmental adversity (French et al. 1966, 1967). This increased survival apparently results from the greater proportion of time spent by rodents in a torpid or inactive condition, during periods of adversity (French et al. 1966, 1967). For example, members of the genus *Perognathus* enter torpor in response to either absence of food or low ambient temperature, and the amount of time spent in torpor has been shown to vary inversely with the quantity of available food (Tucker 1962, 1966; French et al. 1966, 1967). Theoretical discussions of reproductive effort often include the assumption that a cost function is associated with reproduction, and that this "cost" can result in lowered survival rates of reproducers (Williams 1966; Gadgil and Bossert 1970). Such a reproductive cost function has been hypothesized for desert rodents (Rosenzweig 1974), and it is possible that such a mechanism acts to lower rodent survival rates in years of good plant production (and thus high rodent reproduction). Again, regardless of the mechanism involved, it appears that desert rodent survival is inversely related to effective precipitation and plant production.

The relationship of reproduction and survival to rainfall and plant production provides the basis for a demographic strategy exhibited by at least some desert rodents. Maximum reproductive rates and relatively low survival rates seem to occur during periods of high rainfall and plant production, while minimum reproductive rates and maximum survival rates are found during times of drought and poor primary production.

High reproductive rates and low survival rates are generally considered to be correlates of r-selection, while low reproductive rates and high survival rates are usually associated with K-selection (Gadgil and

Bossert 1970; Hairston et al. 1970; Pianka 1970). Desert rodents therefore seem to shift from a relative r-strategy to a relative K-strategy in response to decreasing rainfall and plant production (Fig. 5). Such a dynamic demographic strategy has particular value for inhabitants of unpredictable environments, with high reproductive output permitting exploitation of favorable plant growth and high survival rates allowing animals to persist through adverse periods.

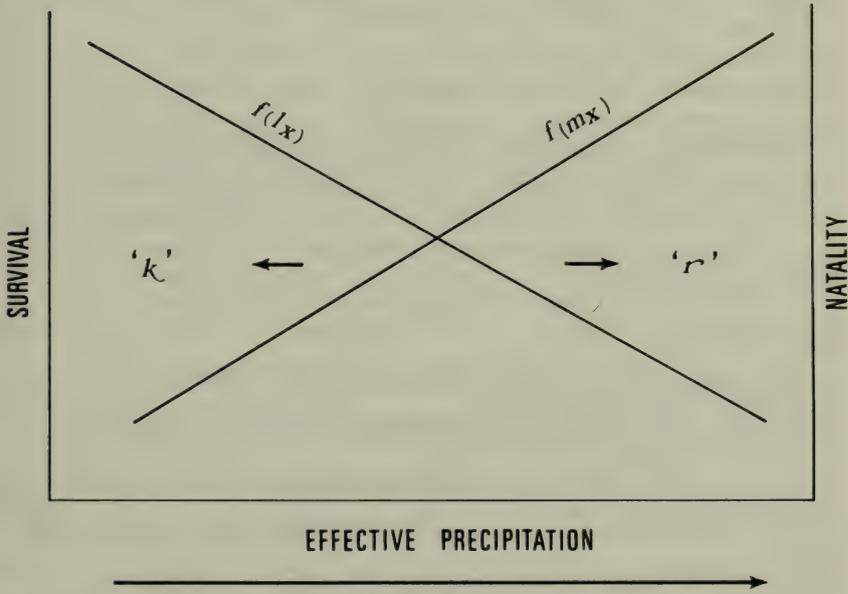


Fig. 5. Temporally dynamic reproductive strategy in desert rodents. See text for discussion.

We have examined possible variations in reproduction through the use of computer simulations and have demonstrated the wide range of possible reproductive effort "options" and resultant demographic consequences for a prototype desert species, *Perognathus formosus*. The simulations indicated that *Perognathus* populations have the capacity either to exhibit high rates of increase during years of favorable conditions (Fig. 2) or to persist during extended adverse periods without reproducing (Figs. 3, 4). Our simulations thus support the general feasibility of a highly variable reproductive strategy.

While dynamic demographic strategies have not previously been discussed relative to r- and K-selection, a similar strategy was described by Margalef (1963) in his discussion of mature and immature ecosystems. For example, it was noted that ecosystem maturity is temporally variable and that certain populations tend to concentrate

reproductive effort during periods of relative immaturity as indicated by high production to biomass ratio (Margalef 1963). It has also been suggested that in environments where any important ecological factor is variable, natural selection will favor "yes-if" genes which cause organisms to reproduce only during periods of favorable conditions (Williams 1966).

In summary, our examination of the demographic characteristics and strategies exhibited by Chihuahuan Desert rodents leads us to doubt the generality of the concept of r- and K-selection. While r-selection is theoretically associated with unpredictable environments, we have noted that species from K-selected taxonomic-demographic groups tend to predominate in the environmentally unpredictable Chihuahuan Desert. More importantly, we suggest that at least some Chihuahuan rodents exhibit a temporally dynamic demographic strategy which involves shifts between relative r- and K-type strategies. While we make no claims regarding the generality of such a dynamic strategy at this point, we suggest that it is especially valuable for inhabitants of unpredictable environments.

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Appendix I

Citations and Corresponding Reference Numbers for Table 2.

- | | |
|--------------------------------|---------------------------------|
| 1. Davis 1960 | 42. Johnston 1956 |
| 2. Baker 1956 | 43. Duke 1944 |
| 3. Asdell 1964 | 44. Day et al. 1956 |
| 4. Warren 1922 | 45. McCulloch and Inglis, 1961 |
| 5. Packard 1971 | 46. Lauenroth and Sims 1973b |
| 6. Packard 1972 | 47. Fisler 1971 |
| 7. Chew and Chew 1970 | 48. Hall 1955 |
| 8. Wood 1965 | 49. Svihla 1931 |
| 9. McCulloch 1962 | 50. Bailey 1926 |
| 10. Edwards 1946 | 51. Leraas 1938 |
| 11. Anderson 1972 | 52. Hoffman et al. 1971 |
| 12. Bailey 1931 | 53. Jameson 1953 |
| 13. Davis 1944 | 54. Layne 1968 |
| 14. Baker 1962 | 55. Terman 1968 |
| 15. Storer et al. 1944 | 56. Beer et al 1957 |
| 16. Miller 1946 | 57. Vaughan 1969 |
| 17. Bond 1946 | 58. Egoscue 1960 |
| 18. Hall 1946 | 59. Clark 1938 |
| 19. Scheffer 1938 | 60. Grant 1972 |
| 20. Douglas 1969 | 61. Lauenroth and Sims 1973a |
| 21. Schramm 1961 | 62. French et al. 1973 |
| 22. Burt 1933 | 63. Davis and Davis 1947 |
| 23. Dixon 1929 | 64. Drake 1958 |
| 24. Howard and Childs 1959 | 65. Blair 1941 |
| 25. Holdenreid and Morlan 1956 | 66. Bailey and Sperry 1929 |
| 26. Hoffmeister 1956 | 67. Svihla 1936 |
| 27. Eisenberg and Isaac 1963 | 68. Rinker 1942 |
| 28. Balda et al. 1972 | 69. Svihla 1929 |
| 29. Reynolds and Haskell 1949 | 70. Dunaway and Kaye 1961 |
| 30. Blair 1943 | 71. Barrett 1968 |
| 31. Holdenreid 1957 | 72. Meyer and Meyer 1944 |
| 32. Vohries and Taylor 1922 | 73. Odum 1955 |
| 33. Bradley and Mauer 1971 | 74. Petryszyn and Fleharty 1972 |
| 34. Johnson et al. 1948 | 75. Feldman 1935 |
| 35. Alcorn 1941 | 76. Vorhies and Taylor 1940 |
| 36. Reynolds 1960 | 77. Spencer 1941 |
| 37. Chew and Butterworth 1964 | 78. Raun 1966 |
| 38. Lidicker 1960 | 79. Johnson, 1952 |
| 39. Reynolds 1950 | 80. Struthers 1928 |
| 40. Reynolds 1958 | 81. Petersen 1973. |
| 41. French et al. 1974 | |

Past, Present, and Future Status of the Desert Bighorn in the Chihuahuan Desert Region¹

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PAST

The existence of desert bighorn sheep in the Chihuahuan Desert region of the United States and Mexico can be traced back to prehistoric times based on Indian pictographs found on historic sheep ranges. One such pictograph of desert bighorn sheep is located in Victoria Canyon in the Sierra Diablo Mountains in Culberson County, Texas, on the Sierra Diablo Wildlife Management Area of the Texas Parks and Wildlife Department.

Carson (1941) stated that the first white men to discover and kill the desert sheep were the Spanish explorers who came through western Texas in the early part of the 15th century. The discovery of valuable minerals and large deposits of salt in the midst of the sheep range caused the first depredation of the desert bighorn sheep in the Chihuahuan Desert region by the white man. For more than 300 years, great wagon trains came up from Mexico to the salt deposits south of the Guadalupe Mountains; the Mexicans refined the salt and carried it back for their use. Hunters supplied these encampments near the salt beds with wild game, and most of the meat supplied is believed to have been from desert bighorn sheep.

In the late 1800s, with the coming of the railroad to west Texas and the discovery of large veins of silver, heavy pressure was again placed on the sheep herds. During 1889 and 1890, when the Hazel silver mine near Van Horn was at its peak operation, bighorns were killed around

¹A contribution of Federal Aid to Wildlife Restoration, Texas Pittman-Robertson Project W-67-D

the vicinity of the mine until their very existence was threatened. As the buffalo herds on the Great Plains decreased, market hunters followed the railroad into the sheep country and continued their trade by hunting sheep, deer, and antelope. The animals were killed during the winter months, placed in refrigerated boxcars, and shipped east to markets. Although the sheep season was closed in Texas in 1903, hunting pressure continued.

The next attack on the sheep came in the late 1930s when domestic sheep were stocked in large numbers in the Van Horn area. At the same time the netwire fence was installed which prevented free movement of the wild sheep. During the period 1938 through 1940, more than 20,000 domestic sheep were stocked on the existing bighorn range.

By 1941, Carson (1941) estimated that there were not more than 150 bighorns left in Texas. Previous estimates in the early 1880s indicated that as many as 1500 bighorn sheep had been present. The last known sighting of native bighorns in Texas occurred in the summer of 1960, when two ewes were sighted in Victoria Canyon in the Sierra Diablo Mountains north of Van Horn by Texas Parks and Wildlife Department personnel.

When the white man arrived in New Mexico (Gordon 1957), "Mexican" bighorns occupied nearly every range of hills and mountains in the southern half of New Mexico. They have disappeared from most areas since 1900. By 1957, bighorns were confined almost entirely to the Big Hatchet and San Andres mountain ranges. C. A. Kennedy (1957), manager of the San Andres Wildlife Refuge, stated that in 1956 a survey of the San Andres complex resulted in the sighting of 157 sheep. An estimate of the number of sheep in the Big Hatchet Mountains in 1957 was set at 50 animals. At the present time, the sheep numbers vary with the existing conditions in these mountain ranges.

As indicated by Mario Luis Cossio (pers. comm. 1974), Director General of Wildlife for Mexico, bighorn sheep occurred in most of the mountain ranges in the Mexican portion of the Chihuahuan Desert at the coming of the white man. One of the last known bands of bighorn sheep was located along the Rio Grande in the vicinity of Santa Elena Canyon on the Mexican side of the boundary. This particular band was last observed about 1925. At the present time, it is doubtful that there are any desert bighorn sheep in the Mexican portion of the Chihuahuan Desert.

PRESENT

An agreement in 1954 between the Fish and Wildlife Service, the Wildlife Management Institute, the Boone and Crockett Club, and the Game and Fish Commissions of Arizona and Texas provided for the trapping of desert bighorn sheep on the Kofa Game Range in Arizona,

and transplanting the animals to a 427-acre holding pasture on the Black Gap Wildlife Management Area in west Texas.

Trapping operations began during the summer of 1956 and were terminated in July 1959. At the end of 1959, nine sheep (four rams and five ewes) remained in the enclosure. During April and May 1960, three lambs were born, and in June of the same year one adult ram and two adult ewes died. Since 1960, the increase in the herd has come from the original three rams and three ewes and their offspring.

The release of desert bighorn sheep from the enclosure on the Black Gap Wildlife Management Area to the immediate area outside the enclosure followed the closing of the 1970 Trans-Pecos deer season. The release of 20 of the adult bighorn sheep from the enclosure would provide a substantial release herd to determine survival in the wild and which age classes would be the best for future releases.

Trapping operations began on 14 December 1970, and were completed on 22 January 1971, when a total of 20 sheep (11 males and 9 females) were released outside the enclosure. Most of the older sheep have become established near the enclosure and have reproduced annually since their release. Five of the released animals were in the yearling age class and were observed approximately 48 km (30 miles) southwest of the release site near the lower end of the Big Bend National Park on the Rio Grande. One of these later returned to the release area.

In 1973, seven sheep (four rams and three ewes) were moved from the Black Gap herd to the Sierra Diablo Wildlife Management Area and placed in a small enclosure on the area. As previously stated, the Sierra Diablo Area was the range of the last known native desert bighorn sheep in Texas. Prior to the release of the sheep from the enclosure to the surrounding area in June 1973, radio-transmitter collars were placed on three of the animals. The released sheep established themselves approximately 6.4 km (4 miles) north of the enclosure in the vicinity of Victoria Canyon.

The New Mexico Game Department has undertaken a project of trapping desert bighorn sheep in Mexico and moving the animals to the Red Rock Game Management Area to be used as brood stock to produce animals for future releases. The releases will be made in former desert bighorn sheep ranges in the hope of establishing new populations to supplement those already in the San Andres and Big Hatchet mountains.

FUTURE

The future of the desert bighorn sheep within the Chihuahuan Desert region is bright at the present time. In Texas, the practice of producing domestic sheep within the historical bighorn sheep range is almost over.

The netwire fences that once restricted the movement of wild sheep have deteriorated so that bighorns will be able to move with little restriction. In some areas, these fences have been completely removed. The attitude of the people is one of protection and reintroduction of the sheep instead of predation, as it has been in the past.

Habitat destruction is the one element that is most threatening to the existing sheep populations and to future releases.

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Mammals of the Chihuahuan Desert Region—Future Prospects

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Man's future nutritional needs will be such as to require extracting higher yields of food stuffs from areas of low rainfall. Many desert soils are potentially highly productive, needing only generous douses of water to allow them to bloom in diverse agricultural crops. This is certainly happening in parts of the Chihuahuan Desert using irrigation waters from such sources as the Río Grande, its major tributaries, the Pecos and Conchos, and such other streams as the Río Nazas and Río Aguanaval which drain into the great interior basins of Durango, Chihuahua, and Coahuila. Networks of canals spread these waters to fields of cotton, grains, livestock forage, vegetables, fruit trees, and grape vines. New dams to impound even more irrigation waters are being constructed at many strategic places along these watersheds. As a consequence, much riparian habitat, adjacent desert, and interior basin environment have been obliterated as habitats for native mammalian life. Of course, how much of the desert will be changed by the almost magical powers of a sustained water supply in the next 20 to 50 years will depend on man's ingenuity to cope with increasing soil salinity, declining sources of water, and the always rising costs of crop production by irrigation.

The sizeable standing crop of native vegetation in the Chihuahuan Desert yields large amounts of plant protein and other nutrients, but much of it is rejected as forage by domestic animals—cattle, goats, and some sheep. Perhaps this avoidance of many desert grasses, forbs, shrubs, and cacti is a good thing for desert mammals from small pocket mice to large collared peccaries. Range managers are studying means to alter plant-species combinations in an effort to increase those more acceptable to livestock. Yet another threat to indigenous mammals is the likelihood that wild or semi-tame Old World hoofed mammals—eland, impala, springbok, black buck, etc.—might be introduced if it could be

demonstrated that one or more of these meat-producing exotics would eat some of the common but unused desert plants.

The obvious and more "natural" approach to this problem of getting higher yields of animal protein per hectare would be to encourage existing game species in combination with the cattle-goat economy. Owners or operators of large desert holdings may in the future find it profitable to protect breeding stocks and harvest only annual surpluses of mule deer and collared peccary along with cattle and goats. The compatibility, possible competition for similar foods, and the maximum per-hectare densities of a near carrying-capacity population of this species-combination have never been examined.

Finally, the accessibility of water has opened arid lands to ever-increasing human habitation. Initially, the attraction was for food-production enterprises. Currently, and increasingly in the future, the clear, sunny skies, cool nights, and invigorating aridity are luring more and more people who seek resort areas and retirement condominiums, with golf courses and pools encroaching on desert areas. Indigenous mammals again will lose ground.

MAMMALS IN DISTRESS

Human land-use practices, current and future, will either discourage or encourage native mammals. With most species, especially the small and inconspicuous rodents, there have been no long-term projects in the Chihuahuan Desert to monitor their population fluctuations. Little is known of the interaction, favorable or otherwise, between livestock production or irrigated farming and many arid-adapted mammals. Most observers will probably agree, although lacking quantitative evidence, that at least the black-tailed jack rabbit (*Lepus californicus*) has thrived in man's presence. The following species include some of those Chihuahuan Desert mammals which have fared poorly as a result of man's occupation. Their future welfare is uncertain; many are presently threatened (Table 1).

Desert Shrew (*Notiosorex crawfordi*). Mammalogists have always had difficulty in capturing this small mammal, although owl pellets containing skulls of this species from such places as Coahuila and Jalisco reveal its widespread distribution on the Mexican Plateau. Our meager knowledge of this curious shrew indicates that it is an insect eater and may inhabit dens of the desert-dwelling white-throated wood rat (*Neotoma albigula*). Neither of these resources seems to be in short supply.

White-sided Jack Rabbit (*Lepus callotis*). This handsome and conspicuous animal is endemic to the Mexican Plateau. Although it prefers the elevated grasslands on the western side, this hare ranges into grass-shrub areas of the Chihuahuan Desert, especially in eastern Durango.

TABLE 1. Threatened mammals of the Chihuahuan Desert region.

| |
|--|
| Desert Shrew (<i>Notiosorex crawfordi</i>) |
| White-sided Jack Rabbit (<i>Lepus callotis</i>) |
| Texas Antelope Squirrel (<i>Ammospermophilus interpres</i>) ¹ |
| Nelson Kangaroo Rat (<i>Dipodomys nelsoni</i>) ¹ |
| Goldman Wood Rat (<i>Neotoma goldmani</i>) ¹ |
| Kit Fox (<i>Vulpes macrotis</i>) |
| Black Bear (<i>Ursus americanus</i>) |
| Mule Deer (<i>Odocoileus hemionus</i>) |
| Pronghorn (<i>Antilocapra americana</i>) |
| Bighorn (<i>Ovis canadensis</i>) |

¹Denotes endemics.

Perhaps livestock grazing may be one of the factors contributing to its decline and apparent replacement by the highly adaptable black-tailed jack rabbit (*Lepus californicus*). The white-sided jack rabbit should be considered endangered throughout its entire range.

Texas Antelope Squirrel (*Ammospermophilus interpres*). Steep, rocky slopes and rimrock of arid desert hills are preferred by this endemic species. Observers have found it common nowhere and spotty in distribution. Its biology needs investigating.

Nelson Kangaroo Rat (*Dipodomys nelsoni*). This nocturnal mammal lives in large mounds scattered at intervals in desert-shrub and desert-grassland situations. Its disjunct distribution in Chihuahua, Coahuila, Durango, San Luis Potosí, and northern Zacatecas may be the result of its incompatibility with livestock production. It is suspected of being endangered in most areas.

Southern Banner-tailed Kangaroo Rat (*Dipodomys phillipsii*). This species, endemic to the Mexican Plateau, occurs in parts of the Chihuahuan Desert region as far north as southern Durango. The biology of this attractive kangaroo rat is obscurely known.

Beaver (*Castor canadensis*). The beaver thrives in semi-aquatic habitat along the Río Grande and some of its tributaries in the vicinity of the Texas-Coahuila-Chihuahua border. Whether it once occurred extensively along the Río Conchos as it flows northeastward from the heart of the Chihuahuan Desert is questionable. However, some of the riparian habitat looks acceptable, and introductions might be considered.

Goldman Wood Rat (*Neotoma goldmani*). This small wood rat is endemic in the Chihuahuan Desert from Chihuahua and Coahuila in the north to San Luis Potosí in the south. It has been taken or observed infrequently, and its ecology is little known. It should be listed as endangered.

Kit Fox (*Vulpes macrotis*). This small, dainty carnivore occurs on the Chihuahuan Desert as far south as Zacatecas, with the subspecies, *V. m. zinseri*, being endemic. Observers indicate that the kit fox is far less common than the widespread gray fox (*Urocyon cinereoargenteus*). For the Chihuahuan area, at least, the kit fox should be carefully watched and considered endangered.

Southern River Otter (*Lutra annectens*). This otter once inhabited the Río Nazas and still lives in streams with Pacific drainages in the Sierra Madre Occidental. Intensive irrigational uses of the waters of streams in the Chihuahuan Desert region will probably preclude the return of this interesting semi-aquatic species.

Black Bear (*Ursus americanus*). The oak and pine-oak slopes of the higher mountains, isolated by and scattered through the Chihuahuan Desert, often support (now and/or previously) black bear. These large mammals are not always restricted in their montane retreats and often descend to the surrounding desert when shrubs are in fruit. In these desert mountains, the black bear must be listed as endangered. Protection from overhunting and possibly some future restocking are necessary if it is to persist in this area.

Collared Peccary (*Pecari tajacu*). The widespread neotropical javelina reaches its northernmost distribution on the Chihuahuan Desert. Its preference for the desert has made it accessible as an easy prey for man, although the animal rarely is extirpated completely locally because of its ability to retreat into rocky areas and dense thickets of thorn brush and prickly pear. If a near carrying-capacity population could be encouraged, this species might be a major source of "wild meat" for local consumption.

Mule Deer (*Odocoileus hemionus*). Vast areas of the Chihuahuan Desert and its arid mountains are completely devoid of this large, meat-producing ungulate. As in the case of the collared peccary, the mule deer should be given enough protection to increase sufficiently to produce sustained annual surpluses. Some restocking will be necessary in parts of Chihuahua, Coahuila, Durango, and Zacatecas. At present, the mule deer must be considered as endangered throughout all of the Mexican part of the Chihuahuan Desert.

White-tailed Deer (*Odocoileus virginianus*). Although not strictly an arid-land species, this deer often lives in oak or pine-oak habitats of the mountainous areas completely surrounded by the Chihuahuan Desert. This diminutive "flag-tailed" deer has been less accessible to hunters in its montane retreats than has been the mule deer of the lowlands. Even so, whitetail populations are low and in need of protection from excessive hunting.

Pronghorn (*Antilocapra americana*). Desert grasslands of the Mexican Plateau were formerly well stocked with pronghorn. Now remnants may

remain only in parts of Chihuahua, possibly Coahuila, northwestern Durango, and San Luis Potosí. Pronghorn must be considered endangered in all Mexican parts of the Chihuahuan Desert. If local protection can be afforded, the pronghorn can be successfully restocked in suitable areas.

Bighorn (*Ovis canadensis*). The "rimrock" uplands that are scattered through the Chihuahuan Desert were once inhabited by bands of "desert" bighorn. This majestic animal's decline has been attributed to many factors, including competition with domestic sheep and persistent trophy hunters. Perhaps some bighorn remain in desert ranges in Chihuahua. When local protection is assured, there is good evidence, based on the Texas experiences (Hailey this volume), that restocking might be successful.

Obviously, the protein-hungry human population in the rural sectors of the Chihuahuan Desert are not apt to change their outlook on the utilization of wild mammal populations overnight. Perhaps the need now and in the immediate future is to persuade operators of large land holdings to restrict hunting of the game mammals and perhaps to agree to accept and sustain breeding stocks of those species extirpated. Small mammal habitats might also be preserved by easing livestock grazing in selected environments. This proposal is at best a "holding action" but follows the same tradition developed elsewhere for protecting scattered populations of mammals and their habitats until such time as they can disperse naturally to adjacent space.

Session III
Botany

Desert Vegetation in the Guadalupe Mountains Region

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The Guadalupe Mountains region possesses a high degree of topographic and edaphic diversity. These factor complexes are situated in a variable, though generally arid climate; and now, as in the past, they provide a setting for marginal interplay of three major biological complexes: the Rocky Mountain Forest, the Great Plains Grassland, and the Chihuahuan Desert. Even a brief inspection of local vegetational patterns discloses that availability of water is the primary determinant of community structure and diversity; therefore an analysis of vegetation must take into account the physical factors governing water utilization by plants. These environmental factors interacting with genetic systems available through processes of selection and dispersal result in the observable mosaic of plant communities. Usually, the variables controlling water availability change gradually over space, creating a continuous gradient along which plant species are arranged according to their tolerances. Whittaker and Niering's study (1965) of vegetation in the Santa Catalina Mountains of Arizona is an excellent example of this phenomenon. Similar to the Santa Catalinas, the Guadalupe is an island of coniferous forest surrounded by desert at lower elevations, and between these extremes is a series of transitional plant associations. The pattern is not static because the climate varies. The presence of alluvial fans, bajadas, and calcareous soils indicates a history of generally arid conditions, but the lake deposits and ancient beaches surrounding the Salt Flat west of the mountains point to periods of more precipitation than the present (King 1948). Van Devender et al. (in press) have found macrofossils of *Pinus edulis* and *Robinia neomexicana* as low as 1525 m (5000 ft) in Williams Cave, south of the mountains and well below the current range of these species. Even at lower elevations both the floristic and physiognomic composition of existing associations implies alternating dominance between grassland and desert-scrub ele-

ments. Undoubtedly, the recent history of intensive grazing has favored predominance of Chihuahuan Desert species, and local variation in stocking practices imposes an additional factor complicating the vegetational mosaic. In historical perspective the region can be seen as a dynamic zone of tension between grassland, forest, and desert.

F. R. Gehlbach (1967) and B. H. Warnock (undated) have both written excellent descriptions of Guadalupe Mountains vegetation including comprehensive classification schemes. In addition, the report of the Guadalupe Mountains National Park Interagency Browse Survey conducted by Michael Glass and Roger Reisch (1974) contains a detailed vegetation map. Accordingly, we attempt to avoid duplicating their efforts in this paper and instead emphasize features not covered by previous authors. The plant names used in this paper correspond to those in Correll and Johnston (1970).

GENERAL FEATURES

To illustrate the general pattern of vegetation we describe a synthetic transect across the southern end of the Guadalupe Mountains. At 1100 m (3600 ft), the Salt Flat is the lowest area on the west side; except for widely scattered bushes of *Allenrolfea occidentalis*, it is barren. Slightly higher saline soils not subject to flooding support an extensive grassland of *Sporobolus airoides*, usually associated with *Atriplex canescens*. Scattered around the basin are low Pleistocene beach ridges dominated by *Coldenia hispidissima*, *Yucca elata*, and other gypsophiles. *Atriplex canescens* occupies the heavy clay of the outermost lake deposits and gives way abruptly to *Larrea tridentata* which dominates most of the bajada. On the lower bajada, *Larrea* is usually associated with *Prosopis glandulosa* var. *torreyana*, while near the base of the mountains *Bouteloua eriopoda* and *Erioneuron pulchellum* are major co-dominants. The alluvial fans along the base of the west escarpment have a heterogeneous vegetation ranging from desert grassland of *Bouteloua eriopoda* with *Krameria glandulosa*, *Larrea tridentata*, and *Yucca torreyi* on xeric sites to riparian associations including *Brickellia laciniata*, *Fallugia paradoxa*, *Rhus virens*, and *Dasyilirion leiophyllum* extending from the canyons down the arroyos.

The vegetation on the west escarpment is a patchwork of species occupying portions of a gradient produced by an integration of elevation, exposure, and substrate. Above the alluvial fans are limestone ledges occupied by *Bouteloua eriopoda*, *B. warnockii*, *Agave lecheguilla*, *Parthenium incanum*, and *Fouquieria splendens*. Between 1675 and 1850 m (5500 and 6000 ft), there are layers of sandstone which have eroded to create a lower slope and somewhat deeper soils. These sites are covered mostly by grasses, usually *Bouteloua hirsuta*, *B. warnockii*, *B. gracilis*, *B. eriopoda*, *Lycurus phleoides*, *Muhlenbergia setifolia*, *Stipa neomexicana*,

and *Aristida glauca*. *Dasyllirion leiophyllum* and low shrubs increase in importance on rocky sites, the most common shrubs being *Leucophyllum minus*, *Dalea formosa*, *Mortonia scabrella*, *Parthenium incanum*, and *Viguiera stenoloba*. Above 1975 m (6500 ft) typical dominants are *Cercocarpus montanus* var. *paucidentatus*, *Muhlenbergia pauciflora*, *Choisya dumosa*, *Forsellesia spinosa*, *Nolina micrantha*, and *Yucca baccata*. At about 2125 m (7000 ft) elevation occur steep talus slopes with dense stands of *Dasyllirion leiophyllum*, and above are limestone cliffs rising over 300 m (1000 ft) to the top of the escarpment.

The high parts of the Guadalupe are a mosaic of coniferous forest, montane grassland, and a chaparral-like association including *Quercus undulata*, *Cercocarpus montanus*, *Rhus aromatica*, and *Ceanothus greggii*.

The east escarpment differs from the west in that it has a more gradual slope. There are also extensive areas of pediment where a relatively thin soil overlays parent rock, as opposed to the deep sediments of the bajadas. In contrast to the poorly developed inclosed drainage pattern on the west, the east slope has a relatively well-defined system of streambeds leading ultimately to the Pecos River. In general, equivalent sites on the east slope seem to support a more mesic community than those on the west. Probably this is due to the general trend of increasing precipitation toward the east and the protection afforded by the mountains from warm, dry winds off the desert to the west.

On the east slope components of the chaparral-like association are gradually replaced by *Dasyllirion leiophyllum*, *Parthenium incanum*, *Mimosa biuncifera*, *Viguiera stenoloba*, and *Xanthocephalum sarothrae*. *Bouteloua hirsuta*, *B. gracilis*, *B. warnockii*, *B. eriopoda*, *Lycurus phleoides*, *Muhlenbergia setifolia*, and *Aristida glauca* are among the more common grasses. Most of these grasses continue to predominate on sediments of the east base, but shrub dominance shifts to *Juniperus pinchotii*, *Quercus pungens*, *Q. grisea*, and *Xanthocephalum sarothrae*, with scattered *Yucca elata*, *Opuntia imbricata*, and *O. phaeacantha*. Lining the arroyos is a riparian woodland often composed of *Quercus grisea*, *Juniperus deppeana*, and *Arbutus xalapensis*. East toward lower elevations *Juniperus pinchotii* decreases greatly, and *Acacia neovernicosa* becomes the dominant shrub. Below 1375 m (4500 ft) *Larrea tridentata* increases in importance along with *Krameria grayi*. On north exposures *Bouteloua eriopoda* and *B. warnockii* share dominance, the latter species being favored by steeper slopes. *Viguiera stenoloba*, *Condalia ericoides*, and *Xanthocephalum sarothrae* are often associated with these grasses. Fine-textured alluvial sediment at approximately 1125 m (3700 ft) supports *Scleropogon brevifolius*, *Hilaria mutica*, *Bouteloua gracilis*, *Prosopis glandulosa*, *Opuntia imbricata*, *Rhus microphylla*, and *Croton pottsii*. Streambeds may be broad, and covered with tussocks of *Sporobolus wrightii*.

About 40 km (25 miles) east of the mountains there is an abrupt change in the vegetation where gypsum outcrops of the Castile Formation are exposed. This rolling plain is covered mostly by *Coldenia hispidissima* and *Bouteloua breviseta*, although some slopes are nearly barren. There are also scattered *Juniperus pinchotii*, *Rhus microphylla*, *Koerberlinia spinosa*, and *Yucca elata*, usually on small pockets of sandy soil. Depressions and sinks contain a more diverse association of *Scleropogon brevifolius*, *Hilaria mutica*, *Atriplex canescens*, *Larrea tridentata*, *Prosopis glandulosa*, and *Rhus microphylla*. The gypsum plain is bordered on the east by low limestone hills of the Rustler Formation, and here *Larrea tridentata* resumes dominance. Toward the Pecos River there is a gradual shift to the *Prosopis glandulosa* grasslands of the Sandy South Plains.

It should be apparent from the preceding overview that delimiting Chihuahuan Desert in this region is arbitrary. Both Gehlbach and Warnock have classified the vegetation of the Guadalupe and the differences between their systems center on this problem. For example, Gehlbach considers the *Dasyilirion leiophyllum*—*Agave lecheguilla* association to represent the Succulent Desert Formation, while Warnock has called the same vegetation part of the Grassland Formation. Shreve and Wiggins (1964) considered the outstanding characteristics of desert communities to be “. . . low but unequal stature of plants, openness of stand, and the mixture of dissimilar life forms.” By these criteria most of the region below 2125 m (7000 ft) qualifies as desert. On the other hand, if the nature of the dominant species is emphasized, much of the east slope can be called grassland. Since the existing schemes leave a latitude of choice and little room for improvement, we prefer to stress the continuous and dynamic nature of the vegetation and avoid classification.

FACTORS INFLUENCING VEGETATION

Gehlbach's analysis of the east escarpment indicated that elevation and exposure are the primary variables interacting to influence vegetation. Our experience leads us to suggest three additional factors to account for variation in the composition of the xeric associations. A reasonably predictive gradient should result from considering the integration of the following variables: elevation, exposure, substrate texture (including depth), total salt content of the substrate, and gypsum content of the substrate.

Elevation imposes a gradient of increasing available moisture with ascent. Primary causes are increased precipitation induced by thermal air currents and cooler temperatures lowering the evaporation rate. The existence of coniferous forest in an otherwise arid region is an adequate demonstration of the influence of elevation.

Vegetational variation with exposure is an expression of differences in evaporation rate caused by solar heating. At about 1725 m (5700 ft) elevation, a sandstone ridge west of Cutoff Mountain has *Bouteloua eriopoda*, *Larrea tridentata*, *Fouquieria splendens*, and *Yucca torreyi* on the south-facing slope, whereas on the northern exposure co-dominants with *Bouteloua eriopoda* are *Bouteloua warnockii*, *Eurotia lanata*, and *Xanthocephalum sarothrae*. Narrow canyon bottoms provide particularly favorable situations for moisture retention because direct solar radiation is minimal and denser cooled air becomes channeled in the canyons as it flows downhill at night. Limestone crevice plants, among them *Salvia summa*, *Perityle quinqueflora*, and *Nama xylopodum*, reach their lower elevational limits in the canyons. A secondary effect of exposure is to modify the extent and duration of critical minimal temperatures. The rapid absorption of heat by south-facing rock ledges during the day can mean daily thawing even with freezing air temperatures. On the east escarpment *Yucca faxoniana*, *Fouquieria splendens*, and *Epithelantha micromeris* occur as high as 2050 m (6700 ft) on south-facing limestone ledges. The overall effect of exposure results in extensive interdigitation of species with differing environmental tolerances.

The importance of substrate texture can be illustrated by a detailed comparison of two study plots established on the west side of the mountains. For analysis, a 20 × 50 m area was divided into a grid of 5-m squares for a total of 20 squares. All species within each square were recorded and a density count made of woody species. To determine coverage eleven 20-m line intercepts were run every 5 m perpendicular to the long axis of the plot, giving a total distance of 220 m. Both plots are located on the bajada at an elevation of about 1225 m (4000 ft). They are separated by approximately 3.5 km and the only major difference is substrate texture. TTU 8-3-74 is on deep, silty soil typical of the middle bajada. The number of species in the plot is 10, and the total plant cover measures 21%, almost entirely *Larrea tridentata*. TTU 8-2-74 is on quartz sandhills derived from wind deposition. It contains a total of 32 species. Total plant cover is again about 21%, but is divided into 11.4% perennial grasses, 7.1% shrubs, 0.6% perennial herbs, and 1.8% annuals. The quartz sand plot has over three times as many species, and dominance is divided among several life forms.

TTU 8-9-74 is located on an alluvial fan about 8 km north of the quartz sand plot. Elevation is about 1200 m (3900 ft), and the slope and exposure are equivalent to the plots above. Although the plot is only half size (20 × 25 m), it contains 41 species. Total plant cover is 24%—2.3% shrubs, 0.4% stem succulents, 18.7% perennial grasses, and 2.9% annuals. The coarser texture of the alluvial fan appears to favor perennial grasses and a greater species diversity. The data are insufficient for conclusions, but hints of the underlying causes are gained by

observation of the sites during rains. As in the rest of the Chihuahuan Desert, much of the yearly rainfall is received from brief, violent storms in the late summer. At the *Larrea tridentata* site, sheets of water run down the bajada, eventually concentrating in the arroyos. However, on the quartz sand there is virtually no runoff; the rain simply sinks into the sand. A study conducted on loess soil in the Negev Desert of Israel (Evenari et al. 1971) showed the greatest runoff occurring on low slopes with few surface stones, a condition approximating the middle bajada. Surface stones appeared to facilitate water penetration by slowing downslope movement and preventing formation of a continuous soil crust after wetting. Other factors being equal, it seems that a greater proportion of the precipitation is available to plants on soils of a coarser texture, and this is reflected by the more complex associations of these sites. Notice that the alluvial fan, with the most rocky soil, also has the greatest number of species.

The limiting effect of high concentrations of salts on water availability is well known. In the Guadalupe Mountains region this factor is most important near the Salt Flat. Communities in this area show a low diversity characteristic of situations with high moisture stress. Much of the *Sporobolus airoides* grassland has been seriously disturbed by grazing, but a relatively undisturbed site was located south of Highway 62 on the west side of the Salt Flat. There are only seven species in the plot, and total plant cover is 16.1%. *Sporobolus airoides* clearly dominates with a coverage of 12.5%. The shrubs *Atriplex canescens* and *Frankenia jamesii* are next in importance with coverages of 1.9% and 1.7%, respectively, and *Yucca elata* is last with about 0.1%. The presence of *Coldenia hispidissima* and *Gaillardia multiceps* here suggests a high concentration of gypsum, a common characteristic of local saline soils.

Gypsum has a profound influence upon vegetation, but the nature of its action is not understood. The abrupt change in vegetation on the edge of gypsum outcrops and the restriction of several species exclusively to gypseous soils indicate selective pressures differing radically from those of other habitats in the region. One of the more unique communities in the region occurs on gypsum outcrops covered by very shallow soils. These have been previously described by Waterfall (1948) and our observations coincide with his. *Coldenia hispidissima* is a major component of such habitats. On two outcrops west of the mountains its coverage is 11.9% and 7.3%, well ahead of any other species. *C. hispidissima* also dominates two plots on the Castile Formation (Fig. 1), the coverages being 12.8% and 10.3%. Average density ranges from 0.9 to 1.8 plants/m². *Bouteloua breviseta* usually follows *C. hispidissima* in coverage with an observed range of 1.1-3.4%. Gypsum outcrops on both sides of the range are characterized by a relatively higher percentage of herbaceous perennial species. On our plots they account for 20-39% of



Fig. 1. Gypsum plain on the Castile Formation. Dominants are *Coldenia hispidissima* and *Bouteloua breviseta* with scattered *Rhus microphylla* and *Yucca elata*.



Fig. 2. Beach ridge southwest of Lewis Well. *Coldenia hispidissima* dominates with scattered *Yucca elata* and *Opuntia leptocaulis*.

the total. The plots east of the mountains have more species, a higher coverage of shrubs, and a higher total coverage than the outcrops on the west side. The Pleistocene beach ridges (Fig. 2) east of the Salt Flat differ from these outcrops in that they tend to have a somewhat more sandy soil and often show greater species diversity. *Coldenia hispidissima* is still dominant, but on our plot cover and density are reduced. Among the common associated species are *Yucca elata*, *Sporobolus nealleyi*, *Bouteloua breviseta*, *Atriplex canescens*, *Ephedra torreyana*, *Krameria glandulosa*, *Opuntia leptocaulis*, and *O. polyacantha*. The beach ridges pass into the gypsum dunes, which are described later.

This completes the discussion of what we feel are the important physical factors influencing vegetation development. However, vegetation is dynamic, and ignorance of past conditions can result in misleading conclusions. Duration and intensity of stock use is an important variable affecting both coverage and composition. A second study plot was set up in the quartz sandhills about 2 km west of the one described above. The boundary fence is down in this area, and there is unrestricted grazing by cattle from the adjacent ranch. The two plots share 21 species, and the east, with a total 32 species, has 5 more than the west. Perennial grass cover is 11.4% on the east and 5.4% on the west. Much of the difference can be accounted for by a sharp decrease in *Sporobolus giganteus* coverage. In addition, *Prosopis glandulosa* increases from 1.8% to 5.5% coverage on the west plot. Increased grazing is implicated as the primary reason for the observed differences between the plots. Another example of livestock impact can be seen at Williams Ranch, where *Larrea tridentata* is concentrated in the old corrals. The precise nature and permanence of changes due to grazing are important topics for future research in this region.

UNUSUAL ASPECTS

The Guadalupe Mountains possess a number of unique botanical features. The most striking are associated with the mountain habitats, but some aspects of the desert area also deserve attention.

Jatropha dioica was first discovered in this area by Roger Reisch and Michael Glass on a small hill on the west bajada 0.8 km north and 3.6 km east of Lewis Well. The small colony occupies a limestone outcrop on the south slope at 1234 m (4050 ft) elevation. A permanent plot was designated to encompass most of the colony, and the resulting data are summarized in Table 1. *Jatropha* leads all other species in coverage; however, its importance decreases rapidly in all directions from the site. The hillside appears to possess no unique qualities except its relatively low elevation. No other locations for *Jatropha* are known from this region, and the locality represents a northern disjunct in the distribution.

Yucca faxoniana is scarce in the Guadalupe Mountains. The largest

TABLE 1. Species found in the *Jatropha dioica* colony. Percent cover on a 220-m line intercept is in parentheses.

| | |
|--|---------------------------------------|
| Shrub (14.9%) | Club moss |
| <i>Jatropha dioica</i> (11.5%) | <i>Selaginella wrightii</i> (0.2%) |
| <i>Larrea tridentata</i> (1.8%) | Leaf succulent (4.7%) |
| <i>Viguiera stenoloba</i> (1.3%) | <i>Agave lecheguilla</i> (4.7%) |
| <i>Fouquieria splendens</i> (0.3%) | <i>Dasyllirion leiophyllum</i> |
| <i>Prosopis glandulosa</i> | Perennial grass (2.0%) |
| <i>Coldenia greggii</i> | <i>Bouteloua eriopoda</i> (0.7%) |
| <i>Parthenium incanum</i> | <i>Sporobolus cryptandrus</i> (0.5%) |
| <i>Ephedra aspera</i> | <i>Muhlenbergia porteri</i> (0.5%) |
| <i>Aloysia wrightii</i> | <i>Setaria leucopila</i> (0.1%) |
| Stem succulent (3.7%) | <i>Trichachne californica</i> (0.1%) |
| <i>Opuntia lindheimeri</i> (2.3%) | <i>Aristida glauca</i> (0.1%) |
| <i>O. phaeacantha</i> (1.2%) | <i>Bouteloua warnockii</i> |
| <i>O. violacea</i> (0.1%) | <i>Aristida pansa</i> |
| <i>O. imbricata</i> | Herbaceous perennial |
| <i>O. leptocaulis</i> | <i>Euphorbia fendleri</i> |
| <i>Coryphantha strobiliformis</i> (0.1%) | Annual |
| <i>Echinocereus pectinatus</i> | <i>Bahia absinthifolia</i> |
| <i>E. triglochidiatus</i> | Suffrutescent perennial (0.6%) |
| <i>E. enneacanthus</i> | <i>Menodora scabra</i> |
| <i>E. horizontalonius</i> | <i>Talinum angustissimum</i> |
| Fern | <i>Polygala scopariodes</i> |
| <i>Notholaena sinuata</i> var. <i>cochisensis</i> (0.2%) | <i>Dyssodia pentachaeta</i> |
| | <i>Hibiscus denudatus</i> (0.6%) |

concentration observed, consisting of about 30 individuals, is at an elevation of 2050 m (6700 ft) near the top of the ridge south of Smith Canyon, about 1.3 km northwest of Frijole Ranger Station. Smaller concentrations occur on the north side of the mouth of Pine Spring Canyon, and on the south rim of Bone Canyon. In Lower McKittrick Canyon grow the largest plants, which have been referred to *Y. carnerosana* in Correll and Johnston (1970). Isolated individuals are widely scattered on rocky slopes and alluvial deposits along both sides of the range. A permanent plot in the largest colony shows *Dasyllirion leiophyllum*, *Cercocarpus montanus* var. *paucidentatus*, *Aristida glauca*, and *Viguiera stenoloba* to be the most important associates. Coverage by growth forms is divided into 14% shrubs and suffrutescent perennials, 14% leaf succulents, 11% perennial grasses, and less than 1% herbaceous perennials. Few young plants have been seen, but they could easily be mistaken for *Yucca baccata*. Furthermore, the large size of the plants suggests that they live for a long time, and a very low rate of reproduction should be adequate to maintain the population at its present level.

The quartz sandhills are an area of wind-deposited sand on the bajada due west of Shumard Peak (Fig. 3). They contain an unusual floristic as-



Fig. 3. Quartz sandhills west of Shumard Peak. *Sporobolus giganteus*, *S. flexuosus*, and *S. contractus* are dominant. The west escarpment including Guadalupe Peak is visible in the background.

semblage differing appreciably from most surrounding areas (Table 2). More open sites support plants usually associated with the Rio Grande Valley to the west, including *Dalea scoparia*, *D. terminalis*, and *Poliomintha incana*. In depressions are species characteristic of sandy habitats to the north and east, among them *Sporobolus giganteus*, *Oryzopsis hymenoides*, *Panicum ramisetum*, and *Penstemon ambiguus*. *Prosopis glandulosa* var. *torreyana* and *Atriplex canescens* are the most common woody plants and the dominant grasses are *Sporobolus flexuosus*, *S. contractus*, and *S. giganteus*. The woody species tend to occur as scattered clusters separated by areas of grasses associated with *Croton dioicus* (Fig. 4). As noted previously, perennial grasses decrease greatly toward the western part of the sandhills.

Gypsophilic plants are among the more unusual elements of the regional flora. Most of the species can be found on both sides of the range, usually in association with *Coldenia hispidissima* and *Bouteloua*

TABLE 2. Species found on quartz sandhills.

| | |
|---------------------------------|---------------------------------|
| <i>Shrub</i> | <i>Croton dioicus</i> |
| <i>Atriplex canescens</i> | <i>Dalea terminalis</i> |
| <i>Artemisia filifolia</i> | <i>Dithyrea wislizenii</i> |
| <i>Chrysothamnus pulchellus</i> | <i>Gaillardia pinnatifida</i> |
| <i>Dalea scoparia</i> | <i>Hymenopappus flavescens</i> |
| <i>Ephedra torreyana</i> | <i>Leuceleone ericoides</i> |
| <i>Krameria glandulosa</i> | <i>Machaeranthera scabrella</i> |
| <i>Lycium berlandieri</i> | <i>Maurandya wislizenii</i> |
| <i>Penstemon ambiguus</i> | <i>Melampodium leucanthum</i> |
| <i>Poliomintha incana</i> | <i>Oenothera pallida</i> |
| <i>Prosopis glandulosa</i> | <i>Rumex hymenosepalus</i> |
| var. <i>torreyana</i> | <i>Sarcostemma cynanchoides</i> |
| <i>Perennial grass</i> | <i>Sphaeralcea incana</i> |
| <i>Bouteloua eriopoda</i> | <i>S. subhastata</i> |
| <i>Cenchrus incertus</i> | <i>Zephyranthes longifolia</i> |
| <i>Muhlenbergia porteri</i> | <i>Annual</i> |
| <i>Oryzopsis hymenoides</i> | <i>Acanthochiton wrightii</i> |
| <i>Panicum ramisetum</i> | <i>Bahia absinthifolia</i> |
| <i>Setaria leucopila</i> | <i>Bouteloua barbata</i> |
| <i>Sporobolus contractus</i> | <i>Euphorbia glyptosperma</i> |
| <i>S. flexuosus</i> | <i>E. parryi</i> |
| <i>S. giganteus</i> | <i>Helianthus petiolaris</i> |
| <i>Leaf succulent</i> | <i>Kallstroemia californica</i> |
| <i>Yucca elata</i> | <i>K. parviflora</i> |
| <i>Stem succulent</i> | <i>Linum aristatum</i> |
| <i>Opuntia leptocaulis</i> | <i>Munroa squarrosa</i> |
| <i>Sedge</i> | <i>Panicum hirticaule</i> |
| <i>Cyperus</i> sp. | <i>Pectis papposa</i> |
| <i>Perennial herb</i> | <i>Portulaca parvula</i> |
| <i>Caesalpinia jamesii</i> | <i>P. retusa</i> |
| | <i>Tidestromia lanuginosa</i> |

breviseta on gypsum outcrops. An exception is *Anulocaulis gypsogenus*, which appears limited to the Castile Formation east of the Guadalupes. In contrast *Selinocarpus lanceolatus* is rare east of the range, as is *Gaillardia multiceps* which has been seen only at a single roadside locality in the Rustler Hills. Both are common immediately west of the range.

The gypsum dunes are a prominent feature of the landscape east of the Salt Flat, the high white dunes being visible from most of the west side. On the northeast corner they are loose, shifting, and virtually barren (Fig. 5), becoming progressively stabilized toward the southwest, where they merge with crusted gypsum ridges. A list of species found in this area is presented in Table 3. Loose sands support an association dominated by *Poliomintha incana*, *Andropogon hallii*, and *Dalea scoparia*. Within the dunes are scattered basins of level, heavily crusted gypsum soil. In this habitat a plot showed a total plant cover of only 6%

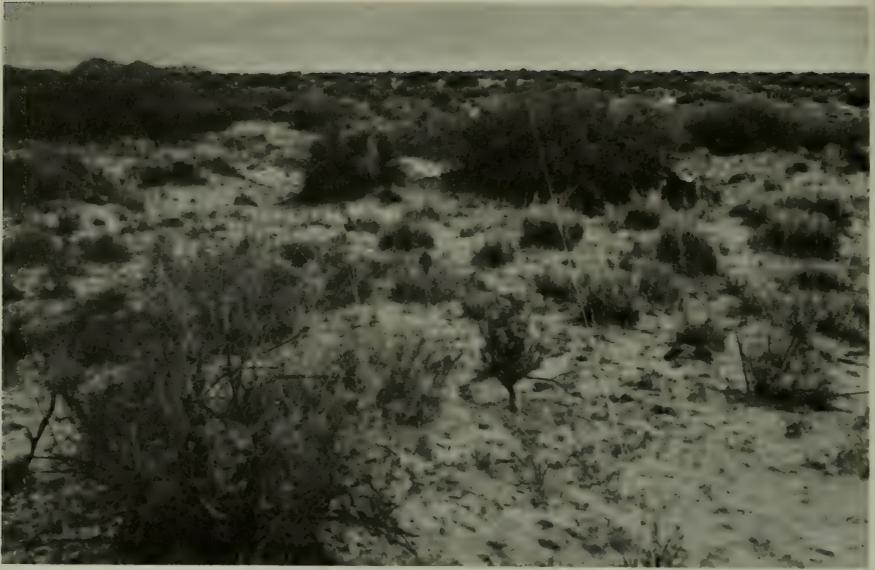


Fig. 4. Quartz sandhills near the park boundary. *Prosopis glandulosa* "hummocks" with *Sporobolus flexuosus*, *S. contractus*, and *Croton dioicus* between.



Fig. 5. Northeast end of the gypsum dunes. The increased vegetative cover to the west is apparent.

TABLE 3. Species found in gypsum sand.

| | |
|--|----------------------------------|
| <i>Shrub</i> | <i>Coldenia hispidissima</i> |
| <i>Dalea scoparia</i> | <i>Dalea terminalis</i> |
| <i>Ephedra torreyana</i> | <i>Dithyrea wislizenii</i> |
| <i>Krameria glandulosa</i> | <i>Gaillardia multiceps</i> |
| <i>Lycium berlandieri</i> | <i>Lepidium montanum</i> |
| <i>Penstemon ambiguus</i> | <i>Machaeranthera scabrella</i> |
| <i>Poliomintha incana</i> | <i>Mentzelia humilis</i> |
| <i>Stem succulent</i> | <i>Nama carnosum</i> |
| <i>Coryphantha scheeri</i> | <i>Nerisyrenia linearifolia</i> |
| <i>Echinocereus triglochidiatus</i> | <i>Oenothera pallida</i> |
| <i>Opuntia imbricata</i> | <i>Selinocarpus lanceolatus</i> |
| <i>O. leptocaulis</i> | <i>Senecio warnockii</i> |
| <i>O. polyacantha</i> | <i>Sphaeralcea subhastata</i> |
| <i>O. violacea</i> | <i>Thelesperma megapotamicum</i> |
| <i>Leaf succulent</i> | <i>Perennial grass</i> |
| <i>Yucca elata</i> | <i>Andropogon hallii</i> |
| | <i>Bouteloua breviseta</i> |
| <i>Annual</i> | <i>Oryzopsis hymenoides</i> |
| <i>Kallstroemia californica</i> | <i>Sporobolus contractus</i> |
| <i>K. parviflora</i> | <i>S. cryptandrus</i> |
| <i>Townsendia annua</i> | <i>S. flexuosus</i> |
| <i>Herbaceous perennial</i> | <i>S. giganteus</i> |
| <i>Abronia angustifolia</i> ¹ | <i>S. nealleyi</i> |

¹A perennial form of this species.

dominated by *Bouteloua breviseta*, *Coldenia hispidissima*, and *Krameria glandulosa*. Trough-like depressions between the low dunes contain dense stands of *Bouteloua breviseta* with a coverage measuring as high as 23%. Associated species include *Krameria glandulosa*, *Ephedra torreyana*, and *Yucca elata*. Where unstable dunes give way to the crusted gypsum ridges, *Sporobolus nealleyi*, *Coldenia hispidissima*, and *Opuntia polyacantha* become dominant. With respect to floristic composition, the gypsum sands appear to represent a gradient of habitats transitional between the quartz sandhills on the east and the gypsum ridges to the south and west. This unusual combination of edaphic factors is reflected by plant associations which are unique to the area.

SUMMARY

The creation of Guadalupe Mountains National Park has assured the protection of examples of most desert communities in the region. However, the gypsum sands lie immediately outside the park on private lands, and although there is no threat at present, should the area become accessible to recreational vehicles the plant cover will be destroyed rapidly. We suggest that the unique nature of these dunes be recognized in planning the proposed paved road through the area. Ex-

cept for *Anulocaulis gypsogenus*, populations of all regional gypsophilic species are protected within the park. The variety of habitats within the park makes it an ideal area for the study of factors affecting plant distributions. In addition, continued monitoring of plots after adequate fencing is established will provide a control for evaluating the impact of grazing on desert vegetation. Obviously, the research opportunities offered within the park have scarcely been tapped, and future studies can add much to our understanding of Chihuahuan Desert vegetation.

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The Natural Products Chemistry of *Larrea tridentata* Cav. in the Chihuahuan Desert

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INTRODUCTION

Larrea (Zygophyllaceae) is composed of four South American and one North American species distributed in the arid and semi-arid areas of the two continents. Two species, *L. cuneifolia* (DC.) Coville (tetraploid, $n = 26$) and *L. nitida* Cav. (diploid, $n = 13$), are restricted to Argentina, a third, *L. ameghinoi* Speg. (diploid, $n = 13$), occurs in Chile as well as Argentina, while a fourth, *L. divaricata* Cav. (diploid, $n = 13$), occurs primarily in Argentina and Chile with a few small, isolated populations in Peru and Bolivia. The fifth species, *L. tridentata* Cav., is unique in that it is found in North America where it occurs as a diploid ($n = 13$) race in the Chihuahuan Desert, tetraploid ($n = 26$) in the more arid Sonoran Desert, and hexaploid ($n = 39$) in the still drier Mojave Desert.

Here we will not attempt to present a detailed account of the natural products chemistry of the creosote bush since we are presently editing a volume on *Larrea* (Mabry, Hunziker, and DiFeo, in press) which will contain a thorough account not only of the chemistry of all the *Larrea* taxa from North and South America, but also details of other aspects of the biology and ecology of the genus. Nevertheless, we do wish to summarize here the rather remarkable chemical story of the diploid *Larrea tridentata* which dominates in much of the Chihuahuan Desert.

At the outset, it should be pointed out that one significant result of our investigations is the discovery that the three euploid levels of *L. tridentata* have, as far as we can determine, an identical (at least qualitatively) natural products chemical pattern; moreover, the patterns are essentially quantitatively the same, with some tendency for the hexaploid

race in the very arid Mojave Desert to have a heavier coat of external resin (presumably as an aid in preventing protoplasmic dessication). Based upon our previous investigations of other species, the similarity of the chemical patterns for the three ploidy races suggest to us a recent autopolyploid origin for the tetra- and hexaploid populations in North America and support the view that all the present North American populations of *L. tridentata* were derived from a single genotype in relatively recent times.

In addition, although the four *Larrea* species in South America exhibit a chemical pattern different from the North American *Larrea*, the chemical data do indicate that the North American diploid race is closely related to the South American *L. divaricata*; therefore, at this time we favor a long distance dispersal mechanism (probably involving migratory birds which frequent salty marshes) for the introduction of seeds of *L. divaricata* or a *L. divaricata*-like plant from South to North America, giving rise initially to the diploid of *L. tridentata*. Subsequent polyploidy occurred as the taxon moved into the two drier deserts in recent times. Our data do not rule out that the diploid may have persisted through the glacial periods in central Mexico. (All of the above topics will be discussed in detail in the aforementioned volume on *Larrea*.) The remainder of this short report will summarize the natural products chemistry of *Larrea* from the Chihuahuan Desert, which in our opinion, represents a major resource of this desert. Indeed, the natural products chemistry of all of the Chihuahuan Desert plants together constitute a remarkable resource since most of these plants produce a high percentage (15-50% of the dry weight of the leaves) of terpenes, phenolics, etc.; this area of chemical production can be expected to become more important as petrochemicals become increasingly scarce.

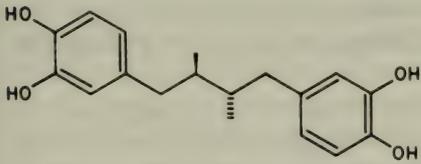
EXTERNAL CHEMISTRY

External Resin on the Leaves of *Larrea*

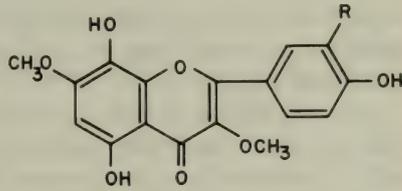
Material representing as much as 15% of the dry weight of leaves of *L. tridentata* can be removed by a 5-minute wash with either ether or acetone. The major component in the external leaf resin is nordihydroguaiaretic acid (NDGA) (I), one of the most powerful antioxidants known. NDGA has been employed at various times as an antioxidant in foods, pharmaceuticals, industrial polymers, lubricants, and rubber. In addition, NDGA serves as an inhibitor of various enzymes and has some antimicrobial and antitumor activity (see Oliveto 1972, for an excellent review of the uses of NDGA).

The external leaf resin also contains an array of flavonoid aglycones and the structures of 19 of these highly hydroxylated and methoxylated compounds have been determined (Sakakibara et al. 1976) including three

new, unusual flavonoid aglycones containing 8-hydroxyl functions (e.g., II and III) which were found to be characteristic of the North American *Larrea* taxa (Sakakibara et al. 1975).



I, Nordihydroguaiaretic acid (NDGA)



II, Herbacetin 3, 7-dimethyl ether, R = H

III, Gossypetin 3, 7, 3'-trimethyl ether,
R = OCH₃

External Wax on the Stems and Leaves

A complex wax mixture which can be extracted from the surface of the stems and leaves of *Larrea tridentata* with petroleum ether has properties much like carnuba wax. The material, which has been found to be composed of esters of long chain acids and alcohols (Table 1) (Seigler et al. 1974), represents about 1% of the dry weight of the plant material examined.

TABLE 1. Relative percentage composition of the wax esters on the stems and leaves of *Larrea tridentata* from the Chihuahuan Desert (Seigler et al. 1974).

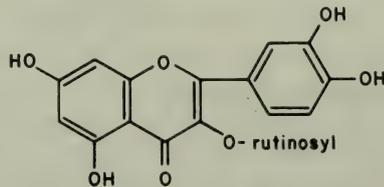
| Wax ester | Acid | Alcohol | Relative percentages |
|-----------------|--|--|----------------------|
| C ₄₆ | C ₂₂ | C ₂₄ | 4.8 |
| C ₄₈ | C ₂₂ , C ₂₄ | C ₂₆ , C ₂₄ | 16.5 |
| C ₅₀ | C ₂₂ , C ₂₄ , C ₂₆ | C ₂₈ , C ₂₆ , C ₂₄ | 27.0 |
| C ₅₂ | C ₂₂ , C ₂₄ , C ₂₆ , C ₂₈ | C ₃₀ , C ₂₈ , C ₂₆ , C ₂₄ | 29.0 |
| C ₅₄ | C ₂₄ , C ₂₆ , C ₂₈ , C ₃₀ | C ₃₀ , C ₂₈ , C ₂₆ , C ₂₄ | 16.0 |
| C ₅₆ | C ₂₆ , C ₂₈ , C ₃₀ , C ₃₂ | C ₃₀ , C ₂₈ , C ₂₆ , C ₂₄ | 6.2 |

INTERNAL LEAF CHEMISTRY

Internal Flavonoid Glycosides

More than 10 flavonoid glycosides, for example, rutin (IV), have been detected in the aqueous 85% methanol extract of the leaves of *L. tridentata*; the structures of all these compounds are under investigation in our laboratory.

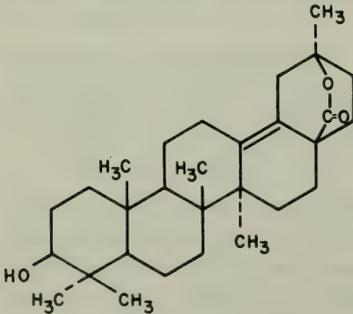
The distribution of these glycosides in the genus *Larrea* suggests to us that the South American diploid *L. divaricata* gave rise to North American *L. tridentata* and, at the same time, provided at least one genome to the South American tetraploid, *L. cuneifolia*.



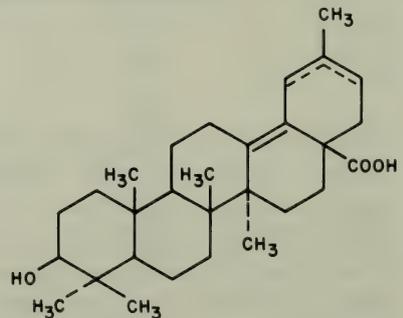
IV, Rutin

Internal Saponins

Saponins (triterpene glycosides) have been reported recently to represent about 10-15% of the dry weight of leaves of *Larrea*; moreover, the structures of two of the sapogenins, which occur internally in the leaves as glycosides, have been determined; namely, larreagenin A (V) and larreic acid (VI) (Habermehl and Möller 1974). We have verified the presence of saponins in *Larrea* but neither the high quantities nor structural types reported by Habermehl and Möller.



V, Larreagenin A



VI, Larreic acid

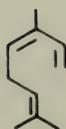
The evolutionary importance of the discovery of saponins in *Larrea*, as well as their potential importance for man, have only now begun to be considered.

Volatile Oils

Steam distillation of fresh leaves of *Larrea* has yielded a complex mixture of more than 400 compounds; yet the total yield of oil is less than 0.5% of the weight of the leaves. A number of these substances (almost 100) in this complex mixture has already been identified (unpublished results from our laboratory) including those shown below; some of these substances may be important as components of flavors and perfumes.

 α -pinene β -pinene

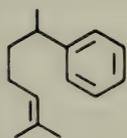
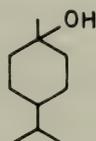
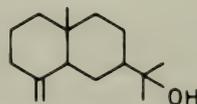
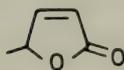
limonene

 β -ocimene

p-cymene



camphene

 α -curcumene β -terpineol β -eudesmol β -angelica lactone

SUMMARY

It was our intention in this short report to focus attention upon the synthetic ability of the creosote bush, *L. tridentata*; it is a rather remarkable chemical factory synthesizing several hundred natural products which together account for between 30-50% of the dry weight of the leaves and stems. Such synthetic ability is characteristic of many desert plants (although we know of none more prolific and diverse than *Larrea*) and together these plant chemicals constitute one of the least recognized resources of the Chihuahuan Desert.

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A Physiognomic Analysis of the Types of Transitional Vegetation in the Eastern Parts of the Chihuahuan Desert in Coahuila, Mexico

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Translated by Anthony J. Lucero, National Park Service

INTRODUCTION AND BACKGROUND

The so-called "Chihuahuan Desert" has been more properly designated as the "arid Chihuahuan zone" by Miranda (1955). This is the criterion which obtains in this present study. This last designation has prevailed to a greater degree in the literature dealing with the ecological aspects and the vegetation of northern Mexico.

The diverse types of vegetation that constitute the ecological and physiognomic mosaic of this extensive arid zone of the North American subcontinent, have merited the attention of several writers concerned with documenting the description of the vegetal cover and its geobotanical interpretation. It is hoped that just as there is already a work dealing with the flora and vegetation of the "Sonoran Desert" (Shreve and Wiggins 1964), we shall soon see a related work dealing with the vast and heterogeneous Chihuahuan arid zone.

Muller (1947) explains that, aside from the fragmentary information provided by Gregg and Wizlizenus, Coahuila State was not given the meticulous attention in the past century by naturalists, and only Pringle in the year 1888, paid attention to the description of the desert shrubs as well as the vegetation of the coniferous and oak forests and the "chaparral." To that could be added Berlandier's (1850) narrative with descriptive facts in the form of "diaries" kept during his trip through northeastern Mexico and parts of Texas in the middle of the 19th century. Also of interest, is Watson's (1882) floristic information which was based on the botanical material collected by Palmer in the northern regions of Mexico.

The interesting aspect in this case is that it appears that Pringle was the first to point out that the northern part—like the southeastern part—of Coahuila belongs to a “transition zone” from the viewpoint of phytogeography, to which Muller (1947), in referring to this great collector, adds that “the forests that he (Pringle) endeavors to include in the transition zone are zones which are not as extensive as shown by the maps.”

THE MOST RECENT LITERATURE

It is Muller (1939, 1947) who treats the aspects of vegetation and climate of Nuevo León and Coahuila with greater causative knowledge; he provides information on the types of vegetation and their relationship to the climate, and makes a profound study of the oaks.

With respect to Chihuahua State, LeSueur (1945) offers a complete treatise on the vegetal formations that embrace a large region located north of the 28th parallel.

I. M. Johnston contributes to the knowledge of the flora of northern Mexico with a series of first studies (1939, 1940a, b, c, 1941a, b, 1943a, b, c, d, 1944a, b, c). With respect to the southern part of the Chihuahuan arid zone, Rzedowski's studies (1956, 1957, 1964, 1966) deserve special mention; he includes—among other regions—the vast territory known as the “Altiplano Potosino” (high plateau of Potosí). Gentry (1957) describes the types of vegetation related to the pasturelands of Durango. Hernandez (1957, 1967) and Tapia-Jasso and Hernandez (1957) contribute agrostological themes concerning the northern part of Mexico. Miranda (1955) defines the forms of vegetal life of the country's arid zones by using physiognomic and ecological criteria which have proved very fruitful for subsequent research. Later, Miranda and Hernandez (1963, 1964) studied Mexico's types of vegetation and undertook aspects of the Mexican arid zones. Pérez-Rosales (1964) initiated studies of the radicular systems and autecological aspects of xerophytes in Coahuila, a subject not well examined yet. Meanwhile, Marroquin et al. (1964) studied the forest resources of economic significance in northern Mexico and prepared maps for distribution showing the most important species for food and forage: candellilla, samandoca palm, gobernadora, guayule, and prickly pear. At the same time, a documented work by Gonzalez and Scheffey (1964) appeared; it dealt with the human geography of the northeast arid zone of Mexico, including socioeconomic aspects with ecological bases.

Some works, related to the central theme that occupies us, exist on a regional and local level. Among these are the thesis by Edwards (1939); the thesis by Rojas-Mendoza (1965) dealing with the vegetation and flora of Nuevo León; Cano and Marroquin (1967) on the botanical aspects of la Sierra de La Paila, Coahuila; the thesis by Capó-Arteaga (1972) on the coniferae of Nuevo León; and Banda-Silva's thesis (1974) on the oaks of Galeana, Nuevo León. De La Cruz and Zapien (1974) summarize the experiences of a decade of experimental works by the Forestry Department in the arid zones of “La Sauceda,”

Coahuila, and Robert (1973) wrote on the distribution and ecology of the *Pinus cembroides* of eastern Mexico.

Exactness of Terms

It is advisable to reconsider the definition of terms to be used to avoid all possible ambiguities that the richness and connotation of technical terminology usually introduces through scientific, as well as popular, ecological literature. An ecotone (Carpenter 1938) is a transition zone between two phytocenosis; it is better defined as "that mixed community formed by the superposition of two communities;" in other words, it deals with "actual areas of transition between two adjacent communities, independent of whether they deal with climax or sere communities." Carpenter (1938) recognizes two types of ecotones: the first type embraces the general area between two major climax communities (for example, between forest and pastureland); the second type applies to "the communities which really prosper in the border zones of two phytocenosis of the first type ecotone."

The term forest (Robert, 1973) does not have a very precise meaning; it is applied to a community part of which is composed of trees and plants. Aubreville (1962) considers a tree—all woody—to be one which has a height of 7 m (23.1 ft) or more; we conventionally consider a tree to be one of 3.5 m (11.55 ft) or more in height.

The term formation in Clements' classic sense has a connotation akin to the one given to the climax communities. Thus, Roberts (1973) uses it in designating collective associations.

Matorral (shrub, brush) is a word which denotes phytocenosis constituted by plants of the middle level (matas) in the sense of Font-Quer (1965, cited by Robert 1973) and can properly be applied to any shrub community, open or closed.

VEGETATION

General concepts

Some technicians view the nomenclature procedure of designating the communities as somewhat trivial and without interest. However, when it becomes necessary to study the literature dealing with the primary and secondary types of vegetation, the climax and disclimax, mixed or transitional, as exist in such a vast region as the Chihuahuan arid zone, it becomes of fundamental interest to know the criteria that botanists who preceded us followed in the designations of communities before proceeding to their reaffirmation with adequate techniques or to their modification if merited by the circumstances. On the other hand, everyone is cognizant of the importance of knowing how to transmit knowledge; thus, the appropriate nomenclature is the best means of sustaining continuity.

Three fundamental criteria have been established (Aubreville 1962; Rzedowski 1965) in order to attain that end: (1) based on the physiognomic or structural similarities (or differences) of the plants, or with bases on the mor-

phological and phytosociological; (2) based on the similarities (or differences) of the ecological conditions; and (3) based on the floristic similarities (or differences).

In this study, we are following the first principle of that criteria, i.e., the physiognomic, but this does not mean that we are negating the validity and importance of the last two. For a more complete and effective physiognomic viewpoint in classifying the vegetal communities see Beard (1973) and Dansereau (1951).

In the Chihuahuan arid zones are found various types of vegetation. Some of them prosper on the fringes of the ecotone zone between the thick shrubs that measure 30 cm to 5 m (1 to 16.5 ft) in height. The associations with heights of 3.5 to 5.0 m (11.5 to 16.5 ft) can be classified under either term, forest or shrub, depending on other inherent characteristics of the dominant forms of life. In effect, there are microhabitats that determine the mean height of the shrub *Larrea* or an oak or pine forest, etc. On the other hand, the term "matorral" (shrub) enjoys vast usage in the geobotanical and ecological literature of Mexico; Aubreville (1962) considers it equivalent to the term *fourre* in French and possibly thicket or dense growth in English. Aubreville suggests conserving the term "maquis" for the communities of small shrubs natural to the Mediterranean (and perhaps to the California region), and desert shrubs and oak forests among the first and the coniferous forests especially as regards the pine forests; and the complex arid transition, difficult to define with precision, between pastureland and oak forest, and between these and the mesophyll forests (LeSueur 1945; Muller 1947; Gentry 1957; Rojas-Mendoza 1965; Rzedowski 1965).

Fasciation in Coahuila

The types of vegetation in the easternmost part of the Chihuahuan arid zone, lying to the southeast of Coahuila, which are treated in this work can best be described as follows: (a) Pinyon forest (study of the Sierra de Arteaga, see Fig. 1); (b) Dense thornless shrubs parvifolious Rosaceae (of the Sierra de Zapalinamé); (c) Grassland with woody shrubs (of the Cañon de San Lorenzo and "Los Angeles," Coahuila); (d) Oak shrubs or "chaparral" (of the Sierra de La Paila and other localities); (e) Mixed desert shrubs (Dr. Arroyo, Nuevo León and Cuernamé, Durango).

Pinyon forest (*Pinus cembroides*). At first sight, the features of this formation would be sufficient to classify it without hesitation as one belonging to the cold temperate regions. In this respect, Robert (1973) studies the ecology of the *Pinus cembroides* forest of eastern Mexico, based on the physiographic-ecological features and explains that the topography of the territory in this country favors the presence of this community in areas climactically conceived as arid. In effect, the simple indexes of aridity (González, 1963) based on the thermal regimen, rainfall, and evaporation indicate a rainfall deficit in the pinyon regions which favors the invasion of xeromorphic elements of the undergrowth

which integrate the pinyon forest. This explains the floristic diversity and the vast ecology (or "valencia") of these mixed and transitional communities (ecotones).

The most conspicuous elements of a xeric nature which usually associate with the pinyon forest are *Yucca carnerosana*, *Juniperus* spp., *Agave* spp., *Rhus* spp., *Berberis trifoliolata*, *Ephedra* spp., and others.

The ombrothermical diagrams prepared by Robert (1973) for pinyon regions such as those of Galeana, Nuevo León in the Sierra Madre Oriental, reveal a long dry spell for a period extending from October to May.

It is apparent that the phytocenosis in which *Pinus cembroides* dominates, is tied to the transition zones and orogenic units that border the Mexican High Plateau in the West as well as in the East. As pertains to the Sierra Madre Oriental, the internal and intermediate watersheds which are sometimes flanked by foothills and mountain ridges with a vegetal cover consisting of desert shrubs, do not permit pasturelands as well developed as those afforded by the western side of the Chihuahuan arid zone. The grasslands which are found in the southwestern part of Nuevo León, north of San Luis Potosí, and adjacent regions of Coahuila and Zacatecas, correspond to the communities conditioned by edafic factors. The most notable case is that offered by the *Bouteloua chasei* grassland.

For Robert (1973), the taxonomic complex represented by *Pinus cembroides* is indifferent to the underlying rocky substratum by virtue of finding itself on soils derived from limestone as well as igneous and volcanic rock. Moreover, there are wild zones in southern Nuevo León where the pinyon forest and its shrubby underbrush (i.e., the subvegetation) prosper in rich lime substratums. Likewise, the crests of the intermediate mountains, as some which link the Sierra Madre Oriental with the Saltillo-Parras axis of southern Coahuila (e.g., the Sierra de Zapalinamé, the Hedionda, and other more isolated ones such as La Paila, north of Saltillo), are often crowned with pine forests in which the pinyon also encounters favorable conditions for its development.

Shelford (1963: 293) cites the community represented by *Pinus-Juniperus* as one which characterizes the interior slopes of the Sierra Madre Oriental, and as a consequence, they become interlaced with the phytocenosis which belong to the western border of the Chihuahuan arid zone. As regards the *Pinus cembroides*, their distribution to the south in Mexico reaches latitude 20°; it embraces reduced and comparatively isolated areas (Robert 1973).

A good example of mixed associations (i.e., transitional) in which *Pinus cembroides* dominates in the presence of *Juniperus* is offered by the Sierra de Arteaga—20 to 25 km (12 to 15 miles) southeast of Saltillo, Coahuila. In these phytocenosis, the diversity of species merits subsequent attention. This list, based on repeated collections by the author, gives an idea:

| | |
|---|---|
| <i>Pinus cembroides</i> | <i>Rhus virens</i> |
| <i>Fraxinus cuspidata</i> var. <i>serrata</i> | <i>Berberis trifoliolata</i> var. <i>glauca</i> |
| <i>Yucca carnerosana</i> | <i>Fraxinus greggii</i> |
| <i>Rhus microphylla</i> | <i>Juniperus</i> spp. |

| | |
|---------------------------------|---|
| <i>Lindleyella mespiloides</i> | <i>Loeselia coerulea</i> |
| <i>Arbutus texana</i> | <i>Nissolia platycalyx</i> |
| <i>Menodora helianthemoides</i> | <i>Tillandsia recurvata</i> |
| <i>Ephedra aspera</i> | <i>Vernonia</i> sp. |
| <i>Parthenium incanum</i> | <i>Bouteloua gracilis</i> |
| <i>Viguiera brevifolia</i> | <i>Bouteloua curtipendula</i> |
| <i>Zexmenia brevifolia</i> | <i>Dyssodia setifolia</i> |
| <i>Quercus supranitida</i> | <i>Stevia berlandieri</i> |
| <i>Sophora secundiflora</i> | <i>Stevia</i> sp. |
| <i>Ceanothus greggii</i> | <i>Hymenoxys scaposa</i> var. <i>linearis</i> |
| <i>Opuntia stenopetala</i> | <i>Pellea</i> spp. |
| <i>Ceanothus ferox</i> | <i>Notholaena</i> sp. |
| <i>Salvia ballotaeflora</i> | <i>Cheilanthes</i> sp. |
| <i>Mortonia</i> sp. | <i>Castilleja</i> spp. |
| <i>Cowania plicata</i> | <i>Lamourouxia</i> sp. |
| <i>Cercocarpus mojadensis</i> | Invasoras: |
| <i>Quercus</i> spp. | <i>Opuntia imbricata</i> |
| <i>Panicum bulbosum</i> | <i>Opuntia tunicata</i> |
| <i>Gnaphalium</i> sp. | <i>Brickellia laciniata</i> |
| <i>Dasyilirion</i> sp. | <i>Baccharis pteronioides</i> |
| <i>Mimosa</i> sp. | <i>Gymnosperma glutinosum</i> |
| <i>Agave</i> sp. | <i>Tecoma stans</i> |
| <i>Chrysactinia mexicana</i> | <i>Hunnemania fumariifolia</i> |
| <i>Hymenoxys acaulis</i> | <i>Cassia</i> sp. |
| <i>Croton</i> spp. | <i>Bromus</i> sp. |
| <i>Phoradendron</i> spp. | <i>Tillandsia usneoides</i> |

As an example, let us cite the mountains of La Paila, La Gavia, La Gloria, etc. (Fig. 1).

In the types of vegetation of Coahuila which Muller (1947) establishes, the pinyon forest is not designated as such but is included in those denominated "montane low forest" and "montane mesic forest," judging from a list of the most dominant species frequently noted by him. For example:

| | |
|--|----------------------------------|
| + <i>Quercus gravesii</i> | <i>Quercus hypoleucoides</i> |
| <i>Juniperus pachyphloea</i> | + <i>Salvia regla</i> |
| + <i>Quercus laceyi</i> | + <i>Garrya ovata</i> |
| + <i>Juniperus flaccida</i> | + <i>Rhus trilobata</i> |
| + <i>Arbutus xalapensis</i> | + <i>Cercocarpus breviflorus</i> |
| <i>Quercus arizonica</i> | <i>Ptelea trifoliata</i> |
| <i>Quercus sinuata</i> var. <i>breviloba</i> | + <i>Bumelia lanuginosa</i> |
| <i>Quercus mohriana</i> | <i>Vitis arizonica</i> |
| <i>Fraxinus cuspidata</i> | |

The species preceded by an asterisk have been collected by Marroquín et al. in the Sierra de La Paila, Coahuila in mixed oak forests, in transition to pastureland

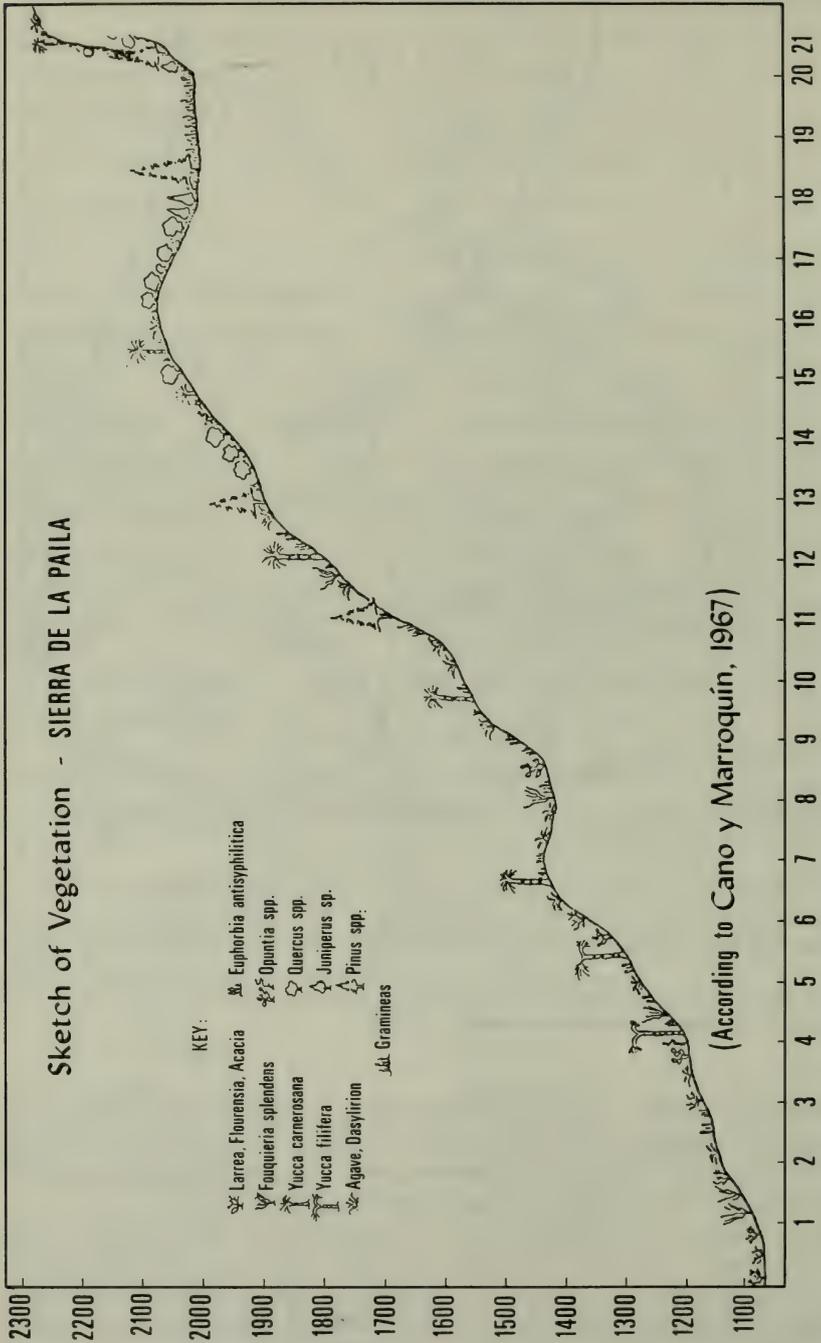


Fig. 2. The vegetation of the Sierra de la Paila, a cross-section (profile) is represented in this sketch by five well-defined types: microphyll desert shrub, "rosetofilo" desert shrub, chaparral, pine-juniper forest, and climax grasslands; the latter occur at altitudes between 1900 and 2000 m.

weather average 20 per year. The rainfall regimen is very variable from year to year but in all cases it is a question of the summer rainfall which ranges from 250 to 600 mm (10 to 24 inches) annually. The total number of dry months is from 6 to 7 per year.

The explanation of why the *Pinus cembroides* forest persists in conditions of an arid climate and the reason that the communities which become successfully intercalated in the forest can be so diverse and floristically rich, probably lie in factors of a historic nature, in conformity with the viewpoint outlined by Rzedowski (1966).

Dense thornless shrubs (parvifolious Rosaceae). This phytocenosis is found in slopes with a northwest facing in the Sierra de Zapalinamé (Fig. 3). The altitudinal sequence is as follows: at the top is found the pine forest which crowns the mountain, followed by fringe shrubs that can be considered akin to the scrub oak; the low oak forest is between points of 1750 to 2200 m (5775 to 7260 ft) in elevation, and following in the lower slopes appear the dense thornless shrubs, parvifolious Rosaceae.

Human influence, land clearing in the past, fires, and now the urbanization of some parts of the Sierra are factors which explain the presence of *Amelanchier denticulata*, *Lindleyella mespiloides*, and *Cowania plicata* in this type of vegetation. It occupies the slopes of the mountain ridges, over the calcareous substratum of shallow soil, furrowed by natural gullies with a great density of plants, and it is very possible that in the past, there existed a *Pinus cembroides* forest (according to De La Cruz, pers. comm.) in transition with more xeric phytocenosis. The prickly shrubs (*Crataegus*) are isolated.

The shrub Rosaceous is characterized by a mean height of 2.00 m (6.6 ft) and even though it interlaces as a subdominant *Berberis trifoliolata* which possesses prickly serrated folioles, it is considered a thornless shrub in its general physiognomy.

The ecological status of the pinyon forest, *sui generis*, in Mexico, makes Robert (1973) believe that this type of vegetation, located between xeric and mesic formations of cold-temperate filiation, exists in these ecotones thanks to the great biotic plasticity of the *Pinus cembroides*. The pinyon forest appears to possess great resistance to climactic conditions marked by a great thermic extension (oscillations which are, in general, characteristics of continental and arid climates), and subject to a variable rainfall regimen. This points out the possibility of using this species as suitable for reforestation. In Buenavista, 7 km (4.2 miles) south of Saltillo, Coahuila, the traditional *Pinus halepensis* Mill. has been used with great success in programs of reforestation on shallow, calcareous soils and sharp slopes.

The climactic pressures, the major ecological characteristics (altitude, thermic, and rainfall regimens), and the floristic composition of herbs and other species which are features of the pinyon forest in the ridges of the Sierra Madre Oriental represent very close similarities to those which govern the distribution of

SIERRA DE ZAPALINAMÉ NORTHWEST FACING SALTILLO

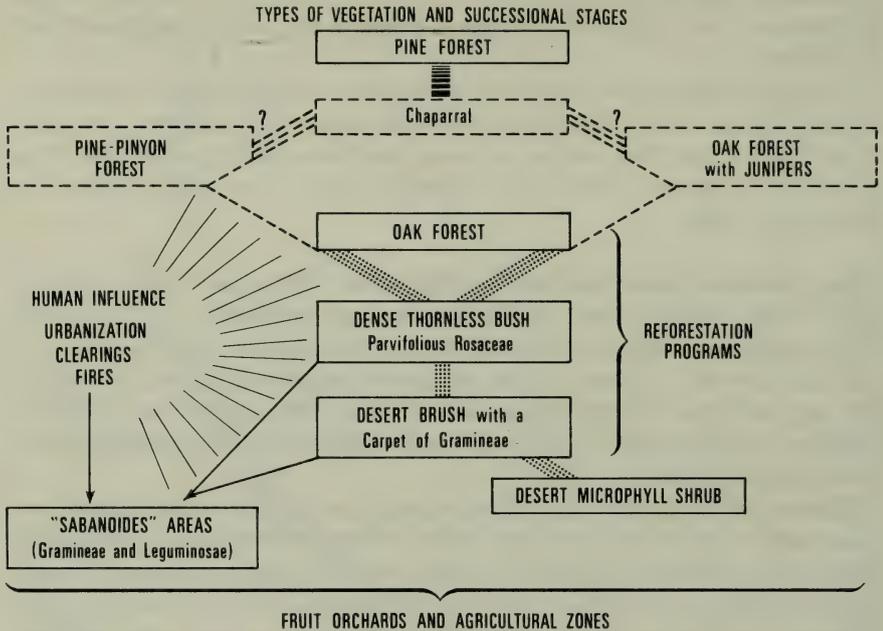


Fig. 3. Fruit orchards and agricultural zones.

The diagram shows the relation between primary and secondary types of vegetation in the Sierra de Zapalinamé, adjacent to the city of Saltillo, between 1 to 2 km (0.6 to 1.2 miles) southeast towards the property of "Lomas de Lourdes." This mountain is connected to the Sierra del Diamante and the Sierra de Arteaga on the east side. The Cañon de San Lorenzo, the entrance to which is located exactly east of Buenavista (Superior School of Agriculture "Antonio Narro") does not exhibit the same succession, since the exposure varies. The altitude ranges from 1,680 to 2,200 m (5,544 to 7,260 ft).

The perennial pine forest (aciculifólio) crowns the sierra. Transitional slopes towards the northwest facing reveal a close affinity to these three phytocenosis: shrub oak forest, pinyon forest and oak forests with junipers. This probable sequence has not been definitely fixed, because it could appear hypothetical.

The low oak forest occupies the middle slopes of the mountain. The oaks are poorly developed, the bark is rugose or smooth, the height is from 2 to 5 m (6.6 to 16.5 ft), sometimes the canopy is closed. The subdominants of the underbrush correspond principally to *Rhus*. The herbaceous stratum is very variable with a great diversity of species.

Human influence is felt from the oak forest down to the lower elevations, thus modifying the physiognomy of the vegetation on the sharp inclines. The disclimax vegetation of the dense-type shrubs occupies a great part of the low elevations and is composed basically of Rosaceae. Reforestation programs are being carried out only in the zone of influence of the Agricultural School "Antonio Narro." Major action, in this sphere, is expected in the region that surrounds the city of Saltillo.

The extensive thorny shrubs, the areas with grassy carpets and a stratum of huizaches (areas subanoides) are the most disturbed communities and grow on the poorest soil. The fruit orchard enclaves, the vineyards and some agricultural lands are located in the areas which are given the greatest attention, with better soil and less pronounced slopes. Cattle grazing is done on the "subanoides" areas.

the shrub oak forest in San Luis Potosí (Rzedowski 1966). This type of vegetation, also known as "chaparral" is found in mountainous regions where a semi-arid and temperate climate prevails; this type of vegetation possesses deciduous foliage but this caducity is of short duration, according to observations by Rzedowski. Likewise, the vegetative tangled growth of some short oaks is a favorable factor in the great resistance of these plants to fire.

The forest formations of Coahuila have been considered as not being homogeneous; they are floristically very diverse and the "isolated clumps" feature that they possess in the midst of arid plains (or "inselbergs") is the reason, according to Muller (1947), that they were overlooked in the past. These floristic elements are also present in the oak forests in the middle elevations of the Sierra, but their frequency is reduced. The Rosaceae possess an interesting phenology; they begin to flower in early spring and in October, they still exhibit that same stage in their life's cycle. They are usually tied to this community: *Chrysactinia mexicana*, *Dyssodia acerosa*, *Eysenhardtia*, *Brickellia veronicaefolia*, *Mimosa* sp., *Croton* spp., *Bouteloua hirsuta*, *Bouteloua gracilis*, and some intermixed. Among these species, several are cited by Rzedowski (1966:181) as indicators of the disturbance in the shrub oak forest of San Luis Potosí.

Sample species found on the northwest slope of the Sierra de Zapalinamé, on the ascent across the oak forest fringe of transition, reveal the following floristic composition:

| | |
|--|---|
| <i>Quercus sinuata</i> var. <i>breviloba</i> | <i>Commelina</i> aff. <i>dianthifolia</i> |
| <i>Quercus endlichiana</i> | <i>Anthericum torreyi</i> |
| <i>Quercus</i> aff. <i>hartwegii</i> | <i>Parthenium confertum</i> |
| <i>Quercus laceyi</i> | <i>Eupatorium</i> spp. |
| <i>Arbutus xalapensis</i> | <i>Senecio</i> sp. |
| <i>Cercocarpus mojadensis</i> | <i>Verbena</i> sp. |
| <i>Garrya ovata</i> | <i>Scutellaria</i> sp. |
| <i>Amelanchier denticulata</i> | <i>Solanum</i> sp. |
| <i>Zexmenia</i> spp. | <i>Cuphea</i> aff. <i>aequipetala</i> |
| <i>Ceanothus coeruleus</i> | <i>Bouvardia ternifolia</i> |
| <i>Conopholis mexicana</i> | <i>Cheilanthes</i> sp. |
| <i>Cowania plicata</i> | <i>Pellaea</i> spp. |
| <i>Berberis trifoliolata</i> | <i>Notholaena</i> sp. |
| <i>Rhus virens</i> | <i>Juniperus flaccida</i> |
| <i>Chrysactinia mexicana</i> | <i>Quercus emoryi</i> |
| <i>Acacia berlandieri</i> | <i>Tragia amblyodonta</i> |
| <i>Panicum bulbosum</i> | <i>Malaxis</i> spp. |
| <i>Piptochaetium fimbriatum</i> | <i>Vernonia</i> sp. |
| <i>Agave</i> sp. | <i>Crataegus greggiana</i> |
| <i>Artemisia ludoviciana</i> | <i>Opuntia stenopetala</i> |
| <i>Brickellia veronicaefolia</i> | <i>Dasylyrion</i> sp. |

Stevia sp.
Lindleyella mespiloides
Dalea sp.
Salvia greggii
Salvia regla
Salvia tiliaefolia
Castilleja latebracteata
Stephanomeria sp.
Desmodium spp.
Linum schiedeianum
Stevia berlandieri
Eryngium gramineum
Clematis pitcheri
Gnaphalium wrightii
Dyssodia porophylla
Loeselia coerulea
Loeselia scariosa
Gymnosperma glutinosum

Crataegus baroussana
Ipomoea sp.
Polypodium sp.
Adiantum sp.
Asclepias sp.
Muhlenbergia sp.
Tagetes lucida
Astragalus sp.
Lamourouxia sp.
Euphorbia sp.
Dahlia coccinea
Galium sp.
Geranium sp.
Bouteloua curtipendula
Acalypha sp.
Silene laciniata
Cirsium sp.
Muhlenbergia rigida

Grassland with woody shrubs. These phytocenosis of transition between the desert shrubs and the grassy communities possess a great diversity of combinations, difficult to discern; this makes generalization equally difficult.

The Experimental Ranch (livestock) Los Angeles, located 34 km (20.4 miles) south of Saltillo, offers hillside areas where the ecotone can be fully appreciated. The grassland *Aristida divaricata*, *Aristida wrightii*, *Aristida barbata*, and other pasturelands are associated with *Yucca carnerosana* and Cactaceae, some of them invaders such as the "clavellinas" and "cardenches"; these other elements occur: *Hymenopappus flavomarginatus*, *Grindelia oxylepis*, *Gaillardia mexicana*, *Mentzelia multiflora*, and *Salvia* aff. *chamaedryoides*. A similar case occurs in the nearby region of Cuencamé, Durango; there the grass *Bouteloua brevisetata* is tied to communities in which *Yucca rigida* appears in a desert shrub complex in which the following species have been identified:

Prosopis sp.
Dalea tuberculata
Hibiscus coulteri
Zexmenia brevifolia
Eysenhardtia polystachya
Cordia greggii
Viguiera stenoloba
Buddleia marrubiiifolia
Viguiera brevifolia
Notholaena sinuata
Tridens pulchellus
 (*Erioneruron pulchellus*)

Enneapogon desvauxii
Tragus berteronianus
Ayenia microphylla
Allionia incarnata
Heliotropium angustifolium
Larrea divaricata
Agave lecheguilla
Mendora scoparia
Lippia berlandieri
Coldenia greggii
Ziziphus obtusifolia var. *obtusifolia*
Linum lewisii

Selinocarpus angustifolius

These appear under disturbing conditions:

*Physalis lanceifolia**Haplopappus spinulosus**Ruellia* sp.*Palafoxia texana**Zinnia pauciflora**Pectis angustifolia**Polygala* sp.*Nicolletia edwardsii**Opuntia imbricata**Dyssodia papposa**Croton potsii* (*C. corymbulosus*)*Porophyllum ruderale**Porophyllum scoparium**Dyssodia porophylla* subsp. *cancellata**Caesalpinia sessilifolia**Trixis angustifolia**Erioneuron pulchellus**Gilia* sp.*Proboscidea parviflora**Opuntia leptocaulis**Opuntia macrocentra*

Shrub oak forest or chaparral. The physiognomic features of the shrub oak have been studied by Rzedowski (1966) under these main guidelines: the subject is a shrub 30 cm to 3.0 m (1 to 9.9 ft) in height, usually dense or very dense; there are places where the canopy formed by these shrubs is so intricate that it becomes impenetrable. The tangled characteristic possessed by some of the species which integrate the chaparral such as *Quercus microphylla* (Fig. 4), *Quercus derrumbaderoensis*, *Quercus cordifolia*, and others in diverse parts of the Sierra Madre Oriental and the mountainous clumps of the High Plateau (e.g., Sierra de Catorce, Sierra de La Paila, Sierra de la Marta, and others), favors the vegetative propagation of these shrubs, which respond to growth even after repeated fires; the shrub oak forests are in general resistant to fire as has been proved in the California region.

Rzedowski (1966) estimates that the shrub oak forests occupy approximately 3% of the entire surface of the state of San Luis Potosí, and "similar to the pinyon forest and many types of grasslands, they are characteristically types of an intermediate climate between the arid zones of the desert shrubs and the semi-humid zone of the oak and pine forests." He adds that these communities require relatively low temperatures. With respect to the altitude, they are found over the 1500 m (4950 ft) elevation, with the annual rainfall being from 400 to 750 mm (16 to 30 inches). The dry season, as in the case of the pinyon pine forests, is equally prolonged.

With respect to other physiognomic features of the chaparral, the plants which form it belong to the "durifolios (or esclerofolios) nanofolios or leptofilos." As regards the geological substratum on which they prosper, Rzedowski (1966) identifies two groups of shrub oak: one which grows on soils derived from igneous mother rock (e.g., rhyolites) and the other which prospers on a natural lime substratum. In reference to the states of Coahuila and Nuevo León, the shrub oak forest exists on limestone substrata of apparently shallow soil at mean altitudes between 1800 and 2800 m (5940 and 9240 ft) (Rojas-Mendoza 1965; Cano and Marroquín 1967; Banda-Silva 1974). Calderón de Rzedowski (1960) contributes to the study of the shrub oak forests in regions bordering the valley of



Fig. 4. *Quercus microphylla*.

San Luis Potosí and furnishes very complete data on the floristic, ecological features, and distribution of oak forests.

It is calculated that the shrub oak forests represent 5% of the cover in relation to the total surface of the state of Nuevo León, according to Rojas-Mendoza (1965:95), who registered the following species: *Quercus cordifolia*, *Quercus saltillensis*, *Q. floculenta*, *Q. pringlei*, and others. Pertaining to the same theme, Banda-Silva (1974) explains that this oak forest crops up as a medium of the oak-pine forest and the pine forest properly said, and indicates that towards the driest part of Galena, Nuevo Leon, these species are found: *Quercus microphylla*, *Q. intricata*, *Q. grisea*, and *Q. supranitida* mixed with *Pinus cembroides*. Also, Banda-Silva (1974:47) observes that the ecotone between the formations denominated "rosetófilo" shrub and oak-pine forest are integrated by the species: *Quercus laceyi* (sensu lato), *Q. graciliramis*, *Q. graciliformis*, *Q. emoryi*, and others.

Physiognomically different from the chaparral, but climactically and floristically related, we have the low oak forest (Fig. 3) which covers the northwest facing of the watershed of the Sierra de Zapalinamé to the southeast of Saltillo, in the direction of the Lomas de Lourdes. The present oaks correspond to the following species: *Quercus sinuata* var. *breviloba*, *Q. laceyi*, *Q. endlichiana*, *Q. aff. hartwegii*, and *Q. emoryi*.

The transition of these oaks toward more xeric vegetative types is seen on the slopes facing the Cañon de San Lorenzo, 3 to 5 km (1.8 to 3 miles) east of Buenavista (Superior School of Agriculture "Antonio Narro"). Muller (in Johnston 1944b) registers samples of oaks—collected by different naturalists in the past—of the following species: *Quercus intricata*, *Quercus saltillensis*, *Quercus laceyi*, *Quercus greggi*. An elder tree is also cited: *Salix lasiolepis*.

Our samples from the lower elevations of the canyon, in rocky terrain offer the following list:

| | |
|-------------------------------|----------------------------------|
| <i>Bumelia lanuginosa</i> | <i>Pellaea microphylla</i> |
| <i>Juniperus flaccida</i> | <i>Notholaena sinuata</i> |
| <i>Arbutus xalapensis</i> | <i>Notholaena aschenborniana</i> |
| <i>Acacia farnesiana</i> | <i>Cheilanthes eatonii</i> |
| <i>Berberis trifoliolata</i> | <i>Eragrostis mexicana</i> |
| <i>Prosopis glandulosa</i> | <i>Erioneuron pilosum</i> |
| <i>Agave asperrima</i> | <i>Chrysactinia mexicana</i> |
| <i>Mimosa biuncifera</i> | <i>Opuntia macrocentra</i> |
| <i>Dasyllirion cedrosanum</i> | <i>Condalia warnockii</i> |
| | <i>Scutellaria suffrutescens</i> |

The invaders *Brickellia laciniata*, *Gymnosperma glutinosum*, *Eucnide bartonioides*, *Aristida* spp., *Opuntia imbricata*, *Brickellia veronicaefolia* and others, complete the landscape of disturbance. The author did not find any significant trees in the sample zone; it is supposed that the oak forest of the Cañon de San Lorenzo has probably been affected by the hand of man; the small isolated trees *Juniperus* and *Bumelia* are vestiges of this action. The slopes more exposed to the sun (i. e., those with a south facing) contain "rosetófilo de sotol" shrubs, lechugilla and "guapilla." It is probable that *Nolina cespitifera* is present, since a species of this genus has been used in the region for making rustic brooms. There is a very poor population of *Yucca carnerosana* in this canyon (very famous as a frequently visited botanical site).

The oak forests of the Sierra de La Paila, northwest of Saltillo, offer very diverse features (Fig. 2). The mountainous clump, partially described by Pérez-Rosales (1964) and by Cano and Marroquín (1967) still merits close attention. The high mountain canyons are interesting because of the existence of endemisms such as *Randia pringlei*, *Emorya suaveolens*, *Bernardia* aff. *myricifolia*, *Vauquelinia heterodon* (also present in the small mountain of Lázaro [locality type] north of Saltillo), and many other rare species such as *Hemichaena spinulosa*, *Echinocereus delaetii*, *Flourensia retinophylla*, *Aristolochia* sp., etc. (Fig. 5).

We can conclude that while *Quercus intricata* (including *Quercus mohriana*) is one of the species most characteristic of the chaparral in Coahuila (Muller, in Johnston, 1944b), in Nuevo León *Quercus hypoxantha* is the most characteristic species (Banda-Silva 1974) (Fig. 6).



Fig. 5. *Echinocereus delaetii*.

The “ericaceas” which usually accompany the oak forests do not seem capable of surviving outside the tree cover when this is adversely affected by man.

With respect to the grasses of San Lorenzo Canyon, Johnston (1943c) cites the following species: *Muhlenbergia emersleyi*, *Muhlenbergia setifolia* (which forms clustered grasslands on the slopes), *Muhlenbergia dubia*, *Setaria grisebachii*.

Mixed desert shrubs. Shrubs are physiognomically classified according to these variables: the mean elevation of the dominant elements; the persistence or caducity of the foliage; the presence or absence of thorns (above all the “caulinars”); the dimensions of the leaves or filioles; the arrangement of the leaves, in their case; the succulence of visible vegetative organs; and aspects of a biological character such as pollination and others.

For Aubreville (1962), “It is useful and necessary to complete the physiognomic terminology by reverting back to the floristic aspects”; this is explained by virtue of the existence of types of species, of genus and even botanical families which characterize the vegetal formations in a precise manner. For this reason, it is suggested, in accordance with the author cited above, that the same



Fig. 6. *Quercus hypoxantha*.

procedure be continued in going ahead with the designation of the vegetal communities: physiognomy; floristic composition; and geography of the place.

With this sequence, we can improve the nomenclatural synecological practice in reference to uniform, regular, or stable communities, as well as to heterogeneous communities (as are many of those which prosper under tropical conditions).

Aubreville (1962) recommends as preferable the use of a physiognomic classification since it is the simplest to establish and renders the greatest service, not only to specialists, but also to many technicians and students.

A case which illustrates these ecotones is that of the slopes north of Dr. Arroyo, Nuevo León, in the grazing region of Santa María, where shrub-like elements characteristic of the microphyll desert shrub share mixed communities which are similar to the submontane shrub that Rzedowski (1956) describes for the region of Guadalcázar, San Luis Potosí. The lower elevation, subject to poor drainage, although very disturbed, consists of clumps of mesquite shrubs with grassy and halophilous elements such as *Maytenus phyllanthoides*. In these elevations, this shrub does not grow more than a meter in height; it tends to spread and ramify close to the ground.

The geographic distribution of *Maytenus* has aroused the attention of several botanists, since it is not known with exactitude whether they are dealing with different species or only ecotypes. The populations of *Maytenus* in the Rioverde region, San Luis Potosí, are more vigorous and reach greater dimensions, not only in height, but also in the cup's diameter, in highly saline conditions and in association with mesquite clumps.

Maytenus has also been collected by the author in the "El Huizache" region, in terrain less dense with mixed shrub complexes, and from the shoulders along the Saltillo-Monclova highway near San Lázaro, as a small tree with a trunk fully developed and a cup of 3 to 4 m (9.9 to 13.2 ft) in height, isolated in the microphyll desert shrub. This apparently erratic distribution of this taxon suggests the carrying out of a detailed study of an "autecológico" type. The distribution pointed out by Standley (1923) is very wide; it is found from Baja California (the type is that of the Bahía Magdalena), Sonora as far as Puebla and Yucatán in Mexico. In Nuevo León, outside of the plains north of Dr. Arroyo, nothing has been collected by the author.

As a continuation, the floristic list of the grazing area of Santa María, Dr. Arroyo, Nuevo León is noted:

| | |
|---------------------------------|---|
| <i>Sporobolus airoides</i> | <i>Chrysactinia mexicana</i> |
| <i>Prosopis glandulosa</i> | <i>Zinnia juniperifolia</i> |
| <i>Leucophyllum zygophyllum</i> | <i>Menodora scoparia</i> |
| <i>Mortonia greggii</i> | <i>Bouvardia ternifolia</i> |
| <i>Parthenium argentatum</i> | <i>Maytenus phyllanthoides</i> |
| <i>Sophora secundiflora</i> | <i>Opuntia cantabrigiensis</i> |
| <i>Viguiera stenoloba</i> | <i>Opuntia engelmannii</i> |
| <i>Fraxinus greggii</i> | <i>Notholaena sinuata</i> var. <i>cochisensis</i> |
| <i>Krameria cytisoides</i> | <i>Sphaeralcea subhastata</i> |
| <i>Larrea divaricata</i> | <i>Paganum mexicanum</i> |
| <i>Cercocarpus breviflorus</i> | <i>Ferocactus pringlei</i> |
| <i>Gochnatia hypoleuca</i> | <i>Baccharis salicifolia</i> |
| <i>Flourensia cernua</i> | <i>Salvia</i> spp. |

| | |
|---------------------------------|--|
| <i>Koeberlinia spinosa</i> | <i>Hechtia</i> sp. |
| <i>Castela texana</i> | <i>Macrosiphonia macrosiphon</i> |
| <i>Rhus microphylla</i> | <i>Castilleja</i> spp. |
| <i>Eysenhardtia polystachya</i> | <i>Artemisia klotzschiana</i> |
| <i>Dodonaea viscosa</i> | <i>Zaluzania parthenioides</i> |
| <i>Salvia ballotaeflora</i> | <i>Flaveria trinervia</i> |
| <i>Dasyliirion longissimum</i> | <i>Flaveria anomala</i> |
| <i>Zinnia acerosa</i> | <i>Croton corymbulosus</i> |
| <i>Coldenia canescens</i> | <i>Clematis drummondii</i> |
| <i>Lycium berlandieri</i> | <i>Hechtia glomerata</i> |
| <i>Condalia ericoides</i> | <i>Taraxacum officinale</i> |
| <i>Yucca filifera</i> | <i>Asphodelus fistulosus</i> |
| <i>Ephedra aspera</i> | <i>Oxalis corniculata</i> |
| <i>Dasyliirion cedrosanum</i> | <i>Artemisia</i> sp. |
| <i>Hoffmanseggia densiflora</i> | <i>Acacia</i> spp. |
| <i>Perezia</i> sp. | <i>Opuntia</i> spp. y <i>Roseocactus</i> sp. |
| <i>Echinoffosulocactus</i> sp. | |

The grasses have not been determined yet.

These ecotones evidently respond to microhabitats in which a durable cover conserves areas which are less dry, or else the edaphic conditions are favorable to the conservation of humidity.

Comparatively more xeric, the Ocampo region, Coahuila, in hillsides adjacent to the area occupied by the Experimental Camp of the Research Center for Arid Zones, northwest of the town of Ocampo, reveals this composition:

| | |
|--|---|
| <i>Mimosa emoryana</i> | <i>Citharexylum brachyantum</i> |
| <i>Tecoma incisa</i> | <i>Krameria interior</i> |
| <i>Cassia bauhinioides</i> | <i>Baileya multiradiata</i> |
| <i>Parthenium incanum</i> | <i>Verbena</i> sp. |
| <i>Zinnia acerosa</i> | <i>Cordia greggii</i> |
| <i>Jatropha dioica</i> | <i>Mimosa lindheimeri</i> |
| <i>Sphaeralcea incana</i> | <i>Acacia vernicosa</i> |
| <i>Dyssodia pentachaeta</i> | <i>Ephedra pedunculata</i> |
| <i>Menodora scabra</i> | <i>Prosopis glandulosa</i> |
| <i>Haplopappus spinulosus</i> | <i>Ziziphus obtusifolia</i> var. <i>obtusifolia</i> |
| <i>Celtis pallida</i> | <i>Acacia constricta</i> |
| <i>Perezia nana</i> | <i>Condalia ericoides</i> |
| <i>Aloysia lycioides</i> (<i>Aloysia gratissima</i>) | <i>Koeberlinia spinosa</i> |
| <i>Hoffmanseggia densiflora</i> | |
| <i>Bahia absinthifolia</i> | and diverse Cactaceae and Grasses |

As a contrast, in the Paso de San Lázaro (Cuesta de La Muralla), the open vegetation of the shrubby type includes clumps of shrubs such as *Rhus virens*, *Vauquelinia heterodon*, *Dodonaea viscosa*, *Mortonia latisepala*, *Rhus pachir-*

rhachis, *Cassia* sp. with pastures and herbaceous plants such as *Cryptantha palmeri*, and others. The shrubs there—on rocky soil—are largely composed of *Larrea divaricata*, *Fouquieria splendens*, *Ephedra pedunculata* which in some areas climb toward the cups of diverse leguminosea like the huizache and mesquite. It is evident that the areas adjacent to the Saltillo-Piedras Negras highway, at the height of the Paso de San Lázaro, have suffered great disturbance. Muller (in Johnston, 1944b) cites *Quercus intricata*, *Quercus gravesii*, *Quercus invaginata*, and other arborescent elements of that locality which is a part of the Sierra de La Gavia.

Johnston (1943c) mentions the following species for the locality of San Lázaro: *Ephedra aspera*, *Pinus cembroides*, *Selaginella wrightii*, *Cheilanthes horridula*, *Notholaena candida*, *Pellaea microphylla*. The following are also mentioned (Johnston, 1943d): *Muhlenbergia rigida*, considered as the dominant grass in the high elevations, *Muhlenbergia monticola*, *Bouteloua radicata*, *Heteropogon contortus*. With respect to the Cyperaceae, Johnston (1944a) cites *Carex schiedeana* of the Puerto de San Lázaro. In the Orchidaceae, he mentions as very rare the *Spiranthes cinnabarina*, identified by L. O. Williams. The sotol *Dasylirion cedrosanum* grows in that locality as well as the *Tillandsia recurvata* (Johnston, 1944a). Johnston (1944b) cites *Phoradendron tomentosum* of the Puerto San Lázaro, as well as the *Aristolochia wrightii*, *Eriogonum greggii*, *Froelichia arizonica*, *Boerhavia gracillima*.

These notes, made on 11 January 1974, strive to show the proper samples found in that famous locality; they were taken in rapid form and without an itinerary. The author is interested in making a more intense collection in that area.

DISCUSSION AND CONCLUSIONS

The physiognomic aspect presents itself as the easiest way of classifying the types of vegetation. In the eastern border of the Chihuahuan arid zones, the communities which we call "mixed" are hard to define in purely qualitative terms. A step forward would be one offered by the quantitative point of view, which is recommended once the natural landscape has been defined.

The nomenclature, which is not an end in itself, merits the proper attention of those engaged in basic research in studies of the vegetation. In general, these studies have far-reaching effects to the degree that the vocabulary used and the names applied to the phytocenosis are the ones which are often passed on to future literature of an applied character. The problems of not finding equivalent terminology between one author and another author, from one country to another country, or from one school to another school should not be an obstacle in the synecological studies.

Several attempts have been made to establish that equivalent terminology of the types of vegetation of Mexico; in that respect, we can cite the tables of equivalence prepared by Rzedowski (1965) and Rojas Mendoza (1965). Aubreville (1962) contributes ideas on tropical synecology.

To date, the terminology established by Rzedowski (1956, 1966) in the description of the vegetation of the arid zones has been very acceptable. The terms, "desert microphyll shrub," desert "rosetófolio" shrub," and "submontane shrub" have facilitated the description of vast arid regions of northern Mexico (Marroquin et al. 1964). Other southern parts of the Mexican High Plateau have been described by using a similar criterion (Rzedowski 1960); toward the west and south, the types of vegetation become grasslands, "crasicaules" shrubs, oak forests, etc. (Gentry 1957; Rzedowski and Mc Vaugh 1966, 1972).

The cases of disclimax vegetation, such as the dense thornless shrub parvifolious Rosaceae, can take root in floristic bases (i.e., the percentage of invaders), the deterioration of the substratum (erosion), the resistance of plants to the trampling by livestock, or the historic factors although this needs the solid scientific bases of auxiliary sciences.

SUMMARY

The designation by Miranda (1955) of "Chihuahuan arid zones" is used instead of "Chihuahuan desert." Several types of vegetation considered as transitional are discussed, especially in the eastern region of the extensive arid zone. The botanical collections made by the author serve as a base, but ample literature is taken into account in order to establish and complement the information.

The region covered embraces parts of southeast Coahuila, citing some areas farther south than Nuevo León and northeast of Durango as points of comparison of the mixed desert shrubs.

The vegetal communities considered from a physiognomic point of view are the pinyon forest, the dense thornless shrub parvifolious Rosaceae, the grassland with shrubs, the chaparral, and the mixed desert shrub.

In the *Pinus cembroides* forest, the xeric ecotones stand out; they were first recorded by the observations of Rzedowski (1966) and later by Robert (1973). The transitions between the oak forest and pinyon forest are very vague; the diversity of the species is very high and the xeric elements stand out sometimes as subdominants (e.g., *Yucca carnerosana*).

The dense thornless shrub parvifolious Rosaceae is a good example of the very peculiar type of vegetation found in the alteration of the oak forest, according to studies of the northwest watershed of the Sierra de Zapalinamé, near Saltillo, Coahuila. The features reveal a cover sufficient to be considered dense, with thornless shrubs predominating (*Cowania plicata*, *Lindleyela mespiloides*, interlaced with *Berberis trifoliolata*, subshrubs, and herbaceae). The term parvifolious is selected from Miranda's (1955) terminology to highlight the reduced foliated surfaces.

Aubreville's (1962) criterion is taken into account to highlight relevant physiognomic aspects, the floristic aspects and, if adequate, the geographic criterion to classify the anterior ones.

The shrub oak forest is discussed on the basis of Rzedowski (1966), Calderón

de Rzedowski (1960), Muller (1939 and 1947), and Banda-Silva (1974). Data on the chaparral of the Sierra de La Paila, Coahuila, are cited in accordance with Cano and Marroquín (1967).

The mixed desert shrub is based on the collections from Ocampo, Coahuila, Dr. Arroyo, Nuevo León, and Cuencamé, Durango. The grassland with shrubs is mentioned as existing (e.g., the Ranch Los Angeles south of Saltillo), but the information is not sufficient to draw any conclusions. Likewise, the grassland *Bouteloua breviseta* in Cuencamé, Durango is considered transitional.

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Aspects of Reproduction in Chihuahuan Desert Nyctaginaceae

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One of the greatest areas of diversity for the Nyctaginaceae is the Chihuahuan Desert region, where 11 genera and about 50 species are found. Twenty-three of these species belong to genera whose distribution is primarily on the Chihuahuan Desert or closely adjacent areas (*Ammocodon*, *Acleisanthes*, *Anulocaulis*, *Cyphomeris*, *Nyctaginea*, *Selinocarpus*). With the exception of the four species in *Anulocaulis*, the 19 in the remaining 5 genera produce a greater or lesser number of cleistogamous flowers (those which remain closed and set seed by self-fertilization) along with chasmogamous flowers (those which open). Except for a few species of *Mirabilis*, section *Oxybaphus*, the phenomenon of cleistogamy in the Nyctaginaceae apparently is restricted to genera best developed in the Chihuahuan Desert.

The first reference known to us to report the occurrence of cleistogamous flowers in the Nyctaginaceae is that of Gray (1853), who observed growing plants of the yet unnamed *Pentacophrys* (= *Acleisanthes*) *wrightii* A. Gray at the Cambridge Botanic Garden. Here Gray commented that plants of this species produced all "precociously fertilized" flowers and that none attained "full development." He also noted in this report that several other species also produced "precociously fructified" flowers. In 1873 he reported that the frequency of cleistogamous flowers (the term introduced by von Mohl in 1863) in some species of Nyctaginaceae shows a seasonal shift, *Oxybaphus nyctaginea* (Michx.) Sweet seeming to shift from chasmogamy early in the season to cleistogamy later, but that *Nyctaginea capitata* Choisy from Texas growing in his garden showed the reverse. Gray (1853) specifically mentioned that "precociously fructified" flowers were not observed on specimens of *Acleisanthes longiflora* A. Gray and made no mention of such on *Selinocarpus* (= *Ammocodon*) *chenopodioides* Gray. Although cleistogamous flowers are frequent in

these species, they are inconspicuous and still are not reported in descriptive taxonomic literature. However, Fowler (1972) mentioned them in *Ammocodon* in her thesis on the taxonomy of *Selinocarpus*.

Our studies have centered on three species, *Ammocodon chenopodioides* (A. Gray) Standl., *Selinocarpus lanceolatus* Wootton, and *Acleisanthes longiflora*, primarily as they occur in southern New Mexico. Data were taken from three populations of *Ammocodon*: One, termed "A Mountain," occurs about 1.6 km (1 mile) E of New Mexico State University in Las Cruces, the other two, called "bajada" and "playa," about 24.1 km (15 miles) N of Las Cruces just E of the Doña Ana Mts. The *Acleisanthes* population sampled lies on the White Sands Missile Range, on the SE bajadas of Salinas Peak in the San Andres Mountains in Sierra County. Because of difficult access, this population could be sampled only twice. The *Selinocarpus* population examined occurs on the gypseous flats on White Sands National Monument.

The characteristics of cleistogamous flowers or plants bearing them, the adaptive significance of cleistogamy, and the effects of uniparental reproduction on population structure have received much attention and are well covered in review form in several places (e.g., Darwin 1897; Heslop-Harrison 1970; Maheshwari 1962; Ornduff 1969 [for autogamous flowers]; Stebbins 1957, 1970; Uphoff 1938). In this preliminary report, we wish to point out the common occurrence of cleistogamy in Chihuahuan Desert Nyctaginaceae, to document the shift from a preponderance of cleistogamic flowers to chasmogamic flowers in two species, the absence of an apparent shift in another, to examine the floral "behavior" and other floral aspects of reproduction, and to discuss the possible adaptive significance of these features in combination.

FLORAL BEHAVIOR, FLOWER VISITORS, AND POLLINATION

Isolated plants of *Ammocodon* grown in the greenhouse, and a single plant of *Acleisanthes longiflora* bearing chasmogamous flowers which was grown in the experimental garden, produced seed when the chasmogamous flowers were self-pollinated and are, therefore, self-compatible. Although self-incompatibility is known for chasmogamous flowers on plants which also bear cleistogamous flowers (Levin 1968), we believe that *Selinocarpus lanceolatus* will also prove to be self-compatible. Self-incompatible Nyctaginaceae are known (Baker 1964; Tillet 1967), but these species bear only chasmogamous flowers.

Ammocodon chenopodioides and *Selinocarpus lanceolatus* are relatively closely related but exhibit divergent floral morphology, whereas the *Selinocarpus* and *Acleisanthes longiflora* are more distantly related but have rather similar flowers. We are thus able to compare two rather contrasting floral types. The chasmogamous flower of *Ammocodon* (Fig.

1, I) is relatively unspecialized, the perianth rose-pink, with a short tube. In this respect it is similar to the flower described for *Mirabilis nyctaginea* (Michx.) MacMillan by Cruden (1973) which is visited by several kinds of insects. *Acleisanthes* (Fig. 1, A) and *Selinocarpus* (Fig. 1, E), conversely, are specialists, their flowers with a long white or cream tubular perianth, comparing well with Baker's (1961) description of hawkmoth-pollinated flowers.

In each species anthesis begins at about sundown (on cloudy days up to 3 hours before in *Ammocodon*; an hour or so before in the other two), other flowers continuing to open from about 1-3 hours after sunset. Flowers of *Selinocarpus* and *Acleisanthes* generally are closed by 1 or 2 hours after sunrise (later on cloudy, cool days) and flowers of *Ammocodon* generally close by 10 or 11 a.m.

The flowers of *Ammocodon* are borne in small umbel-like clusters at the tips and in the forks of the branches of the inflorescence. As the chasmogamous flower begins to open, the style exserts, followed by the exertion of the stamens. Due to the outward spreading of the style and stamens, the anthers and stigma are distantly and almost equally positioned from one another, reducing the chances of self-pollination. Anther dehiscence occurs from about 0.25-1 hour after exertion of the style. The flowers are variously oriented in the cluster and, although this has not been observed, we suspect that because of this varied orientation, an insect visitor approaching the flower may brush against an anther on one flower, the stigma on the next, and so forth, promoting cross pollination.

The reddish color of the perianth of *Ammocodon* is similar to that of *Mirabilis froebelii* (Behr) Greene, which, as Baker (1961) pointed out, can be seen by day-flying insects in the reddish light of evening and early morning, but is also attractive to night-flying moths because of its bluish component. We have observed the following visitors to *Ammocodon* flowers; occasional bumblebees (*Bombus* sp.) in the early morning, a butterfly (*Pieris* sp.) in the late afternoon, and pollen-gathering bees of the Anthophorinae in the early evening. The latter two visitors had a few *Ammocodon* pollen grains on their bodies; no bumblebees were captured. Since the flowers remain open during the night, we believe (but have not observed) that they must be visited by moths of the Noctuidae as Cruden (1973) observed for *Mirabilis nyctaginea* and possibly also Arctiidae, both families common here, and possibly also larger moths of the Sphingidae. Wind has also effected pollination on flowers which were isolated from pollinators. We believe that generally this results in self-pollination.

Subsequent to pollination, the style begins to inroll (Fig. 1, J). This process is well underway in many flowers by sunrise, in others it does not begin until early in the morning. As the style inrolls, the stigma may

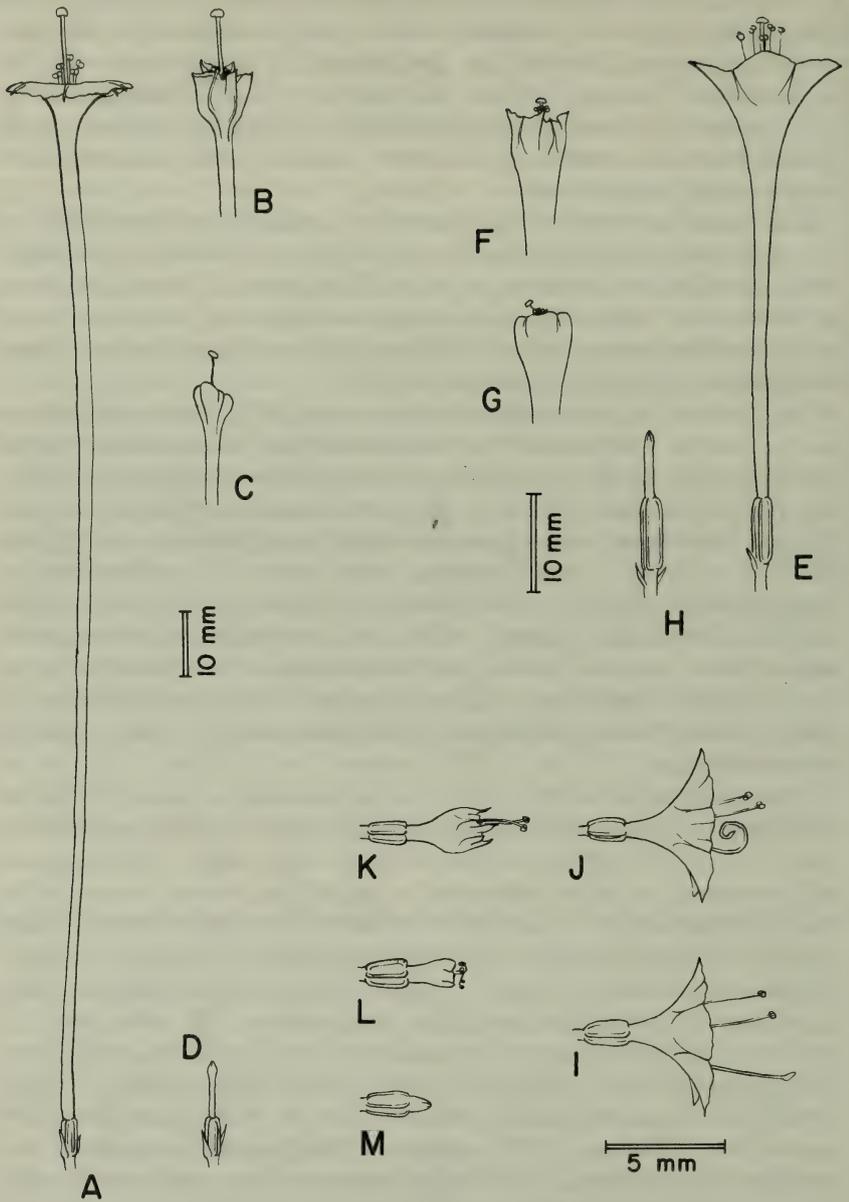


Fig. 1. A-D, *Acleisanthes longiflora*; A, chasmogamous flower; B, C, early and late stages of closure of chasmogamous flower; D, cleistogamous flower. E-H, *Selinocarpus lanceolatus*; E, chasmogamous flower; F, G, early and late stages in closure of chasmogamous flower; H, cleistogamous flower. I-M, *Ammocodon chenopodioides*; I, chasmogamous flower; J, K, L, early, middle, and late stages in closure of chasmogamous flower; M, cleistogamous flower.

contact an anther and pick up pollen. During this time the perianth begins to close, soon enclosing the inrolled style (Fig. 1, K). Eventually, the closed perianth withers tightly at the top of the fruit, the stamens remaining shriveled outside (Fig. 1, L). This sequence of events may inhibit self-pollination and contrasts to that described for the majority of the flowers of *Mirabilis nyctaginea* (Cruden 1973), in which as the style inrolls the stamens follow, the anthers finally lying in proximity to the stigma. Proper operation of the inrolling process of the style in *Ammocodon* seems to depend on pollination. In flowers experimentally kept unpollinated by the isolation of inflorescences in still air, the perianth closed in the morning, but the style failed to inroll in time to be included. However, hand-pollinated flowers, whether selfed or outcrossed, closed normally. It is not known whether flowers which have closed before the style inrolls can later be successfully pollinated and fertilized.

The floral behavior of *Acleisanthes longiflora* and *Selinocarpus lanceolata* is basically similar. As the perianth opens, the style exserts. Anther exsertion and dehiscence occur about one half hour later. Both species generally have five stamens (sometimes more in *Selinocarpus*). Both also have styles which vary about 1 cm in length. In Fig. 1 (A & E) a long-styled form is illustrated for *Acleisanthes* and a short-styled form, for *Selinocarpus*.

The flowers of each species are adapted primarily for moth pollination, but are of very different length, those of *Selinocarpus* ranging from 30 to 40 mm long, those of *Acleisanthes* from 90 to 170 mm. On 11 August 1973, in Hudspeth County, Texas, we observed hawkmoth visitation of flowers of *Acleisanthes longiflora*, once at about 8:00 p.m. and again at 9:00 p.m. Both visits were by *Protoparce quinque maculata* (Haw.); a captured individual had *Acleisanthes* pollen on its head near the base of the proboscis where it could be deposited on a stigma as the moth entered a flower. This and other large sphingids are believed to be the primary pollinators of this species. However, in the experimental garden, wind currents shaking the long, erect flowers also have effected pollination, as have small nectar-seeking ants (*Iridomyrmex*) which crawled all over a flower, some pollen sticking to their bodies as they move about. We have not yet observed pollination of *Selinocarpus lanceolatus*. However, smaller sphingids, *Celerio lineata* (Fabr.), have been captured on another Nyctaginaceae, *Anulocaulis leiosolenus* (Torr.) Standl., which has a floral tube of about the same length as that of the *Selinocarpus*. This species of moth is common in the area, and it and other species of similar size are probably the primary pollinators of *S. lanceolatus*.

When the flower closes, the perianth limb folds inward, pushing the stamens against the style (Fig. 1, B, F). In the short-styled forms, the anthers contact the stigma and self-pollination results. As the perianth continues to wither and tightly inroll, it may cover some or all of the

anthers (Fig. 1, C, G). The stigma remains exerted. We have observed flower closure in a long-styled flower of *Acleisanthes* which had not been pollinated. The perianth enclosed the anthers and self-pollination did not occur; the flower set no seed. Such an arrangement of parts probably aids in inhibiting self-pollination. It is not known whether the stigma remains receptive after the flower closes.

CLEISTOGAMIC FLOWERS; POLLEN CHARACTERISTICS; SEASONAL TRENDS IN CLEISTOGAMY VS. CHASMOGAMY.

The cleistogamic flowers in each of the three species studied are similar in many respects. The basal portion of the perianth, which becomes part of the fruit, develops normally; however, the terminal portion remains as a short greenish tube or dome (Fig. 1, D, H, M). Except for *Acleisanthes* the cleistogamous flowers have fewer stamens than the chasmogamous flowers; five in *Acleisanthes*, two in *Selinocarpus*, and one in *Ammocodon*. In each, the anthers are slightly beneath, but in contact with, the stigma and dehisce prior to pollination. In each species, as is typical of cleistogamous flowers (cl) in general, the pollen:ovule (P:O) ratio of each flower is reduced relative to that of the chasmogamous flowers (ch). We determined the P:O ratios for three flowers of each kind for each species and present the averages here: *Acleisanthes*, ch P:O = 439:1, cl P:O = 104:1; *Ammocodon*, ch P:O = 225:1, cl P:O = 49:1; *Selinocarpus*, ch P:O = 384:1, cl P:O = 42:1. These P:O ratios are lower than that reported by Cruden (1973) for *Mirabilis nyctaginea* (156:1 and 187:1) but considerably above those he reported for cleistogamous flowers of species in other families (ca. 3-6:1). The diameter of these grains was measured also and the expected correlation between style length and pollen grain size of the chasmogamous flowers was found, pollen volume increasing with style length (Covas and Schnaak 1945). Pollen from the cleistogamous flowers is consistently smaller than that from the chasmogamous flowers, although pollen from the former in *Selinocarpus* and *Acleisanthes* is larger than pollen from the latter in *Ammocodon*. Mean pollen diameters ($n = 15$) for each species are: *Ammocodon*, cl 96 μ , ch 107 μ ; *Selinocarpus*, cl 120 μ , ch 132 μ ; *Acleisanthes*, cl 115 μ , ch 161 μ . All means are significantly different ($P < 0.01$). The diameter reported for *Acleisanthes* is larger than that reported by Nowicke (1970) and may merely reflect the different methods of preparation. It is apparent that the cleistogamous flowers represent a considerable savings in terms of volume of pollen produced per flower. In *Ammocodon* a chasmogamous flower produces about 4.2 times the volume of pollen than a cleistogamous flower; in *Selinocarpus* and *Acleisanthes* there is approximately a twelvefold difference.

Three populations were sampled to determine whether the frequency of chasmogamous flowers relative to the total number of flowers

changed during the season. Branches were removed from a plant, pressed and dried, and the two types of flowers later counted. These same samples were also used to determine relative seed set. Sample dates are as follows: for *Acleisanthes*, 6 June, 7 Aug. 1971; for *Ammocodon* "playa," 6, 10 June, 9 Aug. 1973, 25 Aug. 1974, and 13 June, 4 Aug. 1973, 25 Aug. 1974. The springs of 1971 and 1974 were especially dry, whereas in 1973 this portion of the Chihuahuan Desert had a particularly "good" spring. Each summer the rains began on 1 July or shortly after, but in 1973 the precipitation for August was considerably less than normal.

Data from these population samples are presented in Fig. 2. The percent of total flowers counted is presented above the histograms which depict the number of plants bearing a certain percentage of chasmogamous flowers. The differences in actual numbers of flowers counted probably reflect our sampling techniques rather than population trends. However, χ^2 values indicate that the differences in the proportion of chasmogamous flowers in each sample between months in the same year, and between the same months in 1973 and 1974, within the same population, are all significantly different ($P < 0.005$). The same holds true for comparing corresponding sample months between the two *Ammocodon* populations, except in August 1973, which are not significantly different.

The *Acleisanthes* data presented in Fig. 2 are for 69 plants (a road scraper having removed 31 plants of the 100 originally marked for resampling). A strong shift toward chasmogamy between June and August is shown in the total number of flowers and in the number of plants which bear mostly chasmogamous flowers. In the populations of *Ammocodon*, 20 plants were randomly sampled each time. Although the "playa" population shows a slight shift toward chasmogamy in the total number of flowers produced in 1973, 60% of the plants were predominantly cleistogamous. The histograms for this population are bimodal in 1973 and unimodal in 1974, indicating the population as a whole is responding differently to some stimulus(i) in the 2 years. The nearby "bajada" population shows a different response, shifting toward cleistogamy in total number of flowers produced between June and August 1973, but having about an equal number of plants with either a greater proportion cleistogamous or chasmogamous flowers in August. However, in August 1974, it showed a greater total percentage of chasmogamous flowers and, concomitantly, a shift toward a greater number of plants which bore predominantly chasmogamous flowers.

The *Selinocarpus* population we sampled was near an extensively visited area in a National Monument and we were reluctant to take large samples. Instead, we counted the relative number of cleistogamous and chasmogamous flowers on each plant several times during the

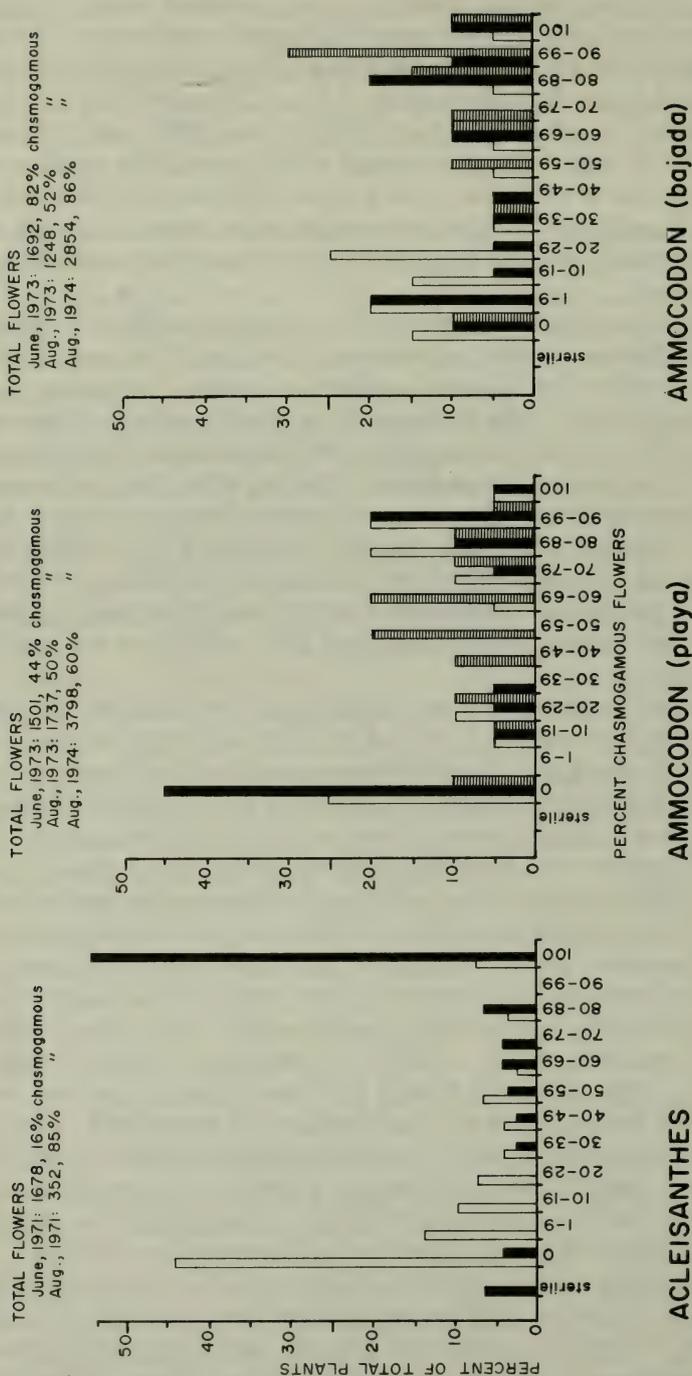


Fig. 2. The percentage of total plants from one population of *Acleisanthes* ($n = 69$) and two of *Ammocodon* ($n = 20$ each) plotted against the percentage of chasmogamous flowers on each plant at various sample dates. White bars represent June sample; black bars represent August 1971 or 1973 sample; hatched bars represent 1974 sample. Total flowers counted in each sample and the percentage of these which are chasmogamous are indicated above each set of graphs.

flowering season. The same was done for a small population of *Ammocodon* near Las Cruces, but from this samples were pressed and dried as before. In each population each plant was marked so it could be followed through a growing season. These data are presented in Fig. 3. As can be seen, the percent chasmogamous flowers on any one plant may vary through the season, plants may respond very differently from year to year, and one plant may respond differently compared to another to the same overall environmental situation (cf., in *Ammocodon* the plants indicated by dark triangles in the boxes). Yet, both populations as a whole seem to show a shift toward chasmogamy later in the summer.

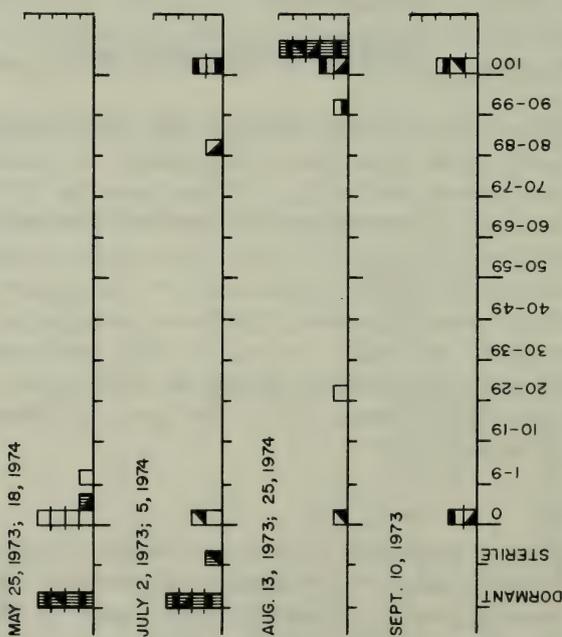
Since these plants show varied responses to the same overall environment, we believe that environmental factors produce different responses from a varied genetic background, combining in a sense the ecological and the genetical cleistogamy reviewed by Uphoff (1938). Some plants will shift toward cleistogamy under one set of conditions, whereas others do so under another; some will bear only one type of flower, others are mixed. That it is not solely an environmental effect but that varied genetics are also involved is illustrated by three seedling *Acleisanthes longiflora* plants which were taken from the same population in Hudspeth County, Texas, and transplanted to within 4 dm of one another in Las Cruces. In its second summer each plant was robust; one produced only cleistogamous flowers, a second a few chasmogamous flowers in July, returning to cleistogamy in August, while the third became predominantly chasmogamous in July and August. Attempts to determine controlling environmental factors for *Acleisanthes* and *Ammocodon* were plagued, however, by breakdowns of our environmental chambers.

Relative seed set for each type of flower was determined by opening fruits of pressed plants from these populations of *Ammocodon* and *Acleisanthes* and is presented in Fig. 4. Where possible, 50 fruits which developed from each flower type were examined. This was not always possible in *Acleisanthes*, which in our June sample had few mature chasmogamous flowers and in August had few cleistogamous flowers. χ^2 values indicate that the apparent differences seen in the histograms are not significant ($P > 0.1$) except for the comparison of the chasmogamous and cleistogamous flowers in *Acleisanthes* ($P < 0.005$, < 0.05 , June and August, respectively). We have not determined relative seed set in *Selinocarpus*.

DISCUSSION

The three species examined, *Acleisanthes longiflora*, *Selinocarpus lan- ceolatus*, and *Ammocodon chenopodioides*, all produce cleistogamous flowers and chasmogamous nocturnal flowers, each of which can be viewed as adaptations to xeric conditions and seasonal drought (Baker

AMMOCODON ("A" Mtn.)



SELINOCARPUS

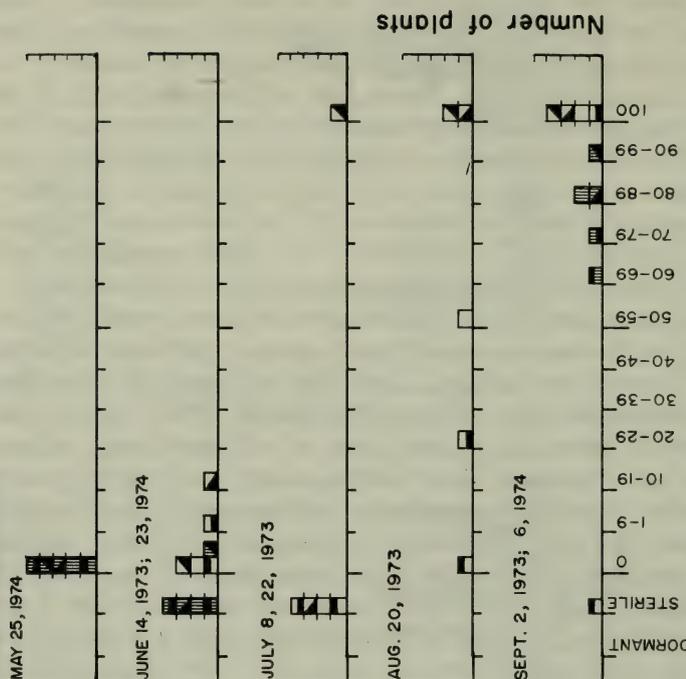


Fig. 3. The number of plants in a sample of five with certain percentages of chasmogamous flowers at various times during the flowering season. Each single box in a bar represents one plant; white bars represent 1973 samples; hatched bars represent 1974 samples. Each box is coded (e.g., with a solid black triangle or rectangle, each pattern for a box corresponding to a single plant) allowing each plant sampled to be followed throughout a flowering season, and also in 1973 versus 1974. In May 1973, individual plants had not yet been tagged for identification and boxes are left uncoded.

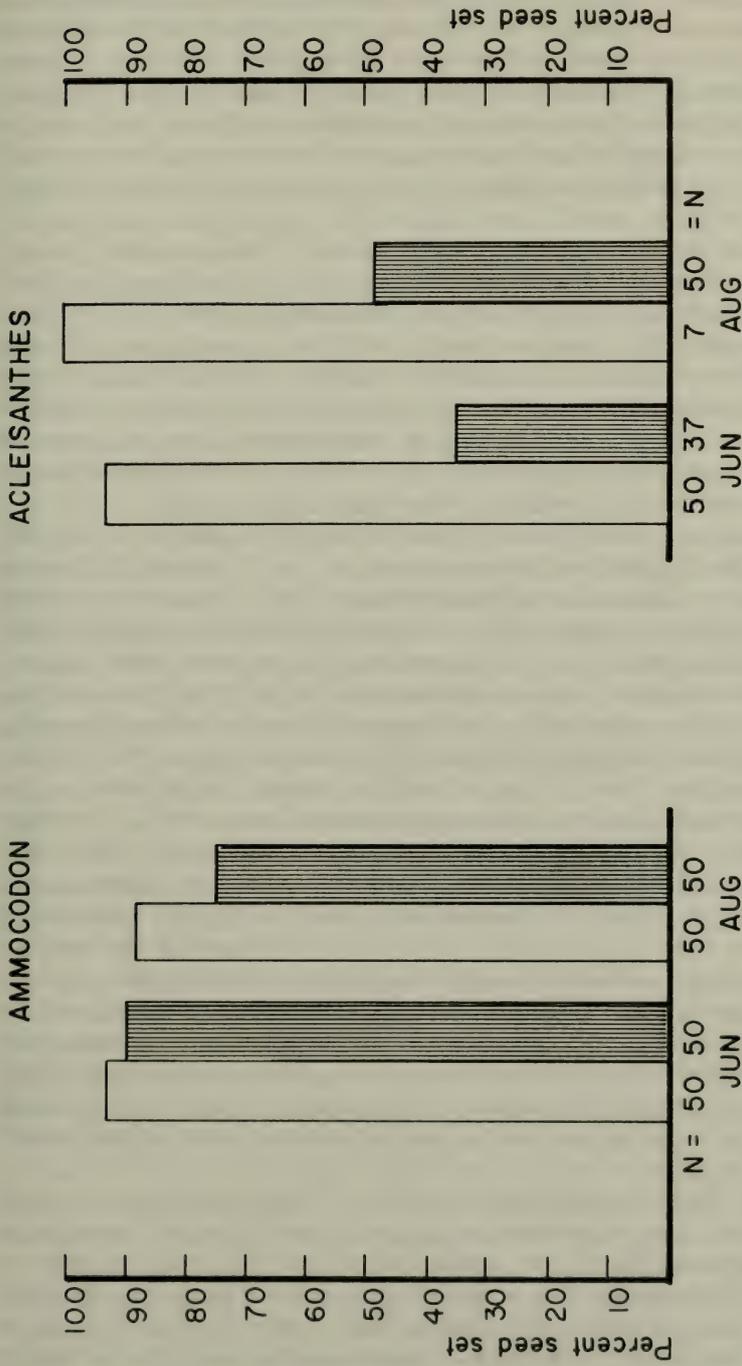


Fig. 4. Percentage of seed set plotted against sample date for *Ammocodon* (playa population, 1973) and *Acleisanthes* (1971). White bars represent cleistogamous flowers, hatched bars represent chasmogamous flowers.

1961; Stebbins 1957). The chasmogamous flowers of *Ammocodon* resemble in many respects the flowers of *Mirabilis nyctaginea* (Cruden 1973) and are probably pollinated by several kinds of insects, whereas in *Acleisanthes* and *Ammocodon* the chasmogamous flowers are specialized and typical of hawkmoth-pollinated flowers (Baker 1961). In the latter species especially, the cleistogamous flowers may also be viewed as insurance mechanisms against the irregularities of moth pollination (Baker 1961).

The information regarding the features of cleistogamous flowers presented here agrees with that presented by other authors (e.g., Ornduff 1969 [for autogamous flowers]; Maheshwari 1962; Uphoff 1938) and for the cleistogamous flowers of *Mirabilis nyctaginea* (Cruden 1973). The perianth is very small, the number of anthers reduced from five in the chasmogamous flowers to two in the cleistogamous flowers of *Selinocarpus*, from two to one in *Ammocodon* (no reduction in *Acleisanthes*), pollen grains are smaller than in the chasmogamous flowers, and there is a lowered pollen to ovule ratio.

The chasmogamous flowers of the three species examined are self-compatible (believed so in *Selinocarpus*) but have features which seem to reduce the chances for self-pollination (cf. Fig. 1). In *Ammocodon* the style curls into the flower before the perianth closes (the stigma sometimes touches the anthers in the process), the stamens remaining outside. This sequence of events contrasts to that of *Mirabilis nyctaginea*, where after the style inrolls, the stamens follow, the anthers becoming positioned near the stigma (Cruden 1973), and is opposite that of *Mirabilis multiflora* (Torr.) Gray, where the anthers are included in the wilted perianth, the style remaining exerted (Cruden 1970). The latter is similar to that which we observed in *Acleisanthes* and *Selinocarpus* where the anthers are partially or wholly covered by the collapsing perianth, the style remaining exerted. In the shorter-styled flower forms of these two species, the anthers contact the stigma when the perianth closes and self-pollination results; in the longer-styled forms no such contact is made and selfing is inhibited. The curling of the stigma into the closing perianth of *Ammocodon* occurs in many Nyctaginaceae with short floral tubes and may aid in preventing desiccation of the stigma before the pollen tube completes its penetration to the ovary; the long tubular perianths of *Acleisanthes* and *Selinocarpus* would afford similar protection.

Baker (1964) and Bateman (1968) have commented on the possible significance of the variable style length of *Mirabilis froebelii*, a species in which there is also genetic self-incompatibility. Bateman suggested it may be a step toward more precise heterostyly, allowing the utilization of more than one class of pollinator until a selectively advantageous specific relationship is established. We believe this not to be the case in

the self-compatible *Acleisanthes longiflora*. As Baker (1961) pointed out, hawkmoth density is often low and on cool nights the moths may not fly at all. Thus, hawkmoth-pollinated plants commonly have various kinds of other mechanisms to insure pollination. The short-styled flowers may be maintained in the population by selection for self-pollination, serving to reduce wastage of the flowers should they not be visited by a pollinator, adding to the insurance of seed set provided by the cleistogamous flowers. The longer-styled forms would encourage cross pollination and be maintained if genetic recombination is adaptively advantageous. This similarity may apply to *Selinocarpus*.

Cruden (1973) reported a shift toward cleistogamy in *Mirabilis nyctaginea* during a season, but noted that two populations of plants might be involved. Our results contrast with this. In each case one population is involved, and if a shift is present, it is reversed. In *Ammocodon* we cannot discern a consistent shift which correlates with the time of the season or climatic conditions, except that very early in the spring plants are mostly cleistogamous. This latter condition was noted by Gray (1873) for *Nyctaginea* and we have noted it in other species of Chihuahuan Desert Nyctaginaceae. Rather than shifting from predominantly one phase to another, *Ammocodon* produces chasmogamous and cleistogamous flowers throughout the season, each kind providing about 90% seed set, individual plants apparently responding differently to microenvironmental situations or to fluctuations in overall environmental conditions. Even though general insect populations are low during the hot dry months of late spring and early summer in the Chihuahuan Desert (J. Zimmerman pers. comm.), enough insects of different kinds may be present to pollinate the chasmogamous "generalist" flowers of *Ammocodon*, maintaining them as adaptive for providing genetic recombination. During periods when insect pollination is reduced, such as during extreme drought or periods of rainy weather, cleistogamous flowers would insure seed set.

Conversely, a strong shift from cleistogamy to chasmogamy is present in *Acleisanthes* and we believe also in *Selinocarpus* (casual observations support the trend seen in Fig. 3). In the spring and early summer, when general insect density is low, the production of a great many specialized chasmogamous flowers which attract hawkmoths (whose density is inherently low to begin with) would serve little purpose. Plants which did so would set fewer seeds relative to those which were cleistogamous and might be selected against. In the southern United States, however, hawkmoths produce two generations of adults per year, the second hatching in the summer from a brood produced in the late spring or early summer (Essig 1958). Thus, the density of hawkmoth population may be considerably higher later in the summer, and a higher percentage of chasmogamous flowers would be beneficial. That there is not a

significant change in seed set ($P > 0.1$, $\chi^2 = 2.01$) is puzzling and may reflect an inherent difficulty in achieving fertilization after pollination in these long fragile flowers, or that few hawkmoths visited this population, most of the seed produced by self-pollination. As Baker (1961) remarked, many flowers in a hawkmoth-pollinated species may not be visited. The absence of a significant shift toward greater seed set in *Acleisanthes* in the presumed presence of a greater number of pollinators may also be misleading since it is gathered from only one population during one summer. However, if our figures do reflect the general situation in this species, it appears that in order to maintain long-term evolutionary flexibility through genetic recombination from cross-pollination *Acleisanthes longiflora* pays a rather high premium by shifting to the production of often barren chasmogamous flowers later in the season. This is illustrated by pollen production alone, where about 23 times the volume of pollen is produced for each seed set in a chasmogamous flower relative to one set cleistogamously.

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Saline Habitats and Halophytic Vegetation of the Chihuahuan Desert Region

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INTRODUCTION

Vegetation within the Chihuahuan Desert is affected by many physical factors of which elevational, climatic, and edaphic factors are the most important. Saline areas, in which the soil contains sufficient amounts of various soluble salts to affect the uptake of water by plants, is one such edaphic phenomenon that has a direct effect on plant distribution in the Chihuahuan Desert. Saline habitats occur throughout the Chihuahuan Desert, and their distribution is a factor of general topography and geology. They occur most commonly around dry lakes, playas, or salinas at the bottom of internally draining basins in which various salts, derived from weathering and leaching of general rock material or older salt-bearing sediments, or derived from previous volcanic activity (Foshag 1926) accumulate either through extensive river systems or through more localized drainage. Salts may also be dissolved from deep or shallowly buried saline deposits of various age and may be carried to the surface by seepage or artesian actions forming saline areas that are not necessarily associated with playas (Ungar 1974). Hot springs present still another source of saline habitats (Foshag 1926; Tamayo 1962). The quantity and quality of salts in the playas and other saline habitats are a reflection of the size, the age, and to a large degree the salinity and depth of underground water (Neal 1969) and the kinds and amount of parent rock material in the drainage area. Salts may also be removed from a basin by entrapment by overlying sediments or removal by wind and other factors (Langbein 1961). The salts may consist of cations of sodium, calcium, magnesium, and potassium and anions of chloride, sulfate, carbonate, and bicarbonate (Neal 1969;

Ungar 1974); and they may differ both quantitatively and qualitatively from basin to basin (Foshag 1926).

The most frequently encountered saline habitats in the Chihuahuan Desert are associated with dry lakes or flats that serve as a sink for salt deposition. These habitats, however, are not uniform but show a gradual increase in soil salinity from the margin of each to the center of deposition, which in a playa is represented by an open, unvegetated flat. Soil salinity also exhibits seasonal variation depending on soil moisture, which, of course, is affected by precipitation and subsequent drying. Upon drying, relative salinity increases, but it does so primarily near the surface due to capillary rise and evaporation of the salt-bearing waters near the surface (Neal 1969). The level of ground water will also affect distribution of plants, as will drainage patterns (microrelief) within the flats and playas. There is also a gradation of soil types from more sandy or sandy-clay loams along the perimeter to finer often impervious clay soils in the center of the playas (Hunt and Durrell 1966; Neal 1969). Development of caliche and the presence of subterranean brine deposits located under some playas may also have an effect on deep rooted plants—phreatophytes, e.g., mesquite. Plant distribution, however, is primarily a reflection of soil salinity, with soil moisture, topography, climate, pH, and biotic factors playing secondary though often significant roles (Ungar 1974).

The physical environment present in saline habitats is very restrictive, for few plants can tolerate moderate to high salinities. Most agricultural crops are affected by salinities in excess of 0.1% (Richards 1954), whereas the most salt-tolerant species have been found in areas with up to and occasionally exceeding 5% salt as measured from saturated soil extracts. The gradual increase of salinities from peripheral higher to central lower areas is reflected by community zonation, with those species capable of tolerating higher soil salinities occurring in the central lower areas. The more recent studies of inland halophytic vegetation in western North America (Bolen 1964; Dodd and Coupland 1966; Hunt and Durrell 1966; Ungar et al. 1969; Ungar 1965, 1967, 1970, and others) have emphasized quantitative vegetative analysis and species-soil relationships, and Ungar (1974) presents a comprehensive review of halophytic communities and their physical parameters. Though these studies have covered only a relatively few areas, they have uncovered some major trends in community structure in inland saline habitats. Vegetation in areas of high salinity is often quite sparse and will consist of one or a few pioneer species that invade saline flats. In western North America these pioneer species include *Allenrolfea occidentalis* (Wats.) Kuntze, *Distichlis spicata* var. *stricta* (Torr.) Beetle, *Sesuvium verrucosum* Raf., which also range into the Chihuahuan Desert, as well as *Suaeda depressa* (Pursh) Wats. and *Salicornia rubra* Nels. Pioneer com-

munities occurring on the open, more saline flats commonly exhibit very low diversity, usually consisting of a single dominant species that occurs in high frequency though often in low density. In less saline areas, community structure may be more diverse, and vegetation is often more dense (Ungar 1974). The pioneer species, however, are not restricted to highly saline habitats but may be found also in areas of quite low salinity as well. Their presence therefore cannot always be used as a direct indication of high salinity. Laboratory growth studies by Barbour and Davis (1970) in coastal halophytes and laboratory and field observations (see Ungar 1974) in inland halophytes have shown that the more salt-tolerant species usually exhibit much better growth under fresh-water conditions, or, in some species, at very low salinities (Mayer and Poljakoff-Mayber 1963) rather than at higher salinities. Barbour (1970) has argued that no halophyte is at present known to be an obligate halophyte, that is, to exhibit best growth at moderately high salinities; and very few are facultative halophytes exhibiting best growth at low salinities. Likewise, studies on seed germination have shown that germination in halophytes is greatest in fresh or sometimes slightly saline water and decreases at higher salinities, although seeds of some species, such as *Suaeda depressa* and *Salicornia rubra*, have some germination in as much as 4% salt (Williams and Ungar 1972; Ungar 1974). Coupland (1950) and Ungar (1964, 1965, 1974) and others have stressed that halophytic species do not grow in saline environments because they require excessive salts, but that they live in these saline habitats because they do not compete well in nonsaline environments; and by living in these saline habitats they escape the competition of the faster growing glycophytes (nonhalophytes). Also, within saline habitats the pioneer species occupy the areas of higher salinity because they are often "out-competed" by the species occupying the less saline peripheral areas. Community structure, then, is a reflection of a species ability to tolerate physical environmental parameters and thus lessen competition.

Most halophytic species have some physiological means of adapting to the high soil salinity (see Caldwell 1974 for review). Many halophytic species compensate for increased soil salinity by accumulating salts in their tissue. This may involve a preferential accumulation of various cations or anions, in some instances, of different types in different plant species growing in the same soil. The increased cellular concentrations allow the plants to maintain turgor as soil salinity increases (Caldwell 1974). Some halophytic species may also have means of avoiding excessively high salt concentrations in their cells. The cell ionic concentrations may be reduced by increased water uptake and the plants may become increasingly succulent, or they may simply grow, which serves to dilute the electrolytes. Some plants, e.g., *Limonium*, *Distichlis*, and *Tamarix*, have salt-excreting glands from which electrolytes are actively

secreted through specialized cells; or the salts may be concentrated in bladder-like trichomes, as noted for a species of *Atriplex* by Mozafar and Goodin (1970). Regulation of salt intake can also occur by ion exchange at root membranes, apparently through a nonmetabolic means (Scholander et al. 1964; Scholander 1968) involving very high negative pressures which bring in fresh water against an osmotic gradient. If internal solutions become excessively saline, complete or partial dieback may result (Chapman 1960).

Saline habitats are not the only type of restrictive habitats in the Chihuahuan Desert. Gypsum areas are also edaphically limiting habitats (Johnston 1941), but they are not as severely restricting as saline habitats. In an outcropping of gypsum, there is often a distinct change in floral diversity, with a number of gypsophyllous species, e.g., *Larrea tridentata* (DC.) Cov., *Atriplex canescens* (Pursh) Nutt., and *Acacia neovernicosa* Isely, that will continue into the gypsum, though in decreased density; that is, many "non-gypsophyllic" species can tolerate gypsum. Few, however, can tolerate saline environments. This is most likely because gypsum ($\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$) has a solubility of 0.24 g/100 cold water while the common salts NaCl and KCl have solubilities of 35.7 and 34.7 g/100 cold water, respectively (Handbook of Chemistry and Physics 1973). The greater solubility of these common salts has a much greater effect on water-uptake capacity of plants.

Little information has been assembled on the distribution of saline habitats and halophytic species in Mexico. Halophytes in effect have been often regarded as insignificant, as exemplified by their omission (Muller 1947; LeSueur 1945) or cursory coverage (Shreve 1939; Marroquin et al. 1964) in previous treatments of vegetation of the Chihuahuan Desert region. The first to make concentrated observations on halophytes was Johnston, who described 10 endemic halophytic species, and his unfinished treatment of the vascular plants of the Chihuahuan Desert region (Johnston 1943-44) included treatments of the two major families containing halophytic species—the Chenopodiaceae and Poaceae. As noted above, most modern treatments of saline environments emphasize community structure as related to soil salinity. This paper will emphasize overall distribution of saline environments and halophytes in the Chihuahuan Desert and the causal factors promoting plant distribution and endemism.

METHODS

An extensive reconnaissance of saline environments was undertaken during September 1974 when many of the lakes contained sufficient water to reduce significance of soil-salinity measurements and also to restrict free access to many peripheral areas of vegetation. Visits were made to Lagunas de Guzman, de Santa Maria, las Palomas, del Rey, del

Coyote, de la Leche, de Jaco, del Guaje, de Viesca, de Mayran and to saline flats near Cuatro Ciénegas, Las Delicias (Coahuila) and Concepcion del Oro (Fig. 2). Additional information on the distribution of halophytic species has been obtained from various floras (Kearney and Peebles 1951; Wootton and Standley 1915; Correll and Johnston 1970), the works of Johnston (1943-44), and herbaria of the University of Texas and Rancho Santa Ana Botanic Garden. Christine Hopkins provided information on distribution of *Suaeda*, and Donald Pinkava provided information of distributions of plants in the Cuatro Ciénegas area. Measurements of soil salinity and gypsum content followed the general techniques given in Richards (1954) except that salinities were determined from saturated soil extracts by a refractometer. Nomenclature follows Correll and Johnston (1970).

RESULTS AND DISCUSSION

Drainage Basins

Saline environments are well represented in the Chihuahuan Desert, for about two-thirds of the desert drains internally. Well over 300,000 km² (115,000 mile²), much outside of the Chihuahuan Desert proper, drain into the desert to form several very large and small lakes and flats. The only significant external drainage is through the Rio Grande (Rio Bravo) and its tributaries.

The 12 major internal drainage basins occurring or extending into the Chihuahuan Desert are illustrated in Fig. 1. Data on the drainage systems, major river systems, lakes present, and total estimated size of the drainage areas are presented in Table 1. This information is taken with some modifications from Tomayo's (1962) comprehensive treatment of drainage areas in Mexico. The internal drainage basins can be divided into two types: (1) those with drainage concentrated in recognizable rivers which terminate in large dry lakes; and (2) multiple drainage basins in which drainage is more local or divided into a number of separate saline flats or dry lakes with independent drainage and in which rivers are lacking or rare. In the Chihuahuan Desert, the first type is represented by the Rio Casas Grandes, Rio Santa Maria (Fig. 3), Laguna de Patos, Rio Nazas, and Rio Aguanaval basins. Each drains through a single major river, or in the case of the Rio Nazas, through a number of tributary rivers. The rivers flow mainly or only during the rainy season; and in most basins the rivers may meander, ramify, and anastomose often in indefinite courses, and much water may percolate down into underground water reservoirs before reaching the lakes. Dams are present on several of these systems, e.g., the Rio Nazas, Rio Santa Maria, which further decrease flow. Some lakes such as Laguna Mayran very rarely contain water for this reason.

The multiple drainage basins occur in areas in which topography

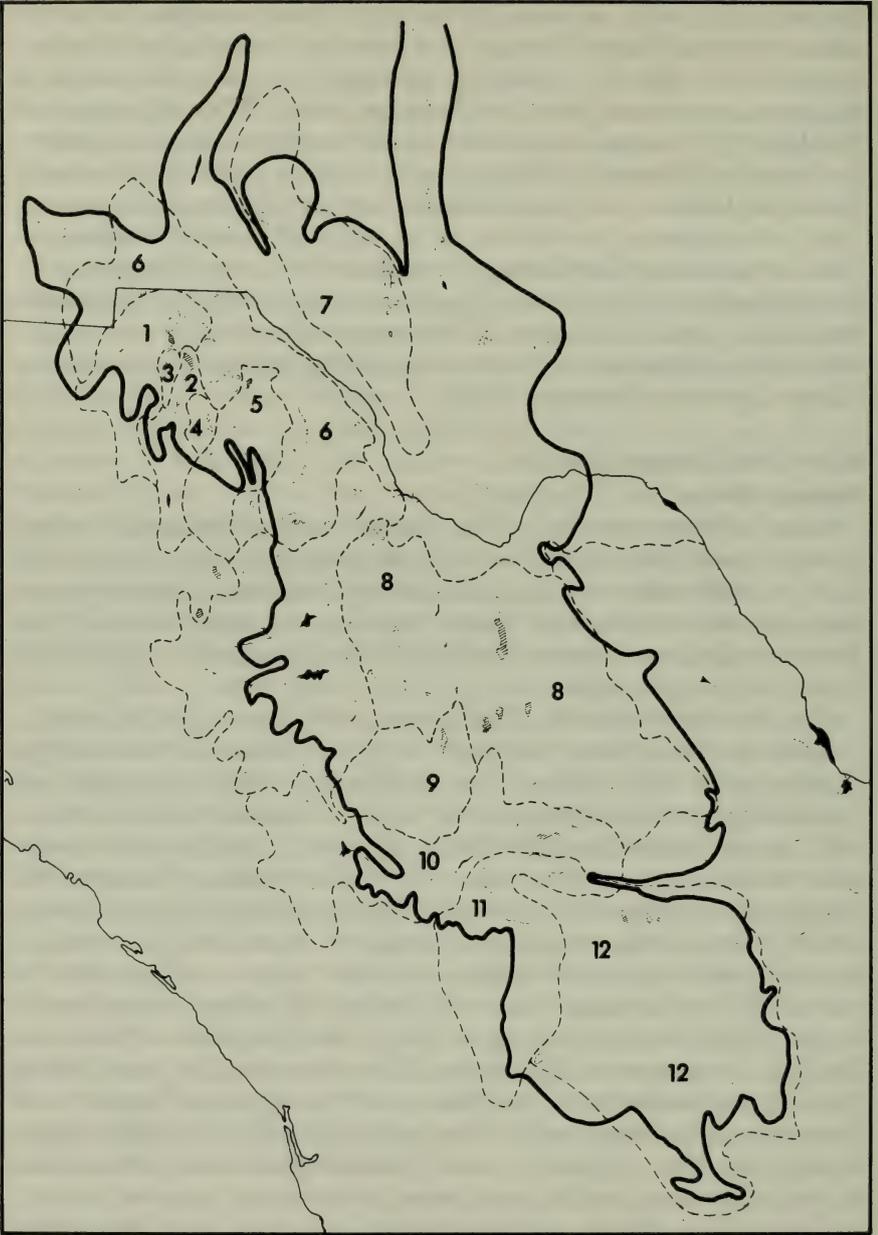


Fig. 1. Map of drainage areas of the Chihuahuan Desert region with outline of Chihuahuan Desert region (shown in bold solid line, from M. C. Johnston); also showing states (delimited with dotted line), rivers (slender continuous lines), saline flats (light diagonal lines), dry lakes or playas (heavier diagonal lines), and permanent dammed lakes (solid black). Numbers refer to drainage basin numbers presented in Table 1.

TABLE 1. Internal drainage basins of the Chihuahuan Desert. Data modified from Tomayo 1962.

| INTERNAL DRAINAGE BASIN | STATES | MAJOR RIVERS AND TRIBUTARIES | | DRAINAGE AREA IN Km ² |
|------------------------------|--------------------|--|---|----------------------------------|
| | | | LAKES | |
| 1. Rio Casas Grandes | Chih. | Rios Piedras Verdes, de Janos to Rio Casas Grandes | Laguna de Guzman and saline flats | 16,600 |
| 2. Rio Santa Maria | Chih. | Rio Santa Maria | Laguna de Santa Maria | 10,680 |
| 3. Fresnal | Chih. | --- | 2 saline flats | 2,110 |
| 4. Rio Bajio de Ojo Caliente | Chih. | Rio Bajio de Ojo Caliente | Several small lagunas: de vieja, la Noria, Ojo Puerco San Cristobal, Victoria Chayote, Colorado | 2,000 |
| 5. Laguna de Patos | Chih. | Rio Santa Clara to Rio del Carmen | Laguna del Patos | 11,880 |
| 6. Llano | Chih., N.M. | Rio Mimbres (N.M.) | Many small playas and flats | 39,000 |
| 7. Tularosa, Trans-Pecos | N.M., Tex. | Chispa Creek (Tex.) | Salt Basin, Tex. | 30,000 |
| 8. Bolson de Mapimi | Chih., Coah., N.L. | --- | Lagunas del Rey, de la Leche, del Coyote, Colorado, de Jaco, del Guaje, de Lagunillo and others; Cuatro Cienegas, Las Delicias, San Marcos, flats | |
| 9. Laguna de Los Palomas | Chih., Dur., Coah. | Rio Cadena | Laguna de las Palomas | 18,800 |

TABLE 1. (Continued)

| INTERNAL DRAINAGE BASIN | STATES | MAJOR RIVERS AND TRIBUTARIES | | DRAINAGE AREA IN Km ² |
|-------------------------|---|--|--|----------------------------------|
| | | | LAKES | |
| 10. Rio Nazas | Dur., Coah. | Rios Tepehuantes, Santiago de Ramos, del Oro to Rio Nazas | Laguna de Mayran | 38,580 |
| 11. Rio Aguanaval | Zac., Coah. | Rio Trujillo to Rio Aguanaval | Laguna de Viesca | 26,500 |
| 12. El Salado | S.L.P., N.L. Zac., Coah. Tam. | --- | Many small flats, playas, Laguna Santa Ana | 92,000 |
| | | | Total | 317,650 ± |

limits development of major drainage systems, and runoff water is deposited in many separate basins which may range from slightly or highly saline flats to large playas, depending upon drainage area and geological factors. The Chihuahuan Desert contains four major multiple drainage basins, two of which extend into or occur in the United States. The Llano basin, occupying much of northern Chihuahua, extends into southwest New Mexico and the Tularosa-Salt Basin is situated in eastern New Mexico and western Texas, west of the Davis-Guadalupe Mountains. The Bolson de Mapimi is a large multiple basin in western Chihuahua and central Coahuila; and the largest of all, El Salado, occurs in eastern Zacatecas, northern San Luis Potosí and extends into parts of Coahuila, Nuevo Leon, and Tamaulipas. These multiple basins are usually defined merely by the fact that they do not drain into adjacent river drainage systems. Of the four major multiple drainage basins, only the Bolson de Mapimi forms a number of distinct, large, dry lakes (Fig. 4). Other basins contain mainly small lakes and saline flats. The Fresnal and Rio Bajio de Ojo Caliente basins are small multiple basins separated mainly because they are delimited by other well-defined river basins.

The major external drainage in the Chihuahuan Desert occurs through the Rio Grande and its tributaries, mainly the Rio Conchos, Pecos River, Rio Sabinas, and the Rio Salado. Other areas drain through the Rio Salinas and the Rio Verde. Not all areas within these drainage basins drain externally. There are many areas of local drainage in which saline environments develop. These desert basins receive water after summer-fall rains. It can be noted that runoff is generally greater after

TABLE 2. (Continued)

| | NEW MEXICO | TRANS-PECOS TEXAS | LAGUNA DE GUZMAN | LAGUNA DE SANTA MARIA | LAGUNA DE LAS PALOMAS | LAGUNA DE JACO | LAGUNA DEL GUAJE | LAGUNA DEL REY | LAGUNA DEL COYOTE | LAGUNA DE LA LECHE | CUATRO CIENEGAS | LAS DELICIAS | LAGUNA DE MAYRAN | LAGUNA DE VIESCA | CONCEPCION DEL ORO | SALINAS |
|---|------------|-------------------|------------------|-----------------------|-----------------------|----------------|------------------|----------------|-------------------|--------------------|-----------------|--------------|------------------|------------------|--------------------|---------|
| <i>A. confertifolia</i> (Torr. & Frem.) Wats. | X | X | | | | | | | | | | | | | | |
| <i>A. elegans</i> (Moq.) D. Dietr. | X | X | | | | | | | | | | | | | | |
| <i>A. muricata</i> Humb. & Bond. ex Willd. | 3 | 3 | | | | | | | | | | | | | | |
| <i>A. monilifera</i> Wats. | * | 2 | | | | | | | | | | | | | | |
| <i>A. obovata</i> Moq. | * | 3 | X | X | | | | | | | | | X | | | |
| <i>A. pringlei</i> Standl. | * | 2 | | | | | | | | | | | | | | |
| <i>A. prosopidium</i> I.M. Jtn. | * | 3 | | | | | | X | X | X | X | | | | | |
| <i>A. reptans</i> I.M. Jtn. | * | 2g | | | | X | | X | X | X | | | | | | X |
| <i>A. stewartii</i> I.M. Jtn. | * | 3 | | | | | | | | | | | | | | |
| <i>A. texana</i> Wats. | ** | 2g | X | | | X | X | | | | | | | | X | |
| <i>Meiomeria stellata</i> (Wats.) Standl. | 3 | 3 | | | | | | | | | | | | | | |
| <i>Salicornia utahensis</i> Tidestr. | * | 3 | | | | | | | | | | | | | | |
| <i>Suaeda jacoensis</i> I.M. Jtn. | * | 2 | | | | X | | | | | | | | | | |
| <i>S. mexicana</i> (Standl.) Standl. | * | 2 | | | | | | | | | X | | | | | |
| <i>S. nigrescens</i> I.M. Jtn. | * | 2 | | | | | | | | | | X | | | | |
| <i>S. n. var. glabra</i> I.M. Jtn. | * | 2 | X | | X | | | X | | | | | | | | |
| <i>S. palmeri</i> (Standl.) Standl. | * | 3 | | | | | | | | | | | | | | |
| <i>S. suffrutescens</i> Wats. | * | 3 | X | X | | X | | | X | X | X | X | X | X | X | |

ENDEMIC, *species; **genus
 SALINITY TOLERANCE: 1, high
 2, moderate; 3, moderate-non

TABLE 2. (Continued)

| | NEW MEXICO | TRANS-PECOS TEXAS | LAGUNA DE GUZMAN | LAGUNA DE SANTA MARIA | LAGUNA DE LAS PALOMAS | LAGUNA DE JACO | LAGUNA DEL GUAJE | LAGUNA DEL REY | LAGUNA DEL COYOTE | LAGUNA DE LA LECHE | CUATRO CIENEGAS | LAS DELICIAS | LAGUNA DE MAYRAN | LAGUNA DE VIESCA | CONCEPCION DEL ORO | SALINAS |
|---|------------|-------------------|------------------|-----------------------|-----------------------|----------------|------------------|----------------|-------------------|--------------------|-----------------|--------------|------------------|------------------|--------------------|---------|
| <i>S. s. var. detonsa</i> I.M. Jtn. | | | X | X | | | | | | | X | | X | | | X |
| <i>S. torreyana</i> Wats. | 2 | X | | | | | | | | | | | | X | | |
| COMPOSITAE | | | | | | | | | | | | | | | | |
| <i>Pseudocappia arenaria</i> Rydb. | 3 | X | | | | | | | | | | | | | | |
| PLUMBAGINACEAE | | | | | | | | | | | | | | | | |
| <i>Limonium limbatum</i> Small | 2 | X | | | | | | | | | X | | | | | |
| GRAMINEAE | | | | | | | | | | | | | | | | |
| <i>Distichlis spicata v. stricta</i> (Torr.) Beetle | 1 | X | X | X | | | | | | | X | | X | | | |
| <i>Eragrostis obtusiflora</i> Scribn. | 1 | X | X | X | | | | | | | | | | | | |
| <i>Monanthochloe littoralis</i> Engelm. | 2 | | | | | | | | | | X | | | | | |
| <i>Reederochloa eludens</i> Soderstrom & Decker | 2 | | | | | | | | | | X | | | | | |
| <i>Spartina spartinae</i> (Trin.) Hitchc. | 3 | X | X | X | | | | X | X | | X | | | | | |
| <i>Sporobolus atroides</i> (Torr.) Torr. | 3 | X | X | X | | | | X | X | | X | | | | | |
| <i>S. regis</i> I.M. Jtn. | * | | | | | | | | | | | | | | | |
| <i>S. spiciformis</i> I.M. Jtn. | * | | | | | | | | | | | | | | | |
| <i>S. wrightii</i> Scribn. | 3 | X | X | X | | | | X | X | | X | | | | | |

ENDEMIC, *species; **genus
 SALINITY TOLERANCE: 1, high
 2, moderate; 3, moderate-non

the approximate areas of saline environments in each of the above-noted basins. Unfortunately, maps currently available do not depict saline environments with sufficient accuracy to provide significant information. It is estimated that approximately 9000 km² (3500 mile²) of saline environments occur in the Chihuahuan Desert region.

Halophyte Distribution

Before discussing halophyte distribution, it is necessary to define the term halophyte. Barbour (1970) reviewed definitions of halophytes and, although general agreement exists that a halophyte is a species that can tolerate salinity, the amount they must tolerate meets with little agreement. Barbour (1970) arbitrarily set the limit at 0.2% for a low saline condition above which nonhalophytic species begin to display declining growth. Some species have also been designated halophytic gypsophylls (Johnston 1943-44; Waterfall 1946), indicating their occurrence in saline gypsum outcroppings. These habitats exist along several playas in the Chihuahuan Desert including Lagunas de Jaco, del Rey, and Cuatro Ciénegas and in New Mexico and western Texas (Waterfall 1946).

As was noted above, saline playas and flats present a gradation of salinity from higher to lower sites of deposition and this is reflected by plant-community zonation. One can, therefore, discuss halophyte distribution in relation to tolerance of salinity and divide the halophytic species into (1) pioneer species capable of tolerating the more saline habitats at the margin of saline flats; (2) those occupying less saline higher sites; and (3) those occurring in nonsaline and slightly saline habitats (Table 2). Numerous studies have shown, however (Ungar 1964, 1965, 1966; Bolen 1964; Flowers 1934), that most salt-tolerant species can also grow at low to nonsaline conditions. The reason they often occur in highly saline areas is, as noted before, considered a factor of competition. For example, *Allenrolfea occidentalis* characteristically occurs in more saline habitats along playas (Ungar 1974). However, near Laguna de Las Palomas near Carrizal, *Allenrolfea* occurs in the ecotone between *Larrea* scrub and other halophytes occurring with *Larrea tridentata*, *Atriplex canescens*, *Lycium berlandieri*, *Prosopis glandulosa*, and *Suaeda* sp. where soil salinity measures 0.3%. Not surprisingly, *Allenrolfea* reached 2 m in height, whereas in saline flats, it seldom exceeds 0.5 m. These apparent differences in salinity tolerance may be genetically based, and possibly ecotypes exist, but most growth studies indicate the contrary (Barbour 1970). The relative tolerance of the more commonly encountered Chihuahuan Desert halophytes is given in Table 2. The species occupying more saline habitats include *Distichlis spicata* var. *stricta*, *Eragrostis obtusiflora*, *Allenrolfea occidentalis*, *Suaeda jacoensis*, *Sesuvium verrucosum*, and *Suaeda palmeri*. The most common species occurring on higher, slightly saline habitats include *Atriplex*

acanthocarpa, *A. obovata*, and *Suaeda* spp. Those occurring in both non-saline and saline soils include several species of *Atriplex* (*A. canescens*, *A. elegans*, and others), *Sporobolus wrightii*, *S. airoides*, and others. Some species have very broad tolerances of substrate. *Suaeda palmeri*, a shrubby species was observed in clay, sandy clay, gypsum, and outwash alluvial soils, with salinities varying from 11.4% to what must have been minimal in areas dominated by *Larrea*, *Fouquieria splendens* Engelm., *Grusonia bradtiana* (Coulter) Britton and Rose, *Hechtia*, etc.

As can be seen from Table 2, the distributions of halophytic species in the Chihuahuan Desert are not uniform but several species have highly disjunct patterns of distribution. This is caused in part by the scattered distribution of saline habitats (Fig. 2) but also by nonvagility of dispersal units, e.g., seeds and fruits. Fruits of *Atriplex* are large and heavy, and except for those species with large wings of the subtending bracts (*A. canescens*), they are not readily dispersed for long distances i.e., between drainage basins. However, one should not underestimate the potential of "dust devils" and high winds as dispersal vectors. *Suaeda*, *Allenrolfea*, *Sporobolus*, and others lack specialized morphological seed-dispersal mechanisms, except that they could be carried in mud on birds' (ducks') feet between adjacent lakes (Van de Pijl 1972). One could also consider that the possible differences in kinds of salts in adjacent drainage basins might affect distribution, but Ungar (1974) noted several studies that have shown that the types of salts present, whether chlorides, sulfates, or bicarbonates, have not been found to affect distributional patterns in halophytes.

Another factor apparent from Table 2 is the depauperate nature of halophytic assemblages. Several playas have as few as five perennial species, e.g., Lagunas de la Leche and del Guaje, though many other species may occur in peripheral areas.

Fig. 3. Lagunas de Guzman and de Santa Maria in northwest Chihuahua terminates the Rios Casas Grande and Santa Maria, respectively. The two lakes, separated spatially by 15 km, have similar floras but on 16 September 1974 Laguna de Guzman (Fig. 3-a) was dry and contained scattered *Sesuvium verrucosum* on the open floor while Laguna de Santa Maria had been wet and contained dense stands of perennial salt grass (*Distichlis spicata* var. *stricta*) (Fig. 3-b) and *Eragrostis obtusiflora* which covered several square kilometers in the north end of the lake bed. One week later, Laguna de Guzman was filled with water due to storms in the foothills of the Sierra Madre Occidental. In the sandy margins of Laguna Santa Maria (Fig. 3-c) are stands of *Suaeda torreyana* contiguous with the flats and extensive stands of sacaton (*Sporobolus airoides*) at higher elevations. The northwest margin of Laguna de Santa Maria contains several springs and two small ponds, one of which (Fig. 3-c) is permanent, slightly saline (0.3%) and contains *Potamogeton pectinatus* L. Both ponds are surrounded by dense stands of bulrush (*Scirpus olneyi*) to 1 m high and an understory of *Eleocharis rostellata* (Torr.) Torr., water parsnip (*Berula erecta* [Huds.] Cov.) and *Erigeron* spp. The *Eleocharis rostellata* also extends into the peripheral stands of salt grass. →





Endemism

Halophytic species in the Chihuahuan Desert occur mainly in two families—the Chenopodiaceae and the Poaceae. Of the 40 taxa noted in Table 2, 25 taxa (62%), including 3 genera are endemic to saline areas in the Chihuahuan Desert region. A total of 26 species of halophytic Chenopodiaceae occurs in the desert; of these, 17 species and one genus are endemic. *Allenrolfea occidentalis* is widespread in western North America and occurs in several localities in the Chihuahuan Desert region. A second species, *A. mexicana* Lundell, has been described from a sandy habitat near Santo Domingo, San Luis Potosí, but this represents only large individuals of *A. occidentalis* and is unworthy of taxonomic distinction. *Atriplex* is represented by 15 taxa in the Chihuahuan Desert. Of these, *A. canescens*, *A. confertiflora*, and *A. argentea* ssp. *expansa* range into the Great Basin; *A. elegans* ranges into the Sonoran Desert; *A. muricata* extends into central Mexico; and *A. semibaccata* (not indicated) is introduced. The remaining eight species have their centers of distribution in the Chihuahuan Desert. *Atriplex canescens*, *A. acanthocarpa*, and *A. obovata* are the most common and variable species. *Atriplex acanthocarpa* occurs in southwest New Mexico, Chihuahua, and western Coahuila and is replaced by intergradations with *A. stewartii* in central Coahuila and an unnamed form in eastern and southern Coahuila, in northern Zacatecas, and San Luis Potosí, where it occurs with the related *A. pringlei*. A total of eight taxa (seven species) of *Suaeda* occur in the Chihuahuan Desert, of which five are endemic. Only *Suaeda suffrutescens*, *S. torreyana*, which range into Arizona, and *S. mexicana*, which is also known from Yucatan, extend out of the Chihuahuan Desert. The taxonomy of the remaining species is complex and in need of systematic study. While *S. palmeri*, *S. mexicana*, and *S. jacoensis* are quite distinct, the other species are poorly defined and were noted not to occur in sympatric associations. *Meiomeria*, a monotypic, endemic genus, is a succulent annual noted by Johnston (1943-44) to be a halophytic gypsophyll. *Salicornia utahensis* has recently been collected in Cuatro Ciénegas by Pinkava.

The Aizoaceae are represented by a widespread pioneer species, *Sesuvium verrucosum*, and the Capparidaceae by two endemic halophytic species: the annual *Cleomella longipes* in Trans-Pecos Texas and New Mexico to Chihuahua, and the suffrutescent perennial *Cleomella perennis*, which ranges from Laguna de Jaco to Durango and the state of Guanajuato. *Pseudocapparia arenaria*, a monotypic, endemic genus of Asteraceae, occurs in saline gypseous areas in Trans-Pecos Texas and adjacent New Mexico, as does the plumbaginaceous *Limonium libatum* (Waterfall 1946). *Limonium* also occurs in nongypseous areas.

The Poaceae also contain many halophytic species, including the

wide-ranging *Distichlis spicata* var. *stricta*, *Monanthochloe littoralis*, and the more restricted *Eragrostis obtusiflora*, which ranges from Arizona to Laguna de Jaco. The dioecious *Reederochloa eludens* is a monotypic, endemic genus known only from saline flats near Salinas, San Luis Potosí and Cd. Durango (Soderstrom and Decker 1966). *Sporobolus* is well



Fig. 4. Lagunas de la Leche, del Rey, and del Guaje occur in the Bolson de Mapimí but differ greatly in vegetative cover. Laguna de la Leche has extensive unvegetated flats (Fig. 4-a). The eastern and lowest margin of the lake contains dense stands of sacaton grass (*Sporobolus wrightii*) where rain water accumulates, thereby reducing salinity during the growing season. The northwest margin of the lake contains an extensive stand of *Bouteloua karwinskii* on slightly higher and less saline (0.2-0.4%) flats. The flats south of the lake (Fig. 4-b) measured 0.5% salinity and contained a dense stand of *Atriplex stewartii* and numerous small perennials such as *Heleotropium* spp., *Hoffmanseggia glauca*, etc. Adjacent, more saline areas contained *Suaeda suffrutescens*. Laguna del Ray, lying 55 km west of Laguna de la Leche, has totally different vegetation with *Sesuvium verrucosum* and *Allenrolfea* in pioneer habitats (Fig. 4-c); and extensive marginal gypseous dunes contain stands of *Sporobolus airoides* (Fig. 4-d), *S. regina* (an endemic species), *Atriplex canescens*, *Ephedra trifurcata*, *Yucca elata*, etc. Other more saline areas contain *Atriplex stewartii*, *A. obovata*, and *Suaeda nigrescens* var. *glabra*. Note the smoke from Quimeca del Rey in the background of Fig. 4-c. The Laguna del Guaje is a very large lake (ca. 175 km²), 80 km north of Laguna de Rey, and contains extensive unvegetated flats and very extensive monospecific stands of sacaton grass (*Sporobolus wrightii*) (Fig. 4-e-f), which occur in the lower areas. The lake is type locality of *Atriplex stewartii*. *Atriplex obovata* is also present, but *Distichlis*, *Allenrolfea*, and *Suaeda* are not known from the lake. Only 65 km to the west lies Laguna de Jaco, type locality of *Atriplex reptens*, and *Suaeda jocoensis*, and which also contains *Distichlis*, *Allenrolfea*, and *Suaeda suffrutescens*. →



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represented around saline environments, including *S. airiodes* and *S. wrightii*, the most commonly encountered, and *S. spiciformis* and *S. regis*, endemic to southern Coahuila.

There is a large number of additional species that occur on or around saline flats and playas. None of these is restricted to saline habitats. The annual and many of the herbaceous perennial species develop on these saline sites only after rains decrease total salinity, and they usually die back as salinities increase. Certain of these species apparently can tolerate quite high salinities, for they will occur in the open non-vegetated playas where few other plants grow. A number of grasses, mostly annual, can be included in this group, e.g., *Leptochloa fascicularis* (Lam.) Gray, *L. uninerva* (Presl.) Hitchc. and Chase, various species of *Panicum*, including *P. obtusum* H.B.K., *Sporobolus pyramidatus* (Lam.) Hitchc., and *Chloris virgata* Swartz. *Bouteloua karwinskii* (Fourn.) Griffiths, a species not always associated with saline environments, forms extensive stands along Laguna de la Leche; and Johnston (1943-44) reports *B. trifida* Thurb. in Wats. from slightly saline soils in the same area. Other species of *Bouteloua*, *Erioneuron*, *Aristida*, *Muhlenbergia*, as well as *Hordeum jubatum* L., and *Polypogon monspeliensis* (L.) Desf. also occur in saline habitats in the area. Three species of submerged aquatics, *Zannichellia palustris* L., *Ruppia maritima*

L., and *Potamogeton pectinatus* L., have been recorded in saline and brackish waters in the Chihuahuan Desert (Johnston 1943-44). A large number of annual and perennial herbs may also occupy these sites, such as *Allionia incarnata* L., *Boerhaavia* sp., *Dyssodia aurea* (Gray) A. Nels., *Heliotropium curassavicum* L., *H. glabrisculum* (Torr.) Gray, *H. molle* (Torr.) I.M. Johnst., *Hoffmanseggia glauca* (Ort.) Eifert., *Salsola iberica* Sennen and Pau.L., *Tidestromia lanuginosa* (Nutt.) Standl., and *Trianthemum portulacastrum* L. This group also includes some shrubby species such as *Lycium berlandieri* Dun., *Isocoma wrightii* (Gray) Rydb., *Tamarix gallica* L., the very common *Prosopis glandulosa* Torr. var. *glandulosa* and *P. glandulosa* var. *torreyana* (L. Benson) M.C. Johnst., and a large number of cacti, including *Opuntia leptocaulis* DC., *O. macrocentra* Engelm., *Coryphantha macromeris* (Engelm.) Lemaire, and others. *Echinocactus texensis* Hopffer and *Ariocarpus kotschubeyanus* (Lemaire) Schumann were observed in very saline flats in the playa of Laguna de Viesca.

One can note that of all saline areas indicated in Table 2, the Cuatro Cienegas basin contains the highest concentration of halophytes. This could be the result of the large area of saline habitats available in the basin, the more plentiful supply of subterranean water available, or the long time that these habitats have been available for colonization. Meyer (1973), on the basis of studies of fossil-pollen chronology, noted that the vegetation now present on the floor of the Cuatro Cienegas basin has been more or less similar since mid-Wisconsin time, ca. 30,000 years ago. The Cuatro Cienegas basin has a number of additional species on gypsum and occasionally on saline-gypseous soils. These include a species of *Oenothera*, *Machaeranthera restiformis* Turner, *Tidestromia rhizomatosa* I. M. Johnst., and others.

It is important also to note that saline playas are not isolated habitats but are often associated with sand dunes which have their own distinctive floras. The saline habitats associated with dry lakes are extreme deposition habitats. Other basins may be only slightly saline or nonsaline and, if they contain underground fresh water, may contain vegetation dominated by the phreatophytic *Prosopis glandulosa* and an assemblage of other characteristic species, including *Atriplex canescens*, *Flourensia cernua* DC., *Parthenium incanum* H.B.K., *Lycium berlandieri*, and others. Still other basins or flats contain dense stands of Tobosa Grass (*Hilaria mutica*). These flats generally have a clay to sandy-clay soil and are not significantly saline. Soils in a Tobosa Grassland south of Escalon, Chihuahua, contained only 0.2% salts.

Of the 40 primarily halophytic taxa noted above as occurring in the Chihuahuan Desert, 25 (62%) are endemic or range only slightly outside the Chihuahuan Desert region, and this includes three endemic genera—*Reederochloa*, *Meiomeria*, and *Pseudocappia*. The last two are considered halophytic gypsophylls.

While the total endemism found on saline areas in the Chihuahuan Desert is not as great as that encountered on gypseous habitats, the percent of endemism is significant, especially because we are considering such a small flora. First we may ask, why are there so few plants occurring in saline habitats? The obvious response is that it is the result of the severity of the habitat and the few groups of plants that have means of tolerating such osmotic potentials. But why should there be endemism? These isolated saline playas and flats not only exhibit adaptation of plants to extreme environments but present a series of disjunct habitats comparable to islands in a sea, vernal pools in the California grasslands, or mountain peaks of a cordillera, between which gene flow is restricted by spatial isolating mechanisms (Grant 1963). The intermittent and often local rainfall may cause adjacent playas to fill at different times or only rarely, resulting in temporal isolation for an indefinite period and in different blooming times in adjacent flats. The populations are often subject to bottle-necks in size depending on weather conditions. Populations may be extensive or occasionally very localized, thus affecting the rates of evolution and resulting in independent adaptation and possible development of distinct ecotypic or morphological differences between populations. In small, fragmented populations, genetic drift (Grant 1963) may result in interpopulation variation. All this occurs in a field in which selection due to aridity is severe and competition is very high. These factors may, as Stebbins (1952) suggested, serve as a stimulus to plant evolution. In this regard the saline playas and flats present an opportunity to study evolutionary factors. Saline habitats present an untapped laboratory of evolution.

Man's Utilization

One would expect that these biologically hostile habitats would be of little economic value and would escape man's often destructive activities. However, man is using and modifying these habitats. Vegetation around lakes is subjected to grazing by livestock even though vegetation may be sparse and many plants cannot be used as forage. The internal salt concentrations of *Allenrolfea* and *Suaeda* and salts deposited on leaves of *Distichlis* usually make these plants unfit as forage. In these species, salinity provides protection, just as spines protect cacti from herbivores. Some species of *Atriplex* also concentrate salts particularly on their outer surface, but new growth and fruits may be heavily grazed by livestock (Wootton and Standley 1915), as will *Sporobolus* and new growth of *Distichlis*. The endemic genus *Meiomeria stellata*, a rare, highly succulent annual, may be vulnerable to extinction by overgrazing. Automotive travel and road building over dry lakes can modify drainage patterns and affect distributions of plants which often concentrate in slightly wetter basins within playas. The most significant encroachment

on dry lakes at present is associated with commercial salt-extraction techniques which pump up brine for evaporation in surface pools. Commercial salt works are presently located at Lagunas de Jaco, del Rey, and de las Palomas. These are relatively small operations run as "ejidos." Their main effect is in modifying drainage and through a concentration of people who in turn concentrate herbivores. The potential exists for large-scale exploitation, however. There is a large factory at Laguna del Rey (Quimica del Rey S.A.) which uses the brine in production of commercially pure magnesium oxide from magnesium ore mined at Sierra Mojada. The industry's effect on the lake vegetation is in itself small, but it is a big and expanding operation which emits a continuous plume of smoke (mostly particulate matter) which affects visibility throughout the area. Thus far, no surface mining of salt crystals has occurred and it is doubtful that any commercially extractable surface salts would occur in the Chihuahuan Desert.

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Aspects of the Plant Biology of the Gypsum Outcrops of the Chihuahuan Desert

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INTRODUCTION

Many excellent reports have been presented before this symposium. The three preceding papers of this session have been particularly good, and it might seem that this effort will be made more difficult under the circumstance of having to follow them. However, in actuality this report has an advantage over most of the earlier presentations. The biological aspects of gypsum endemism constitute one of the most exciting stories of modern evolutionary and floristic biology.

Gypsum deposits (hydrous calcium sulfate) presumably were formed by precipitation from ancient seas, perhaps as old as the Permian period. Through geologic time these deposits were covered by strata of various origins, and were subsequently exposed to plant habitation in more recent times through the action of simple erosion as well as more complex geological events. It is difficult to date the time at which gypsum exposures became available to habitation. Some portions of original deposits supposedly have been redistributed by erosional activities perhaps more than once in geological history. We assume that gypsum habitats were exposed from mid-Tertiary to Pleistocene times, depending upon the outcrop in question.

The gypsum exposures are found throughout the Chihuahuan Desert region, and elsewhere in the western United States and Mexico. Some of the gypsum exposure are extensive, covering many square kilometers in surface area, and other are less than 100 m (330 ft.) in largest diameter. Regardless of size, the island-like exposures always support communities (florulas) of plant species which are characteristic of gypsum soils.

Some species that occupy the gypseous substrates are facultative in that they may also live on surrounding soil types.

The plants which occupied gypsum outcrops originally must have been recruited from surrounding habitats (Johnston 1941). However, considerable speciation has occurred in connection with the limiting edaphic conditions of gypsum soils. For example, related species of many different genera are found on disjunct gypsum outcrops as though speciation had occurred subsequent to spatial isolation. Indeed, a few genera are mostly or completely gypsophilous. Several hundred gypsophilic species representing about 150 genera and about 50 families of flowering plants are currently known.

The reality of plant gypsophily was first discussed by Johnston (1941) who studied the phenomenon at numerous sites in the Mexican states of Coahuila, Nuevo Leon, San Luis Potosí, Zacatecas, and Chihuahua. Johnston pointed out that "Gypsophilous plants have been ignored by ecologists and plant-geographers, who have failed to recognize them as a small, but very interesting and noteworthy element in the xerophytic floras of northern Mexico and adjacent United States." Although Johnston's firsthand knowledge of gypsophily was confined to Mexico, he correctly surmised from existing collections that gypsum habitats also existed north of the Rio Grande. Waterfall (1946) extended this work by carrying out extensive studies of gypsum sites in southeastern New Mexico and Trans-Pecos Texas, and he compiled what have proved to be rather thorough lists of gypsophilic taxa for the major outcrops in the region investigated. We are aware of few publications dealing with plant gypsophily between 1946 and the time we initiated our studies in about 1969 (Shields 1956). However, two relatively minor vegetative surveys of gypsum areas were accomplished prior to Johnston's original study. Emerson (1935) compiled a list of species known to grow in the White Sands area of New Mexico. Campbell and Campbell (1938) published a range management survey of gypsum soils on the Jornada Plain in New Mexico, but listed only eight angiosperms which occur there.

Previous collectors have gathered specimens from gypsum exposures but many of them evidently failed to recognize them as gypsum substrates, as evidenced by such label data as "dry calcareous soil," "calcareous," "chalky," "limy," or even "saline" (Johnston 1941). Until the past few years, however, the gypsum outcrops in Mexico were not extensively collected, and many localities were not known. We have opined that botanists often have ignored gypsum sites which may appear to be nearly devoid of vegetation, except upon close examination, especially during relatively dry periods.

Our recent investigations have borne out the reality and the uniqueness of gypsophily. We have found an interesting array of gypsophilic taxa to inhabit every island-like exposure in the Chihuahuan Desert, and

numerous previously undescribed taxa have come from the efforts. Other recent workers, especially M. C. Johnston and his associates collecting for the nascent *Flora of the Chihuahuan Desert*, have added significantly to the knowledge of gypsum florulas within the desert region.

PHYSIOGNOMY OF GYPSUM EXPOSURES

Selenite, which is pure rock gypsum, is virtually colorless and translucent, but pure deposits are seldom found (Stone 1920). Nearly all gypsum deposits contain oxides, carbonates, or other impurities which cause them to range in color from white through gray to nearly black. More infrequently pink or reddish, yellow, brown, and even pale blue deposits are found. Selenite usually is so soft (2 in Moh's scale) that it can be scratched with the fingernail.

Most gypsum exposures in the Chihuahuan Desert are whitish or grayish in appearance. The soil from such deposits is usually rather compact superficially, but is friable, and most characteristically, gypsum soils exhibit a distinctive hollow sound when "pounded or stamped upon" (Johnston 1941). The latter trait probably results from the numerous cavities (subterranean water channels) which permeate thick deposits of gypsum. Erosion and other geological events have caused some exposures to be diluted variously so that they are scarcely recognizable by the above criteria. In such cases gypsophilous plant associations are most reliable in indicating the presence of gypsum in the soil.

Large gypsum deposits may occur as small mountains, ridges, cliffs, or as large flats in desert plateaus or bolsons. Smaller deposits or localized outcroppings also are variable in structure. In a few areas, especially those near salt lakes or flats, gypsum may be in the form of a fine granulated "sand" and may even occur as magnificent white dunes such as those at White Sands, New Mexico, and near Cuatro Ciénegas, Coahuila.

The Cretaceous clays mostly exposed near the Rio Grande between El Paso and Big Bend Park in Texas, Chihuahua, and Coahuila, constitute another type of gypseous substrate. These areas often have been referred to as "Painted Deserts" or "Badlands" in that the hills which comprise them may be of multicolored clays which are nearly devoid of vegetation. These clay hills, which are most commonly brownish in color, may be mixed with shale and gravel and may or may not be gypseous enough to support gypsophilic vegetation. The clays and shales evidently were not gypseous at the time of deposition, but may have had thin deposits of crystalline gypsum intermixed with them by erosional activities, depending upon the geological structure at particular localities. Again, gypsophilous plant associations are most reliable in indicating the presence of gypsum in the soil.

GYPSUM LOCALITIES

Most of the major gypsum deposits of the Chihuahuan Desert in New Mexico and Texas are specified by Waterfall (1946). Generally speaking, the exposures are found as part of the Jornada del Muerto in Socorro County, New Mexico, and in various localities south to the Texas border. In southeastern New Mexico, exposures are extensive in Chaves and Eddy counties, especially in the Pecos River drainage area. In Trans-Pecos Texas, major deposits continuous from New Mexico are found on both the west and east sides of the Guadalupe Mountains, and extend southward for about 72 km (43.2 miles) in Culberson County. Numerous beds, ridges, and smaller outcroppings occur in Reeves, Ward, Pecos, and Crane counties. Near Finley in Hudspeth County, gypsum is quarried from an extensive deposit. As mentioned previously, the Cretaceous gypseous clays are exposed at various localities on both sides of the Rio Grande from El Paso to Big Bend Park.

Many of the major gypsum sites of the Chihuahuan Desert in Mexico are indicated by Johnston (1941). In Nuevo Leon prominent exposures exist between Monclova and Monterrey and in the vicinity of San Roberto; in San Luis Potosí, vicinity of Matehuala and Huizache; in northern Zacatecas, vicinity of Sierra Hermosa and Concepcion del Oro; in Coahuila between San Pedro and Cuatro Ciénegas and near Cuatro Ciénegas; and in Coahuila and Chihuahua, many sites generally north of Torreon and east of Cd. Chihuahua, in the large and unpopulated area south and west of the Big Bend of the Rio Grande.

PLANT GYPSOPHILY

Both Johnston (1941) and Waterfall (1946) were impressed by the dramatic specificity of certain gypsophilic species, and cited examples of species which were noted to be growing side-by-side, but not transgressing, in gypseous and nongypseous soils. We have also noted numerous examples of this remarkable gypsum specificity. Where the contact between gypsum and nongypsum exposures is sharp, the delimitation of gypsophilous and nongypsophilous vegetation usually is equally abrupt. However, the margins of many gypsum exposures have been diluted by the erosion and intermixing of soil types. In these instances there may be a mixture of vegetation types, and we have surmised that the percentage of gypsum in the mixed soils is somewhat relative to the number of gypsum endemics that occur there. We recognize that certain species seem inflexible with regard to their requirements for gypsum (see Appendix) while others are somewhat facultative in this respect. We also suppose that the genotypes of certain species are in themselves variable with regard to gypsum requirements.

Johnston (1941) concluded that plants found on beds of gypsum are of two sorts, "those tolerating gypsum, and those demanding it." The

species tolerating gypsum were construed by Johnston to be the taxa that were typical of nongypseous soils, but which also grew in marginal gypsum mixtures and seemed to be unaffected by differences of the substratum. The species demanding gypsum are those which never seem to grow beyond the margins of gypseous soil. We suggest that there is a third group of genotypes, those which prefer gypsum, and are more often found on gypseous substrata, either mixed or "pure," than on other soil types. In support of our suggestion, we offer the following theoretical explanation. Johnston (1941) believed that the gypsum flora, over a period of evolutionary time, was "recruited" from communities common to the desert region (other than halophytes), and we agree with this thesis. However, in view of the successful speciation episodes which have occurred in connection with gypsophily, it is plausible that some of the nongypseous elements of the desert flora have been recruited from gypsophiles. For example, most of the species of *Neorisyeria* are obligate gypsophiles (Bacon 1975), and it appears likely that most taxa of this genus evolved in response to the edaphic restrictions of gypsum. But one species, *N. camporum*, is equally frequent upon concentrated, dilute, or nongypseous substrates. It is likely that other facultative taxa also have undergone adaptation to nongypseous soils.

OTHER BIOLOGICAL ASPECTS OF GYPSOPHILY

Polyploidy

For many years biologists have been interested in the distribution and percentages of polyploid species in the world flora (DeWet 1971; Grant 1971; Gustaffson 1948; Haskell 1952; Johnson et al. 1965; Johnson and Packer 1965; Löve and Löve 1943, 1953; Pojar 1973; Stebbins 1942, 1950, 1971). It has been suggested that polyploids might enjoy a selective advantage over their diploid ancestors and thus be effective pioneers of new habitats, and those habitats which are more extreme than is typical of parental species. Chromosomal surveys have suggested that there is a significant and progressive increase in polyploid percentages with an increase in northern and southern latitudes (Löve and Löve 1943, 1967; Johnson et al. 1965) and with higher altitudes (Löve and Löve 1967). In 1969 we undertook a chromosomal survey of gypsophilic species in the Chihuahuan Desert, hoping to test the idea that harsh, extreme, or "new" habitats might support a higher percentage of polyploid species. Gypsum habitats certainly may be considered "harsh" by comparative standards in the Chihuahuan Desert. In 1971 Stebbins observed that the lowest percentages of polyploidy seem to be found in the floras of temperate and subtropical areas and that the percentage of polyploidy increases both toward cooler and tropical areas. Stebbins further suggested that the best way to test the environmental factors

which might cause an increase in polyploidy was to assess the phenomenon "in different habitats within the same climatic zone." Chromosomal surveys of gypsum florulas within the Chihuahuan Desert would seem to fit the ideal situation expressed by Stebbins.

After evaluating more than 100 chromosome counts from gypsophilic taxa, and nearly 600 counts from nongypseous species of the general Chihuahuan Desert region, we have found that there is a marked difference in polyploid percentages of the two floristic types. The percentage of polyploidy is lower among the gypsophiles than surrounding, nongypseous species. The exact percentages, other data, and a discussion of this subject are presented elsewhere (Powell and Sloan 1975). Essentially, we believe that relative habitat stability of the gypsophiles and environmental instability in the nongypseous flora are responsible for the differential percentage of polyploids.

Speciation

Gypsum endemism offers a unique opportunity to study various evolutionary phenomena, including speciation. During the early years of exploring gypsum habitats, we became conditioned to *expect* to find undescribed species everytime we came upon an exposure that had been isolated from extensive collecting. Let us emphasize at this point that we are not talking about "shady" species of unclear distinction, but some of the most clearly marked taxa one could imagine. Some of the gypsophiles, for example, *Haplopappus restiformis* and *Argemone turnerae*, might even be described as bizarre by comparison with related taxa. Of course, many gypsophilic taxa and populations exhibit nebulous variation from related entities on disjunct outcrops, and we are still in the process of evaluating such cases, but one could expect to find cryptic species among them. Indeed, recent monographers of such groups have found just that (Bacon 1975 in *Nerisyrenia*; Richardson 1975, in *Coldenia*).

Probably more important than the recognition of undescribed taxa is the investigation of phenomena involved with speciation. The edaphics of gypsum clearly represent stringent isolating barriers, and island-like exposures are usually separated by many miles. The forces of speciation are thus relegated to relatively small populations, and these forces presumably operate independently in separate gypsum habitats. Our geologist colleagues tell us that it is very difficult to date the exposure (or deposition) of particular gypsum habitats. But if this could be done, at least relative times of exposure in disjunct habitats, then we would have a chance to measure the rates of speciation among many different taxa, which occur on separate outcrops, in context with the evolutionary factors which were involved.

Distribution

When the floristics of gypsum habitats are well enough understood, it would be interesting to investigate the factors which have effected the distribution of species from one isolated exposure to another. We would assume that wind and small animals might have accounted for the distribution of certain species, but surely not for all of the gypsophiles over the distances involved. The associations of avifaunas, if any, with gypsum florulas and their roles in disseminating propagules are not at all well known. We can imagine that whirlwinds, so common during hot months in the Chihuahuan Desert, might be effective in carrying seeds for many miles, but as yet we have not devised an experimental procedure to test this idea.

Coevolution

The gypsum florulas would appear to be particularly well suited for coevolutionary studies. Again, it is the strict endemism of gypsophiles on separated exposures and the limited number of floristic elements which offer the most cogent advantages for such investigations. Furthermore, we propose that much biological information is likely to come from the correlation of co-evolutionary data and the secondary compound chemistry of gypsophiles because the plant associations are so clearly delimited. At present, very little information relative to the above is available to biologists.

Physiology and Gypsum Edaphics

Precisely why certain species exhibit obligate gypsophily is not understood. Whether they require relatively high amounts of sulfates, which seems most obvious, or whether other edaphic factors are more important, is not known. Johnston (1941) observed that there is an absence of gypsophiles in gypsum substrata that are mantled by as much as 1.54 cm (0.616 inch) of nongypseous soil and concluded from this that gypsophily must be "associated with an inability of their seeds to germinate or their seedlings to become established in a completely nongypseous surface layer of soil." We have tested this logical hypothesis and have not found it to obtain under unnatural, experimental conditions in the laboratory and greenhouse, although Farhadnejad (1975) has conducted more precise tests which show a correlation of gypsum concentration and seed germination in gypsophilic and nongypsophilic species of *Gaillardia*. We have repeatedly germinated seeds of gypsophiles such as *Anulocaulis* on moist filter paper, and on various soils, including gypsum, and have seen them grow to maturity with characteristic vigor. We suggest, therefore, that other aspects of soil chemistry are important in gypsophily, and point to the interesting parallel where plants specific to serpentine soils were shown to be those which are

tolerant of low calcium contents of the soil (Kruckeberg 1954; Walker 1954). At any rate, the subject of plant gypsophily is one which deserves the attention of physiologists and modern-day ecologists.

ENDANGERED GYPSOPHILES

Several of the gypsum endemic species are so limited in distribution that there is reason to consider that their ultimate survival is endangered. Taxa such as *Strotheria gypsophila*, *Isocoma gypsophila*, *Sartwellia gypsophila*, *Thelesperma scabridulum*, *Gaillardia powellii*, *G. gypsophila*, *Sophora gypsophila*, *Argemone turnerae*, and others occur in small exposures that are likely to be affected by such anthropocentric activities as highway or road expansion, gypsum mining, or other commercial developments. We hope that the scientific community will become aware of the delicate nature of the endangered biological entities and the unique gypsum communities and do what might be appropriate to prevent their destruction.

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Appendix

Representative List of Gypsophiles

The following alphabetical list of gypsophilic taxa is representative of the gypsum florulas of the Chihuahuan Desert. The list is not intended to be a complete account of gypsum vegetation. Some of the species included here are facultative gypsophiles and are not restricted to gypsum; seemingly "obligate" gypsophiles are marked with an asterisk.

AIZOACEAE: *Sesuvium verrucosum* Raf.

AMARANTHACEAE: *Tidestromia lanuginosa* var. *carnosa* (Steyerm.) Cory, *T. gemmata* Johnst.

AMARYLLIDACEAE: *Cooperia* sp.

ANACARDIACEAE: *Rhus aromatica* Ait., *R. microphylla* Engelm., *R. virens* Gray.

BERBERIDACEAE: *Berberis* sp.

BORAGINACEAE: *Coldenia gossypina** (Woot. & Standl.) I.M. Johnst., *C. hispidissima** (Torr.) Gray; *Heliotropium curassavicum* L., *H. greggii* Torr.; *Cryptantha jamesii* (Torr.) Pays.

CARYOPHYLLACEAE: *Drymeria elata** I.M. Johnst., *D. lyropetala** I.M. Johnst.; *Paronychia jamesii* T.&G.

CELASTRACEAE: *Mortonia* cf. *scabrella* Gray.

CHENOPODIACEAE: *Allenrolfea occidentalis* (Wats.) O. Ktee.; *Atriplex canescens* (Pursh) Nutt., *A. reptans* I.M. Johnst.; *Suaeda suffrutescens* Wats.

COMPOSITAE: *Aphanostephus ramosissimus* DC.; *Artemesia bigelovii* Gray, *A. ludoviciana* Nutt.; *Baccharis texana* (T.&G.) Gray; *Bahia absinthifolia* Benth. var. *dealbata* Gray, *B. pedata* Gray; *Bartlettia scaposa** Gray; *Brickellia* sp.;

- Chaetopappa pulchella* Shinnery; *Dicranocarpus parviflorus** Gray; *Dyssodia acerosa* DC., *D. gypsophila** Turner; *Ericameria triantha** (Blake) Shinnery; *Flaveria anomala** Robins., *F. chloraefolia* Gray, *F. oppositifolia* (DC.) Rydb.; *Gaillardia gypsophila** Turner, *G. multiceps** Greene, *G. powellii** Turner, *Gaillardia* sp.; *Gutierrezia microcephalum* (DC.) Gray; *Haploesthes greggii* Gray, *H. robusta** I.M. Johnst.; *Haplopappus johnstonii** Blake, *H. restiformis**, *H. scabrella* Greene; *Isocoma gypsophila** Turner, *I. wrightii* (Gray) Rydb.; *Leucelene ericoides* (Torr.) Greene; *Machaeranthera gypsophila** Turner; *Parthenium incanum* HBK.; *Perezia nana* Gray; *Perityle vaseyi* Coult.; *Psathyrotes scaposa** Gray; *Pseudoclappia arenaria** Rydb., *Pseudoclappia* sp.*; *Psilostrophe tagetinae* (Nutt.) Greene; *Sartwellia flaveriae** Gray, *S. mexicana** Gray, *S. puberula** Rydb., *Sartwellia* sp.*; *Senecio warnockii** Shinnery; *Strotheria gypsophila** Turner; *Thelesperma megapotamicum* (Spreng.) Kuntz., *T. longipes* Gray, *T. ramosius** Blake, *T. scabridulum** Blake; *Xylorhiza wrightii** (Gray) Greene.
- CRUCIFERAE: *Lepidium montanum* Nutt.; *Lesquerella fendleri* (Gray) Wats.; *Nerisyrenia camporum* (Gray) Greene, *N. castillonii** Rollins, *N. gracilis** I.M. Johnst., *N. gypsophila** Bacon, *N. incana** Rollins, *N. linearifolia** (Wats.) Greene; *Streptanthus carinatus* Wright.
- EUPHORBACEAE: *Croton dioicus* Cav.; *Euphorbia astyla* Engelm. ex Boiss.
- FOUQUIERIACEAE: *Fouquieria shrevei** I.M. Johnst.
- FRANKENIACEAE: *Frankenia jamesii** Torr., *F. gypsophila** I.M. Johnst., *F. leveritchii** Turner, *F. margaritae**.
- GENTIANACEAE: *Centarium calycosum* (Buckl.) Fern.
- GRAMINEAE: *Aristida pansa* Woot. & Standl., *A. reverchonii* Vasey; *Bouteloua breviseta** Vasey; *Hilaria mutica* (Buckl.) Benth.; *Muhlenbergia arenacea* Buckl., *M. porteri* Scribn., *M. villiflora* Hitchc.; *Scleropogon brevifolius* Phil.; *Sporobolus cryptandrus* (Torr.) Gray, *S. nealleyi** Vasey, *S. wrightii* Scribn.
- HYDROPHYLLACEAE: *Nama carnosum** (Wooton) Hitchc., *N. havardii* Gray, *N. hispidum* Gray, *N. purpusii* Brandeg., *N. serpylloides** Gray, *N. stenophyllum** Gray ex Hemsl., *N. stevensii** Hitchc., *N. stewartii** I.M. Johnst.; *Phacelia gypsogenia** I.M. Johnst., *P. integrifolia* Torr.
- LABIATAE: *Hedeoma* sp.; *Tetraclea coulteri* Gray.
- LEGUMINOSAE: *Dalea filiciformis** Robins. & Greenm.; *Krameria grayi* Rose & Painter; *Sophora gypsophila** Turner & Powell.
- LILIACEAE: *Allium* sp.; *Yucca elata* Engelm.
- LINACEAE: *Linum puberulum* (Engelm.) Heller.
- LOASACEAE: *Cevallia sinuata* Lag.; *Eucnide lobata*; *Mentzelia humilis** (Gray) Darl., *Mentzelia* sp.; *Petalonyx crenatus** Gray ex S. Wats.
- MALVACEAE: *Sphaeralcea subhastata** Coulter.
- NYCTAGINACEAE: *Abronia nealleyi** Standley; *Acleisanthes longiflora* Gray; *Al-lionia incarnata* L.; *Ammocodon chenopodioides* (Gray) Standl.; *Anulocaulis eriosolenus** (Gray) Standl., *A. gypsogenus** Waterfall, *A. leiosolenus** (Torr.) Standley, *A. reflexus** I.M. Johnst.; *Selinocarpus angustifolius** Torr.,

*S. gypsophila** Fowler, *S. laceolatus** Wooton, *S. parvifolia** (Torr.) Standl.
*S. purpusianus** Heimerl.

ONAGRACEAE: *Calylophus hartwegii* Benth. var. *filifolius** (Eastw.) Munc;
Gaura coccinea Nutt.; *Oenothera brachycarpa* Gray.

PAPAVERACEAE: *Argemone turnerae** Powell.

PLUMBAGINACEAE: *Limonium limbatum* Small.

POLEMONIACEAE: *Gilia rigidula* Benth. *G. stewartii* I.M. Johnst.; *Loeselia havardii* Gray.

POLYGALACEAE: *Polygala* sp.

POLYGONACEAE: *Eriogonum fimbriatum* Hess & Reveal, *E. turneri** Reveal.

RESEDACEAE: *Oligomeris linifolia* (Vahl) Macbr.

ROSACEAE: *Vauquelinia angustifolia* Rydb.

SCROPHULARIACEAE: *Castilleja* cf. *lanata* Gray.

ZYGOPHYLLACEAE: *Larrea divaricata* Cav.; *Peganum harmala* L., *P. mexicanum* Gray; *Sericodes greggii** Gray.

*Vegetation and Flora of the Cuatro Ciénegas Basin, Coahuila, Mexico*¹

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The unique aquatic features of the bolsón of Cuatro Ciénegas provide habitats for a varied and most interesting Chihuahuan Desert flora. The small basin, encircled by mountains in central Coahuila, Mexico, lies about 75 km (45 miles) W of Monclova and about 270 km (162 miles) SSE of Big Bend National Park. Municipio de Cuatro Ciénegas de Carranza (26°59' N, 102°04' W), north-central in the basin, prospers near the mouth of the Río Cañon which flows through Cañon del Agua, north puerto between Sierra de la Madera (in part locally called Sierra de Antejo) and Sierra de la Menchaca (Minckley 1969) (Fig. 1).

The Cuatro Ciénegas basin, measuring approximately 40 km (24 miles) east to west and 25 km (15 miles) north to south, is nearly bisected from the south by outjutting Sierra de San Marcos. Elevation above mean sea level ranges from about 740 m (2442 ft) on the grassy basin floor to more than 3000 m (9900 ft) atop conifer-capped Sierra de la Madera. The basin is bounded on the east by Sierra San Vicente and Sierra de la Purísima and on the west by Sierra de la Fragua. The railway, Ferrocarriles Nacionales de Mexico, parallels the east-west roadway from Puerto Salado to Puerto de Jara. A paved road extends from Municipio de Cuatro Ciénegas southward along the west flank of Sierra de San Marcos to San Pedro via Puerto San Marcos.

The Cuatro Ciénegas basin has abundant water, much of it subterranean. There are seven major epigeal drainage systems, the largest being Río San Marcos (locally Río Mesquites), some 2-20+ m (6.6-66 ft) wide, to 2.5 m (8.25 ft) deep, carrying clear water through open bays via travertine chutes at rates from nearly 0 to 75 cm/sec, respec-

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tively (Minckley 1969). Originally, this system, according to Rodriguez González (1926), had no outlet from the basin but rather drained through intermediate lagunas into a large depression in the eastern lobe of the basin, giving Municipio de Cuatro Ciénegas its name. The basin is now drained by a series of canals which ultimately pass eastward through Puerto Salado to the Rio Grande. Origin of the basin's rivers are springs, cool or thermal (to 31°C according to Minckley 1969), emerging from travertine-lined tubes or from pits (pozos, or locally "posos"). Río Churince originates from a large poso and terminates in a large, shallow, mineralized lake, Laguna Grande. Evaporation results in nearly pure gypsum salts drying along the shores and these are blown by winds into a very complex series of dunes of varied ages, particularly to the north and west.

There are also several subterranean channels, notably along the bases of mountains. Localized foundering of the roofs of these channels has resulted in hundreds of pits or posos. Minckley (1969) postulates that this may be due in part to the lowering of the water table and general sag of the basin floor. Posos vary in depth from less than a meter to more than 10 m (33 ft) and in diameter from but a few centimeters to more than 200 m (660 ft) via slumping of the walls. The larger ones are called lagunas or sometimes retain the name of poso. Progressive foundering of subterranean channels in a linear series of posos may lead to an open channel occupied by swift-flowing streams, which in time meander and widen due to slumping, undercutting, and deposition.

Usually a poso will have an inflow and an outflow. If the outflow is plugged, water will overflow the banks and produce travertine deposits, even cone springs such as Poso Escobeda; if the inflow is stopped, eutrofication will follow resulting in extensive marshes (Minckley 1969). Large downflow lagunas, upon evaporation, salinize and form barrial lakes or playas such as Laguna Grande and Laguna Salada. Waterways are subject to great modifications by salts, principally sulfates (Minckley and Cole 1968). Stabilized posos and narrow channels may be reroofed by successive development of vegetation mats over the water and the deposition of salts.

Río Cañon, however, is a very different system. Its fresh water forms well-developed pools and riffles and supports a rich, wooded vegetation along its banks. It is the source of water for the town and for irrigation. Although the central basin's rivers are used also for irrigation, fallow fields south of town, some blown into dunes, testify apparently to the accumulation of salts from these sources.

Well-developed and arroyo-dissected bajadas rise above the basin floor. Towering above these tapering bajadas are the massive limestone sierras. These generally northwest-southeast-oriented mountains lie at the eastern edge of the Basin and Range Province and the Central

Plateau, just west of the Sierra Carmen axis, an effective barrier keeping moisture-laden winds from the Atlantic Ocean and the Gulf of Mexico from passing onto the arid Central Plateau, much as the Sierra Madre Occidental in Chihuahua forms a barrier to western winds (Muller 1947). The mean annual precipitation is less than 200 mm in the basin (Shreve 1944).

COLLECTIONS

The first significant collection of vascular plants from the Cuatro Ciénegas basin was made by Ivan M. Johnston, 24-26 August 1938. Within the next 3 years, additional specimens were prepared by Leroy H. Harvey, Ernest M. Marsh, Jr., Cornelius H. Muller, and Stephen S. White, all in 1939, and again by Johnston in 1941.

Nearly 25 years lapsed before the vegetation and flora were again intensively investigated, notably by teams of researchers from Arizona State University (W. L. Minckley, myself, and our students), from the University of Texas, Austin (M. C. Johnston, B. L. Turner, and their students) and from the Desert Botanical Garden, Phoenix (H. S. Gentry and Rodney Engard). Many other collections have been made, e.g., by J. Henrickson, A. M. Powell, N. Boke, F. L. Wynd, and Jean Graber.

To better understand the montane flora, I have included collections from three cañons west-northwest of Cañon del Agua, primarily along the north- and northeast-facing slopes of the Sierra de la Madera. These are from south to north, Cañon de Pajarito, Cañon de la Hacienda, and Cañon de la Charretera. Also considered is a collection from the north-facing slopes of Sierra de la Menchaca by Elena Arnold.

VEGETATION

The vegetation of the Cuatro Ciénegas basin and surrounding mountains may be divided into the following major groupings: (1) basin grasslands; (2) aquatic plants; (3) sedge borders and marshes; (4) gypsum dune plants; (5) transition; (6) Chihuahuan Desert scrub; (7) chaparral; and (8) montane forests.

An interesting series of vegetational changes may be witnessed by observing posos of varying ecological maturities. The newly founded poso has essentially no more floristic representation than the constituents of the surrounding basin grasslands, primarily *Sporobolus airoides* (Torr.) Torr., *S. wrightii* Scribn., *Muhlenbergia asperifolia* (Nees & May) Parodi, *Distichlis stricta* (Torr.) Rydb., and *Monanthochloe littoralis* Engelm. The slumping banks are soon populated by sedges (e.g., *Eleocharis cellulosa* Torr., *E. rostellata* [Torr] Torr., *E. caribaea* [Rottb.] Blake, and *Carex pringlei* Bailey), additional grasses (*Phragmites communis* Trin., *Spartina spartinae* [Trin] Merr., and *Setaria geniculata* [Lam.] Beauv.), and associated species (e.g., *Polygala turgida* Rose, *Cynan-*

chum angustifolium Pers., *Eustoma exaltatum* [L.] G. Don, and *Sabatia stellaris* Pursh). As the poso matures and enlarges, the number of species present appears to be additive, for even in the most advanced stages of development the early invaders are still represented, though in lesser numbers. The mature posos, such as Poso de Los Fresnos and Poso de Anteojo, contain the aquatics, *Nymphaea ampla* (Mart. Solms in DC., *Utricularia obtusa* Sw., and *Chara* spp. The shores support grasses and sedges including now *Fimbristylis thermalis* S. Wats., *Fuirena simplex* Vahl, and *Schoenus nigricans* L. as well as herbs, *Heliotropium curassavicum* L., *Bacopa monnieri* (L.) Wettst., *Ludwigia octovalvis* (Jacq.) Raven, *Anemopsis californica* (Nutt.) Humb. & Arn., *Mentha rotundifolia* (L.) Hudson, *Ipomoea sagittata* Poir., and *Eupatorium betonicifolia* Mill., plus woody *Prosopis glandulosa* Torr., *Acacia greggii* Gray, *Fraxinus berlandieriana* DC., and *Salix nigra* Marsh.

Other aquatic plants growing in the basin rivers and lagunas are *Najas marina* L., *Ruppia maritima* L., and *Potamogeton nodosus* Poir. in Lam., plus in Rio Canon, *Nasturtium officinale* R. Br., *Najas guadalupensis* Moreng, and *Zanichellia palustris* L.

White gypsum salts, blown from evaporating lake beds, notably of Laguna Grande, form dunes adding relief to the otherwise relatively flat basin. Active dunes up to 609.6 cm (20 ft) high encroach upon streams, posos, older dunes, and the surrounding plains. Mesquite trees, *Prosopis glandulosa*, often nearly completely buried by sand, *Acacia greggii*, *Yucca treculeana* Carr., and *Varilla mexicana* Gray are important in stabilizing the dunes.

Upon stabilization, a grayish crust forms at the surface, apparently via recrystallization. Occupying these sites are gypsophilous species (see Johnston 1941; Turner 1972a,b, 1973), particularly some bizarre endemic composites, *Machaeranthera restiformis* Turner, *M. gypsophila* Turner, *Gaillardia gypsophila* Turner, *Dyssodia gypsophila* Turner, and *Haploesthes robusta* I. M. Johnst. Also present are *Selinocarpus purpusianus* Heimerl., *Nerisyrenia incana* Rollins, *Petalonyx crenatus* Gray., *Coldenia hispidissima* (Torr. & Gray) Gray, *Euphorbia astyla* Boiss., *Fouquieria splendens* Engelm., *Opuntia leptocaulis* DC., and *Echinocereus enneacanthus* Engelm. Also represented are species of the lichen genera *Acarospora*, *Dermatocarpon*, *Peltula*, and *Collema* (Thomas Nash III pers. comm.).

Encircling the basin and its lagunas is an interrupted band of shrubs and small trees as hammocks of *Condalia warnockii* M. C. Johnst., *Suaeda palmeri* (Standl.) Standl., *Allen rolfea* sp., *Atriplex canescens* (Pursh) Nutt., *Flourensia cernua* DC., *Acacia greggii*, *A. schottii* Torr., and *Prosopis glandulosa* which forms a dense bosque near Santa Tecla.

The bajadas and lower mountain slopes and arroyos support a rich

and varied Chihuahuan Desert scrub flora. Dominant are *Larrea tridentata* (DC.) Cov., *Agave lecheguilla* Torr., *Agave falcata* (Engelm., *Opuntia* (*Grusonia*) *bradtiana* (Coulter) Brandg., *Jatropha dioica* Cerv., *Euphorbia antisiphilitica* Zucc., *Selaginella lepidophylla* (Hook. & Grev.) Spring, *Parthenium incanum* H. B. K., and *Dyssodia pentachaeta* (DC.) Rob. var. *belenidium* (DC.) Strother.

The chaparral zone is best developed on northerly and easterly exposures in protected arroyos and canyons and in areas near the montane forests. The often dense growth is predominantly oaks (*Quercus glaucoides* Mart. & Gal., *Q. gravesii* Sudw., *Q. greggi* [DC.] Trel., *Q. hypoxantha* Trel., *Q. intricata* Trel., *Q. invaginata* Trel. and *Q. pringlei* von Seem.), heaths (*Arbutus xalapensis* H.B.K. and *Arctostaphylos pungens* H. B. K.), pines (*Pinus cembroides* Zucc.), and numerous shrubs and small trees (e.g., *Rhus aromatica* Ait., *R. virens* Lindh., *Forestiera angustifolia* Torr., *Fraxinus greggii* Gray, *Rhamnus betulaeifolia* Greene, *Amelanchier denticulata* [H. B. K.] Koch, and *Cercocarpus mojadensis* Schneid.).

The montane forest is comprised of *Pinus arizonica* Engelm., *Pinus strobiformis*, Engelm., *Pseudotsuga menziesii* (Mirb.) Franco, *Abies coahuilensis* I. M. Johnst., *Cupressus arizonica* Greene, as well as junipers, oaks, and various shrubs and herbs.

The known vascular flora of the Cuatro Ciénegas basin and surrounding mountains consists of approximately 650 taxa in 105 families. Meyer (1973), in comparing modern pollen rain with late-Quaternary deposits from the basin floor, has found that local habitats and their vegetation have been equivalent, if not identical, for the last 30,000-40,000 years.

This area is type locality for the following 20 taxa: *Abies coahuilensis* (Pinaceae); *Quercus greggii* forma *subglabra* Muller and *Q. filiformis* Muller (Fragaceae); *Suaeda suffrutescens* Wats. var. *detonsa* I. M. Johnst. (Chenopodiaceae); *Berberis pinifolia* (Lundell) Muller var. *coahuilensis* Muller (Berberidaceae); *Tidestromia rhizomatosa* I. M. Johnst. (Amaranthaceae); *Nerisyrenia incana* Rollins (Cruciferae); *Nama serpylloides* Gray var. *confertum* I. M. Johnst. (Hydrophyllaceae); *Opuntia anteojensis* Pinkava (Cactaceae); *Tiquilia turneri* A. Richardson (Boraginaceae); *Dyssodia gypsophila*, *Gaillardia gypsophila*, *Haploesthes robusta*, *Machaeranthera restiformis*, *M. gypsophila*, *Chaetopappa pulchella* Shinnars (Compositae); *Andropogon maderensis* Swallen, *Muhlenbergia pubigluma* Swallen, *Sporobolus spiciformis* Swallen, and *Stipa alta* Swallen (Gramineae).

Because of the large number of endemic taxa of both plants and animals (see Minckley 1969), the unique aquatic habitats, as well as the scenic value, there is an urgent need to preserve at least a portion of this ecosystem before an important part of man's heritage is lost.

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Brief Resume of Botanical, Including Vegetational, Features of the Chihuahuan Desert Region with Special Emphasis on Their Uniqueness¹

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INTRODUCTION

The Chihuahuan Desert region (Fig. 1) is the generally very arid region lying in north-central Mexico and extending northward through Trans-Pecos Texas to southern New Mexico. It is a bluntly and irregularly cuneiform territory pointed south-southeastward to near the city of San Luis Potosí in the state of San Luis Potosí. At 31°N latitude, the broadest portion, the east-west dimension is approximately 620 km (372 miles). The greatest linear measurement from a point in New Mexico on the Rio Grande at 34°30' N latitude south-southeastward to the farthest desertic locality in San Luis Potosí is approximately 1550 km (930 miles). The total area is approximately 505,000 km² (202,000 miles²), or four-fifths the size of Texas. For reference purposes, the locations of some towns in the region are shown on another map (Fig. 2).

Although abortive attempts have been made by others to determine some climatic parameters and to use them to define the "Chihuahuan Desert," the Chihuahuan Desert region (hereafter abbreviated to CDR) is here defined geobotanically. The western margin of the CDR is drawn (Fig. 1) at the hazy eastern margin of the vast zone of short grama grassland or pastizal occupied in substantial part by species of *Bouteloua*. These grasslands gradually give way eastward to shrub-desert

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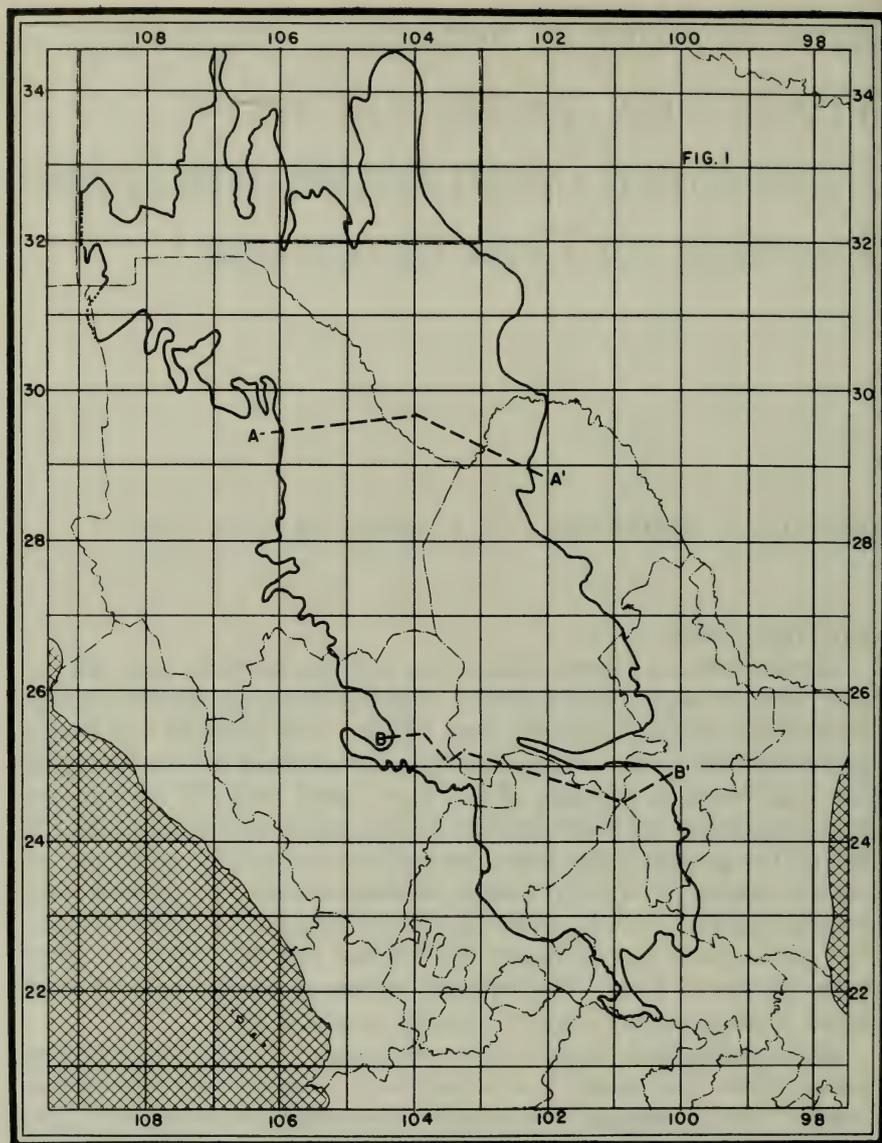


Fig. 1. Map showing by continuous line the outline of the Chihuahuan Desert region. The locations of the transects A-A' and B-B' are indicated.

community types. The zone of intergradation is so broad that it is everywhere difficult to draw a demarcation on a map, so the boundary in Fig. 1 should be considered approximate and suggestive. This seems to be true in part because of the expected interdigitation and localiza-

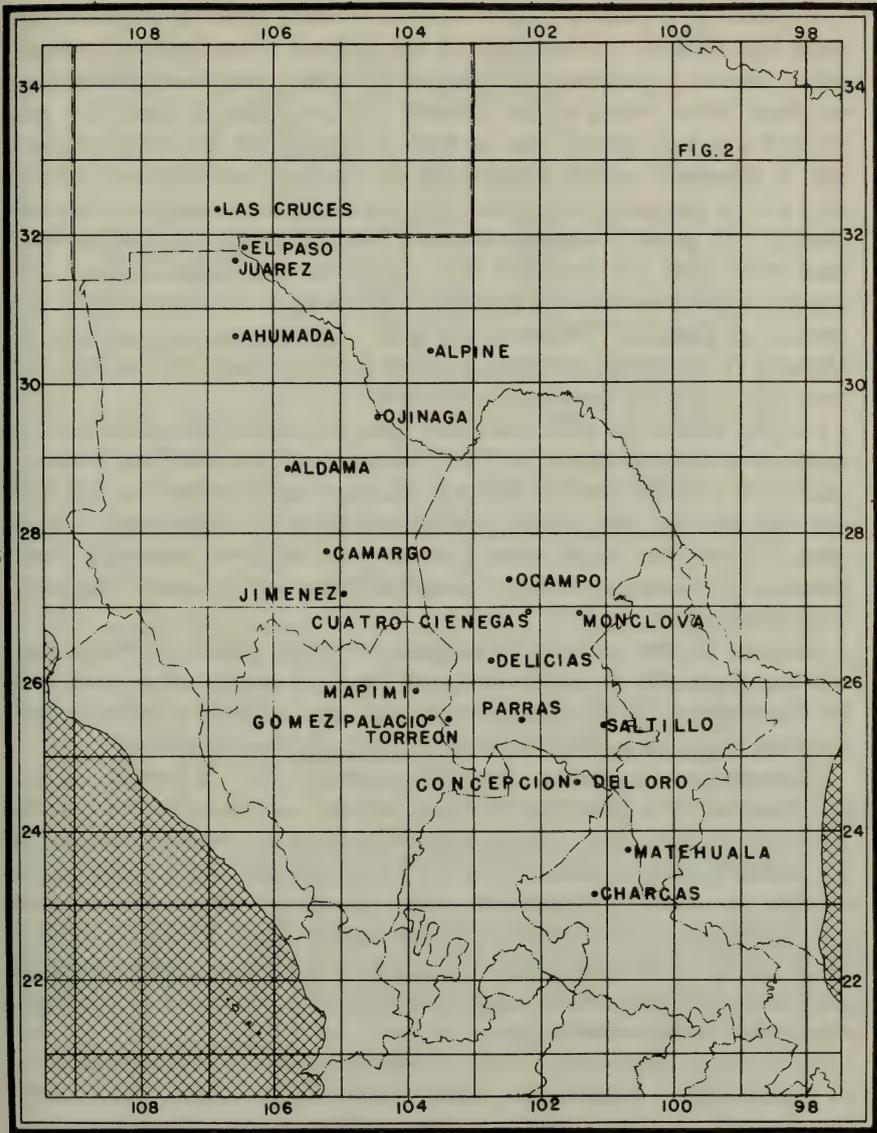


Fig. 2. Map showing the locations of some towns in the Chihuahuan Desert region.

tion of community-types on irregular terrain (grasslands on the broad, flattish, deeper-soiled interflumes, shrub-desert on the dissected terrain) but also partly because of destructive overgrazing which encourages erosion and growth of shrubs in previously continuous grassland.

The southern boundary of the CDR in Zacatecas and western San

Luis Potosí is, if possible, even less well defined than the western one, again due possibly to centuries of agricultural abuse and increasingly dense human population, far greater than the land can sustain on a renewing basis. Much of the "desert" of northeastern Zacatecas and western San Luis Potosí may well have been, some hundreds of years ago, a grassland, which would befit the present geobotanical setting, viz., a high plateau of extrusive igneous rocks with adequate summer rainfall. The present inclusion in the CDR may be the result of agricultural abuse that has modified the vegetation. The present biotic ambiguity of the area could be explained in this way, for floristically it is a mixture of grassland elements with a few desert elements; similarly D. Morafka (pers. comm. 1973) has faunal evidence that the area does not clearly fit either the grassland or the desert.

On the north the CDR extends into the Pecos and Rio Grande drainage systems to about 34°30' N latitude and between these rivers it extends northward into the internal drainage basins known as Salt Flat and the Jornada del Muerto. Northwestward, in southwestern New Mexico it becomes localized or "patchy." On all these borders it intergrades with grama grasslands or in a few places with montane chaparral community-types.

Between 31°30' and 34° N latitude the CDR grades northeastward into the grasslands of the Sandy South Plains, a southward extension of the Great Plains. On the loosest sandy soil some of these grasslands even resemble midgrass prairies with much *Schizachyrium scoparium*.

The eastern boundaries of the CDR south of 31°31' N latitude are largely marked by a gradation to chaparral-like woodland formations on limestone or dolomite. This gradation occurs at the western margins of the Edwards plateau from 30° to 31°30' N latitude and at various calcareous mountains, collectively called the Sierra Madre Oriental, in Mexico south of 29° N latitude. The transverse Sierra Madre Oriental at about 27°15' N latitude, which in its western extremity consists solely of the Sierra de Parras, strikes deep into the CDR, dividing it into floristically rather different subregions.

In San Luis Potosí near 22°30' N latitude, 100°30' W longitude, and in southwestern Tamaulipas occur intermontane basins which some workers include in the CDR by virtue of the presence of scattered *Larrea tridentata* plants, but the predominance in them of elements of non-desert formations dictates their present exclusion from the CDR.

COMMUNITY-TYPES

Within the CDR as thus circumscribed occur a number of community-types, the most important of which are summarized in Fig. 3. In this figure, the lines emphasize the possibilities of intergradation between types. It is not possible within the present limits of time and space to

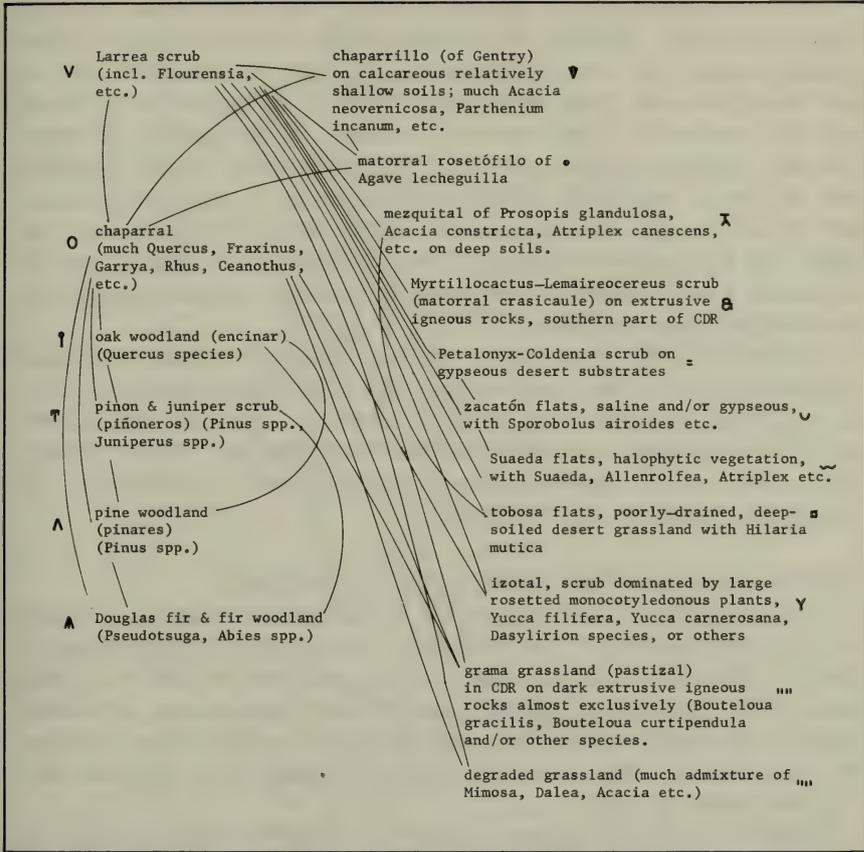


Fig. 3. A scheme summarizing some of the more important community-types of the Chihuahuan Desert region. The lines emphasize the occurrence of intergradation between the community-types. The montane woody community-types are at the lower left, roughly in inverse order to their usual altitudinal zonation. The more edaphically controlled desert and grassland community-types are at the top and right, in some cases with geobotanical annotations, and in some cases with the Spanish equivalents shown parenthetically. The symbols shown peripherally are those used in the transects (Fig. 4, Fig. 5).

discuss these community-types in detail. The unifying and widespread vegetational matrix is the microphyllous desert scrub dominated by *Larrea tridentata* or creosote bush. Next in coverage is a shrub-desert community-type called by H. S. Gentry "chaparrillo," occurring on calcareous rocks, either limestone, dolomite or bedded volcanic ash, in which *Acacia neovernicosa*, *Parthenium incanum*, and often *Viguiera stenoloba*, along with some *Larrea tridentata* are some of the most abundant dicotyledonous species; a subtype of this is found on bedded limestone or dolomite where rosetted monocots such as *Hechtia* predominate.

The community-types at the lower left of Fig. 3 are those found at higher elevations. Of these, the chaparral and the near-chaparral types grading toward the izotales or toward the matorral roseto-filo are the next most prevalent types in the entire CDR following the *Larrea* scrub and the chaparrillo. They occupy vast areas of moderately to highly elevated mountain slopes and tops. The relationship of the chaparral and the izotal, especially the izotales dominated by *Yucca carnerosana* and *Dasyilirion* spp., is complex and requires careful study. It seems at times that the monocotyledonous dominance in certain places may be correlated with a history of fires which temporarily at least suppress the woody dicotyledonous plants.

It should be emphasized that an intensive study of Chihuahuan Desert vegetation has not been undertaken, the observations presented here having been incidental to floristic research. Intensive descriptive, statistical-analytical, and experimental treatments are sorely needed. The works of J. Marroquin near Saltillo and J. Henrickson on halophytic vegetation are a beginning.

COMPLEXITY OF THE VEGETATIONAL MOSAIC

The complexity of the vegetational mosaic needs emphasis as a basis of an understanding of the difficulty encountered in attempting to describe the CDR and as a signal of the enormity of the tasks lying ahead. The topographic, edaphic, and climatic complexities, of course, underlie the vegetational complexity. To give some hint of the complexity, two transects (Fig. 4 and Fig. 5) are presented, their locations having been shown in Fig. 1.

Profile A-A' (Fig. 4) passes through the Big Bend region, starting on the west, outside of the CDR, at the Sierra de los Burros which is at the margin of the zone of *Bouteloua* grassland, and passing eastward, out of the CDR again, in chaparral on one of the several mountain ranges shown on maps incorrectly as "Sierra del Carmen." The average elevation of the transect is low, about 1200 m, in spite of the fact that some of the mountains reach 3000 m. The Rio Grande and its tributaries have eaten through all these areas and now have rather steeply entrenched canyons, the most scenic being the vertical limestone walls of the Rio Conchos where it traverses the Sierra del Cuchillo Parado and Sierra de Peguis west of Ojinaga; and the Rio Grande itself where it flows between the Dead Horse Mountains and the Sierra del Carmen just downstream from Boquillas del Carmen.

The only basins of internal drainage on this profile are the Laguna del Cuervo (extreme west) which has an extensive area of tobosa (*Hilaria mutica*) and zacatonal (*Sporobolus airoides*), and the basin at the extreme eastern end which is diluted CDR vegetation with zacatonal and tobosa. *Bouteloua* grassland is found at the western end on the Sierra de

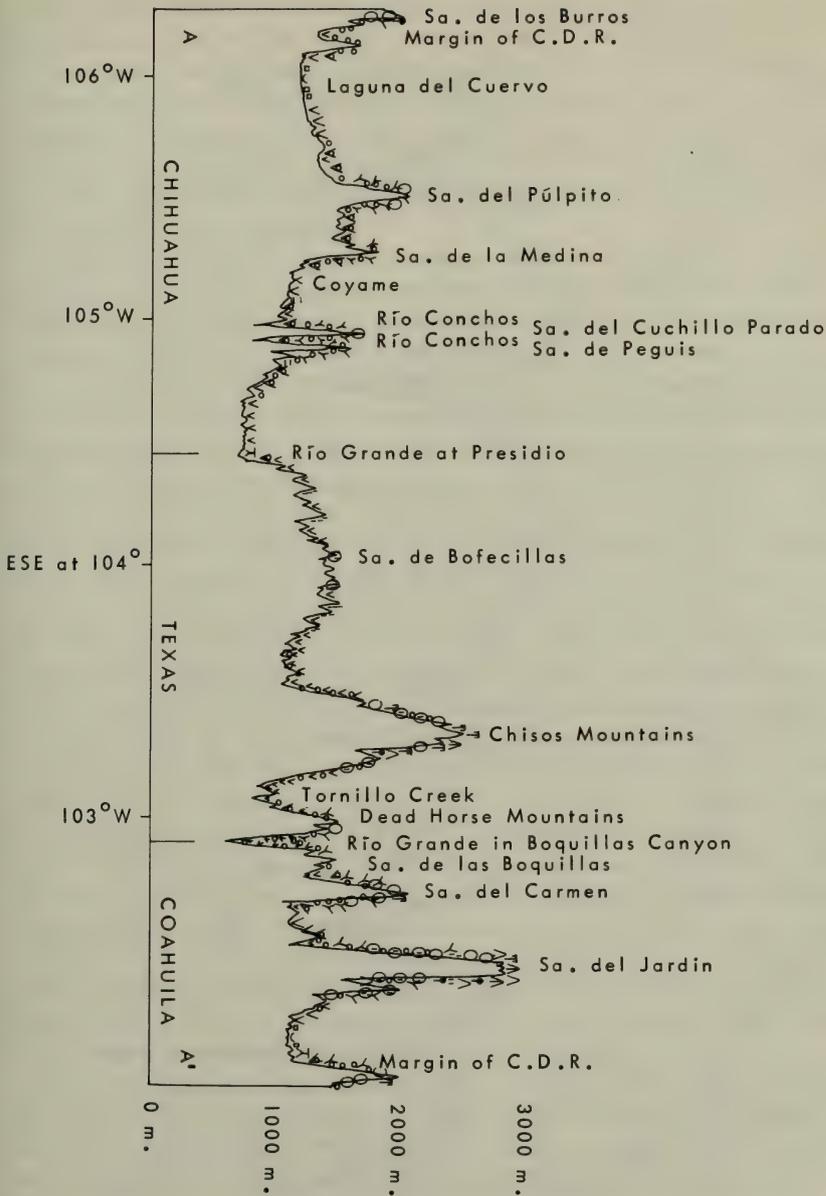


Fig. 4. Transect A-A' showing topography and vegetation through the Big Bend region.

los Burros and in patches at outcrops of basic extrusive igneous rocks above approximately 1300 m (4290 ft), e.g., in the Bofecillas and Chisos mountains of Texas and the Sierra del Jardin (perhaps better called the Fronterizas) in Coahuila.

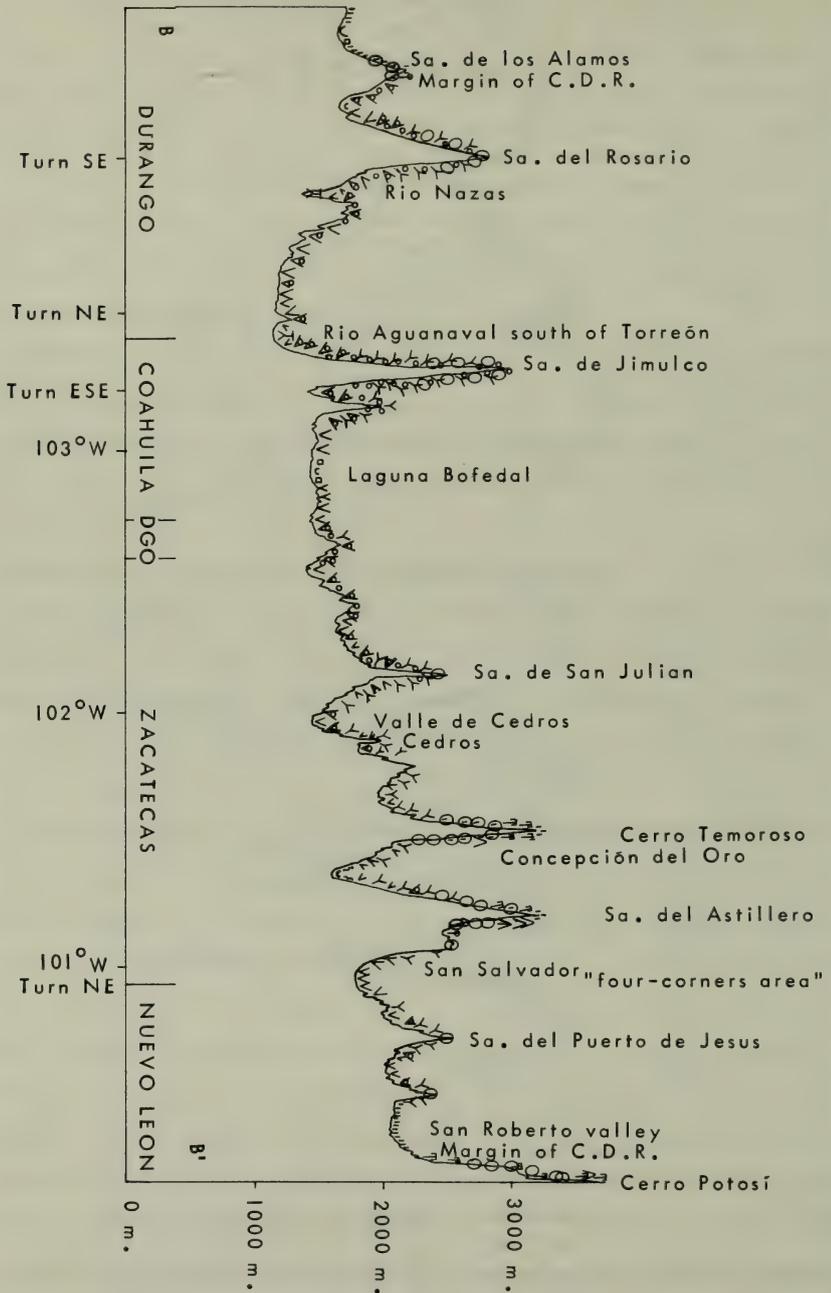


Fig. 5. Transect B-B' showing topography and vegetation in the Chihuahuan Desert region at approximately 25° N latitude.

Any one of the mountain ranges or valleys or bolsons would have to be shown on a scale that would resolve elements as small as 100 m in extent if the true vegetational mosaic is to be revealed. The dominance of the desert scrub community-types and their intergradation upward in elevation to monocotyledonous-rosette communities and then to chaparral is to be noted. The small areas of grama grassland in the Bofecillas and Chisos mountains and the Fronterizas scarcely show up on a profile drawn to this scale.

Profile B-B' (Fig. 5) passes through parts of Durango, Coahuila, Zacatecas, and Nuevo Leon, the average elevation being about 800 m higher than that in the previous profile, and the whole lying south of the latitude of the Transverse Sierra Madre Oriental. The low elevations in the western moiety with very extensive desert scrub are in the drainages of the Nazas and Aguanaval rivers which pour northward into the Bolson de Mapimi and the Laguna de Mayran areas. In fact, none of this profile is drained into ocean or gulf; it is all internally drained. The western moiety is so dry that even the high ranges (Sierra de Jimulco, more than 3000 m [9900 ft]) have no forest. Proceeding to the eastern moiety of the profile, the ranges are higher and more mesic with some forests. Particularly to be noted are the large expanses of izotal, here for the most part dominated, at least visually, by the large joshuatree-like *Yucca filifera* which is best developed here, some of the plants being up to 16 m in height. These izotales of *Yucca filifera* are mostly at about or just under 2000 m in altitude. The scrub-desert community-types are more and more restricted as one proceeds into the eastern moiety of the profile. In the far eastern portion can be found a kind of marginal zone of high gypsum llanos (San Roberto valley) which are unlike anything else in the CDR, having a gyp-grama matrix and many different grasses and herbs, including an endemic genus and at least 10 other endemic species. Second only to the San Roberto Valley in floristic interest are the limestone deserts of the Nazas and Aguanaval river drainages, where *Colubrina viridis* and *Franseria dumosa* occur; these species are known elsewhere at lower elevations and on the western side of the Sierra Madre Occidental in the Sonoran Desert region.

It may be reiterated that these profiles give only a hint of the difficulties lying ahead in providing even the most elementary description of the CDR vegetation, not to mention an understanding of the dynamic interrelationships of the community-types and their environments.

FLORISTIC RELATIONSHIPS

A high desideratum would be to give here a complete discussion of the vascular flora of the CDR. This is not possible for several reasons. In the first place, such data will be relatively complete only when the manuscript of the *Chihuahuan Desert Flora* is assembled, an occurrence

which is anticipated about 3 years from now. Limitations of space and time, of course, prevent a full exposure even of the floristic data which have been gathered together so far.

The floristic relationships of the calcareous uplands of the CDR are primarily with the Sierra Madre Oriental, one of the oldest and richest centers of plant evolution in North America in Tertiary and Quaternary times. In fact, the northern part of the CDR, north of 25° N latitude, can be thought of largely as an expanded or flabellated Sierra Madre Oriental in which the individual mountain ranges instead of lying juxtaposed are spread apart. Upwards of 1000 species of the calcareous uplands show this floristic near-continuity with scarcely any specific, much less generic, differentiation. Floristically, the next most closely related region is the limestone Edwards Plateau, which is a sort of disjunct piece of the Sierra Madre Oriental piedmont. In affirming the relationships of the CDR to the Sierra Madre Oriental, it is almost redundant to mention the Edwards Plateau.

The next most striking floristic affinity is to the Sierra Madre Occidental and can be noticed in those disjunct masses of dark extrusive igneous rock such as the Sierra de Rancheria in Chihuahua, the massive Davis-Bofecillas region of western Texas and the Fronterizas of Coahuila. These rock masses are simply like chips of the Sierra Madre Occidental displaced eastward.

In order of diminishing importance, the next affinity to be mentioned is that to the lower Rio Grande plains or Tamaulipan scrublands. A rather large number of species is shared, possibly as many as 300. In some cases, for example *Zanthoxylum fagara* and *Karwinskia humboldtiana*, it is questionable whether this should be considered an affinity to the Tamaulipan scrublands, but rather may be an indication of marginal similarity to the North American Arid Tropical Scrub which is widespread in the West Indies, Central America, and both eastern and western coastal plains of Mexico. On the other hand, a large number of basically CDR plants seem to have "spilled over" onto the coastal plains in the neighborhood of the Rio Grande. Perhaps this can be explained ultimately in terms of dynamic paleoclimatology.

ENDEMISM AND UNIQUENESS

The endemic taxa, the unique floristic elements of the CDR flora, including at least 1000 species, deserve special emphasis. These are not uniformly distributed over the CDR. Some are widespread, others localized. The distributions of 52 selected species are mapped (Fig. 6 through 16) to give a feeling for the variety of distributional patterns (if "patterns" do indeed exist).

The ranges of the widespread though edaphically somewhat restricted *Sartwellia puberula* and *S. mexicana* (Fig. 6) are illustrative of CDR

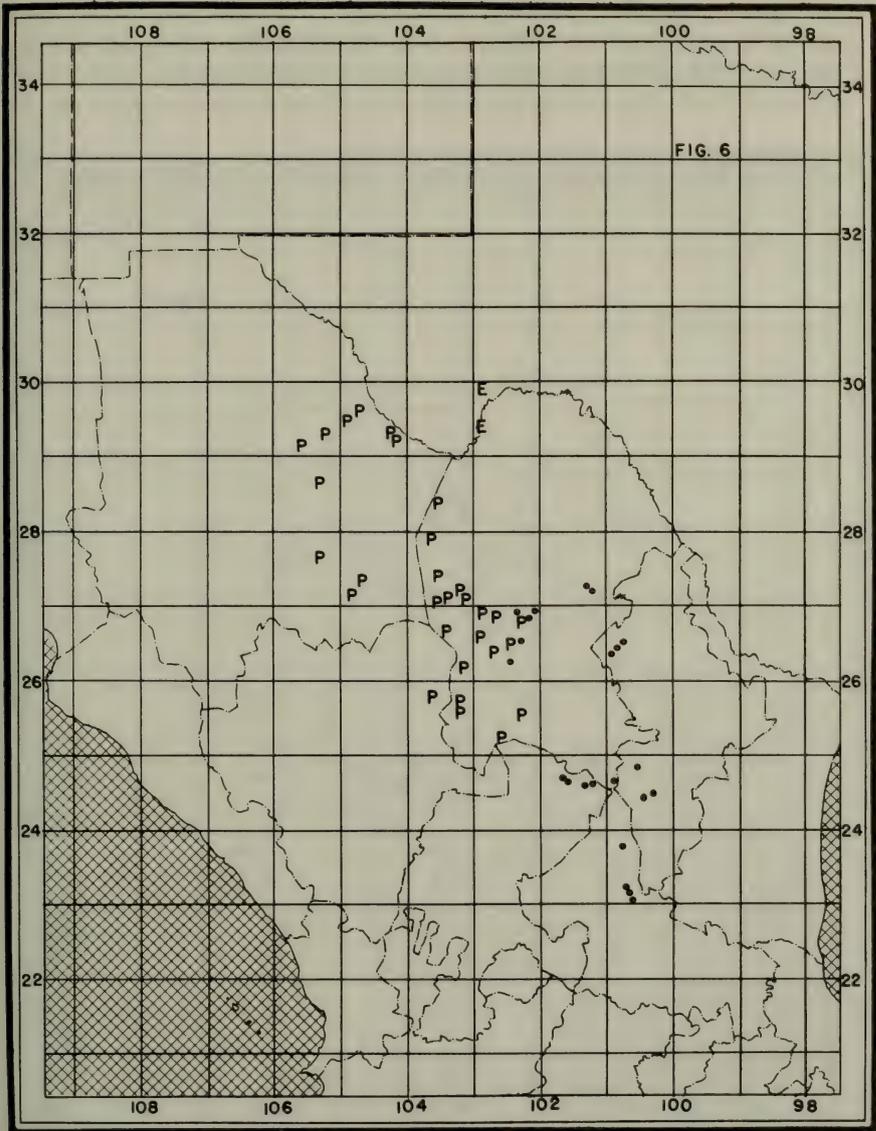


Fig. 6. Map showing distribution of three species of plants endemic to the Chihuahuan Desert region. E, *Phyllanthus ericoides*. P, *Sartwellia puberula*. Small circles, *Sartwellia mexicana*.

“wide” endemics. Both species tend to be found on gypsum deposits. Another gypsophilic taxon is *Varilla mexicana* (Fig. 7), which shows a massing in southwestern Coahuila, an oft-repeated tendency. *Acleisanthes acutifolia* (Fig. 9) is almost a CDR marker species as to its

total distribution, but the known localities are few and scattered. *Ziziphus lloydii* (Fig. 10) widely marks the southern subregion of the CDR, south of the Transverse Sierra Madre Oriental, and is one of the

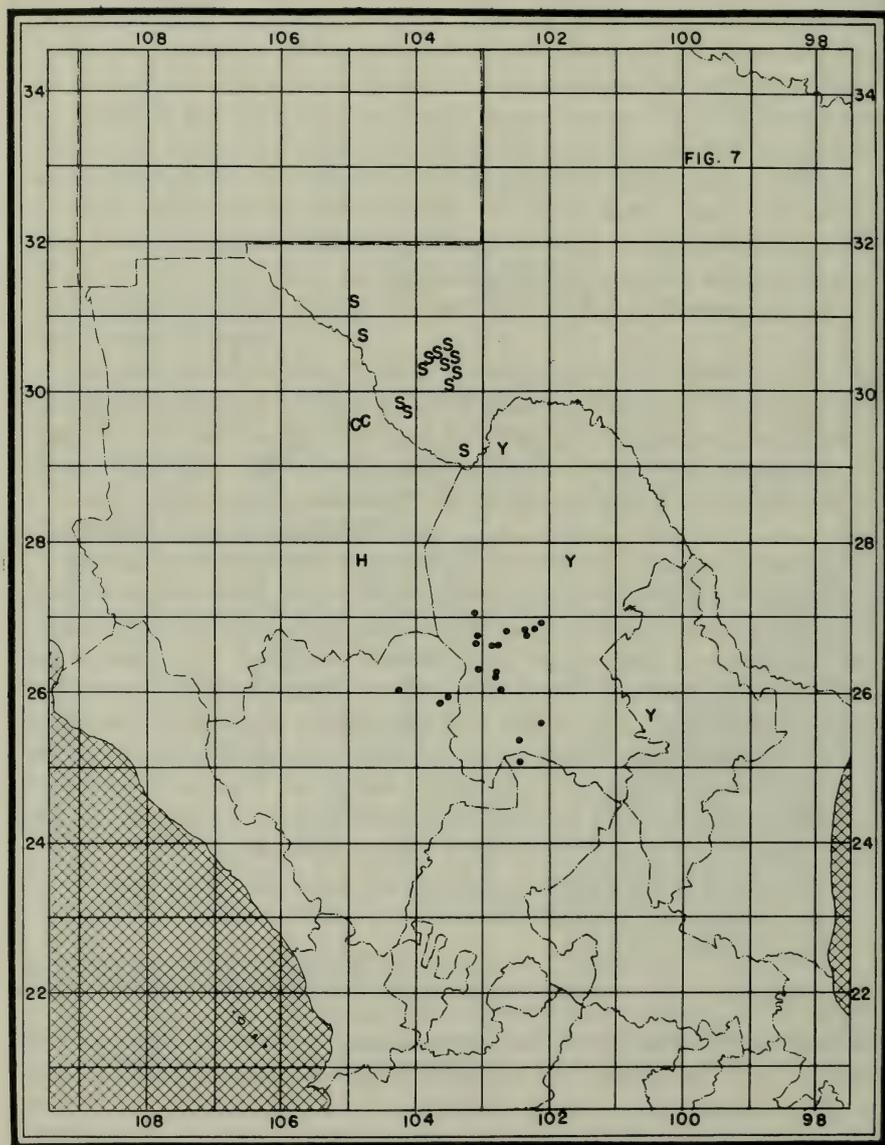


Fig. 7. Map showing distribution of five species of plants endemic to the Chihuahuan Desert region. C, *Canotia wendtii*. H, *Euphorbia henricksonii*. S, *Senecio millelobatus*. Y, *Styrax youngae*. Small circles, *Varilla mexicana*.

very few species to exhibit this type of distribution. *Tetracoccus fasciculatus* (Fig. 9) is one of the few species massing in southeastern Chihuahua and with stations far to the east in eastern Coahuila and Nuevo Leon, where it was first discovered. *Acacia crassifolia* (Fig. 8) has

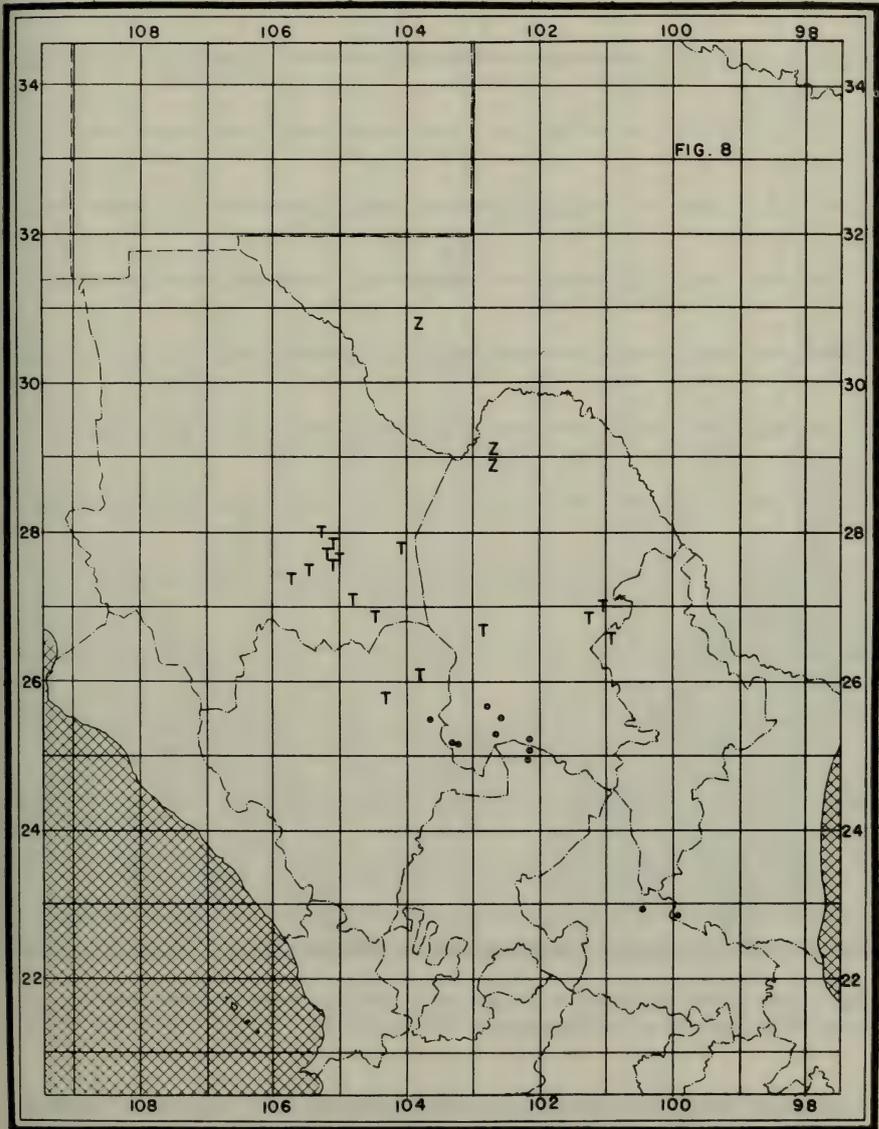


Fig. 8. Map showing distribution of three species of plants endemic to the Chihuahuan Desert region. T, *Tetracoccus fasciculatus*. Z, *Zanthoxylum parvum*. Small circles, *Acacia crassifolia*.

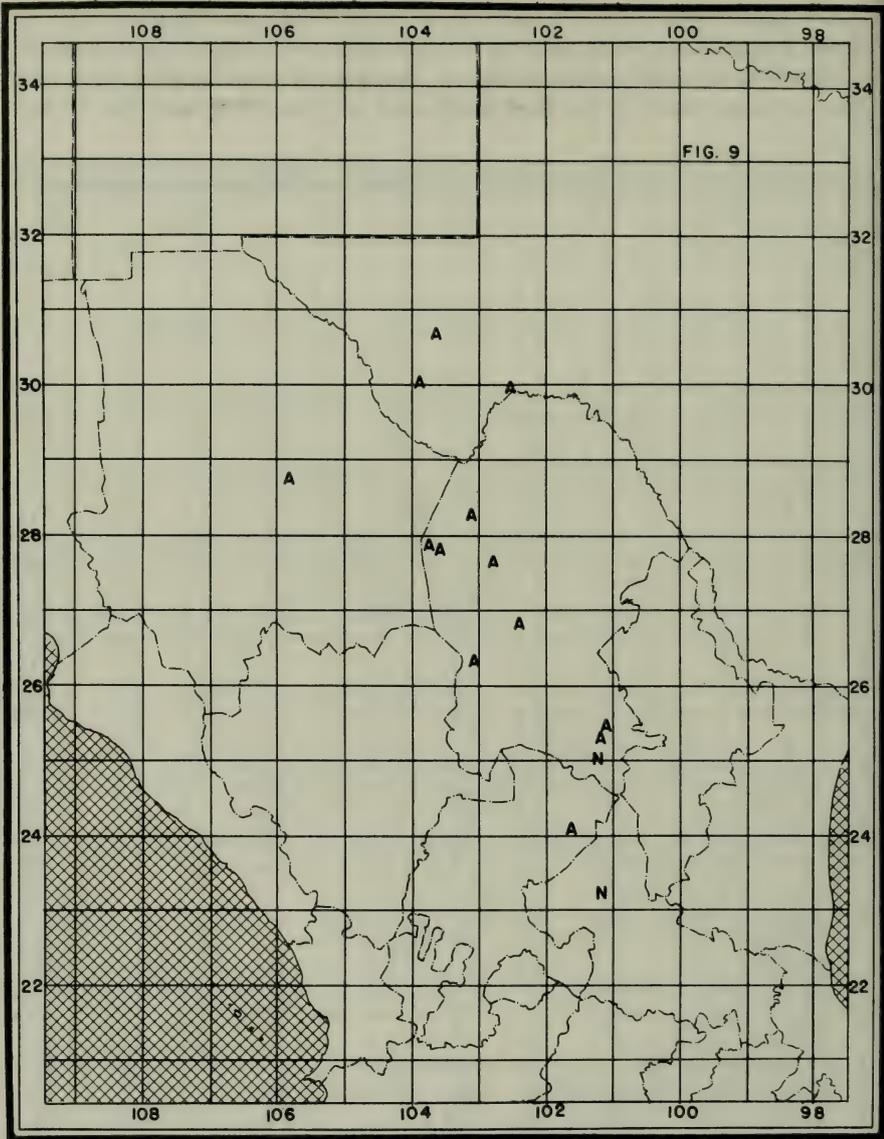


Fig. 9. Map showing distribution of two species of plants endemic to Chihuahuan Desert region. A, *Acleisanthes acutifolia*. N, *Acleisanthes nana*.

a curious disjunct pattern of a sort also exhibited by *Bonetiella anomala* and a few other species of limestone mountains; these species apparently cannot occur on the igneous-rock substrates of the intervening area. *Bartlettia scaposa* (Fig. 12) illustrates a species favoring sandy soils

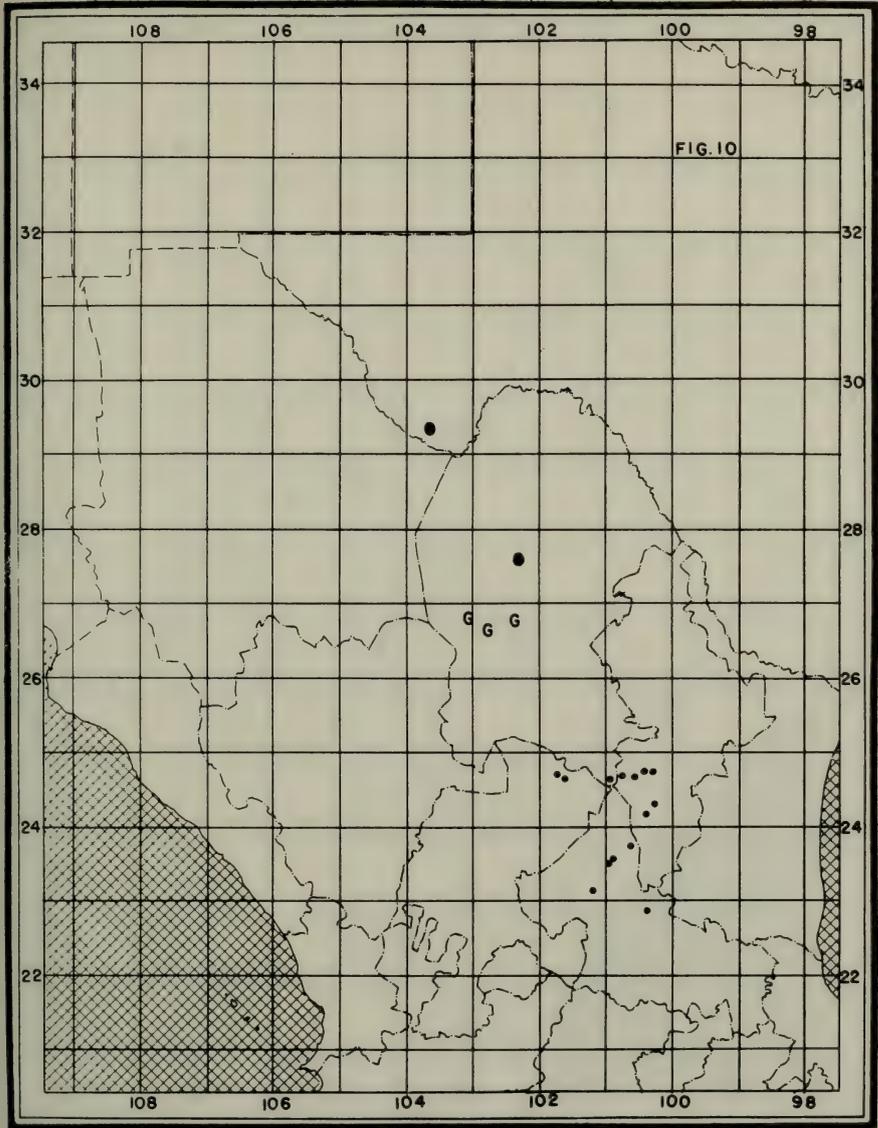


Fig. 10. Map showing distribution of three species of plants endemic to the Chihuahuan Desert region. G, *Dyssodia gypsophila*. Ovals, *Genistidium dumosum*. Small circles, *Ziziphus lloydii*.

derived from igneous rocks, but it has a uniquely spotty or disjunct pattern which appears to be real and not merely a revelation of incomplete collecting. An unusual type of restriction is displayed by *Senecio millelobatus* (Fig. 7) in its restriction to igneous-rock mountains in Texas.

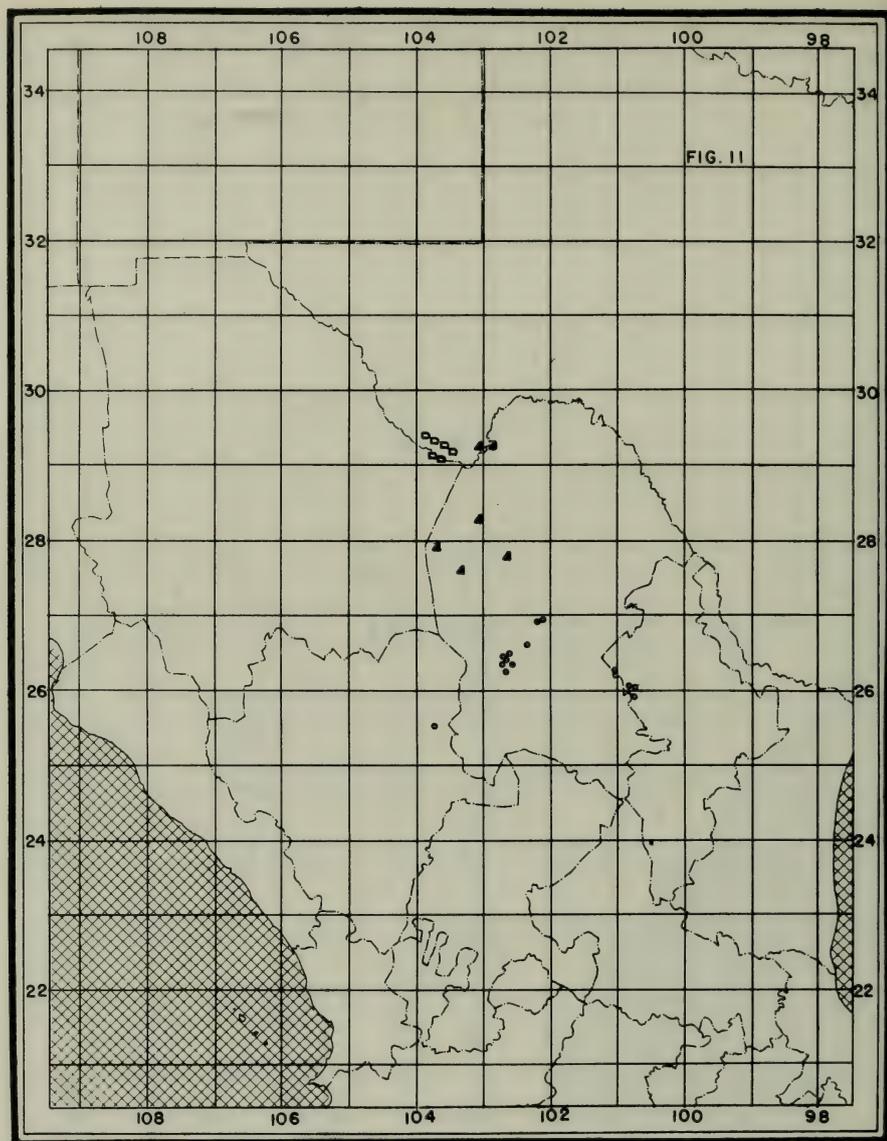


Fig. 11. Map showing distribution of three taxa of plants endemic to the Chihuahuan Desert region. D, *Euphorbia perennans*. Triangles, *Euphorbia chaetocalyx* var. *triligulata*. Small circles, *Euphorbia fruticulosa*.

A rather large number of species are restricted to the Big Bend region, for example, *Phyllanthus ericoides* (Fig. 6), *Zanthoxylum parvum* (Fig. 8), *Euphorbia perennans* (Fig. 11), *Polygala maravillasensis* (Fig. 12), *Galium carmenicola* and *G. correllii* (Fig. 13), *Breweria ovatifolia*

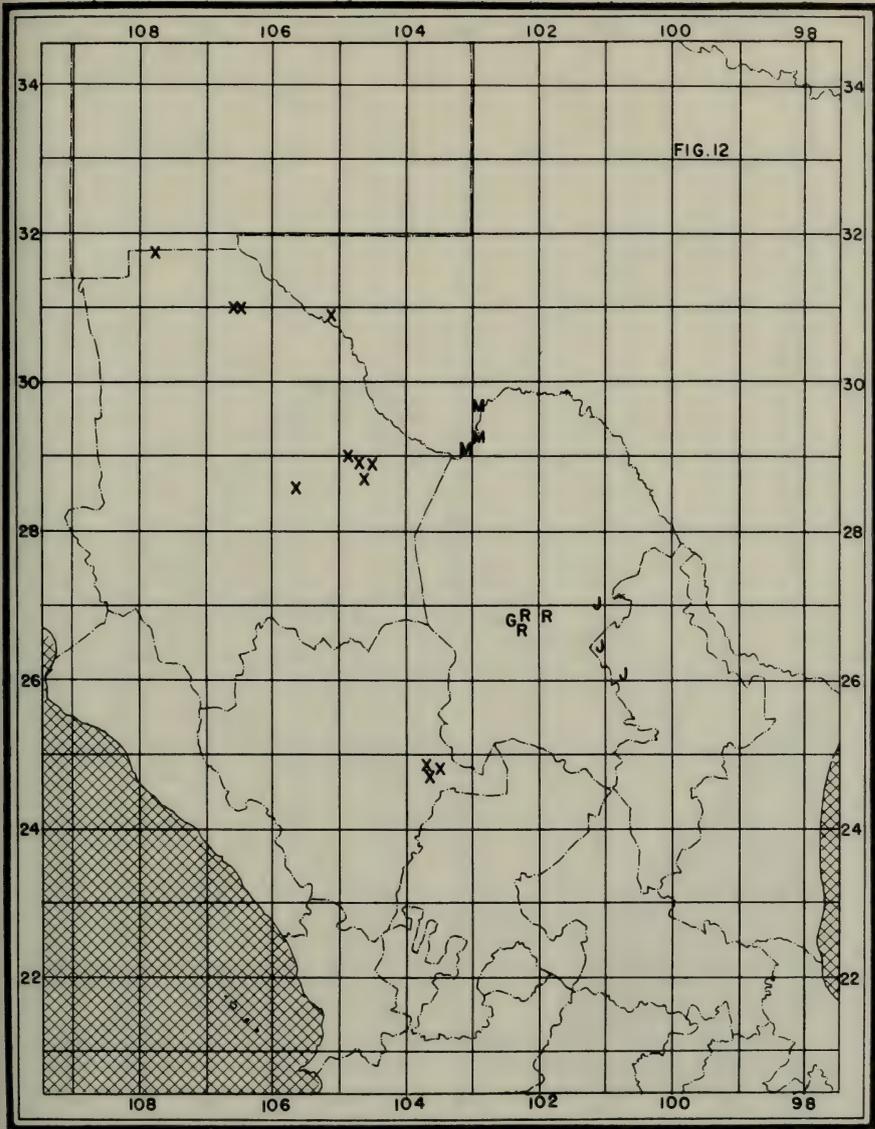


Fig. 12. Map showing distribution of five species of plants endemic to the Chihuahuan Desert region. G, *Machaeranthera gypsophila*. J, *Machaeranthera johnstonii*. M, *Polygala maravillasensis*. R, *Machaeranthera restiformis*. X, *Bartlettia scaposa*.

(Fig. 14), *Tidestromia gemmata* and *T. carnosa* (Fig. 15), and *Quercus hinckleyi* (Fig. 16). Probably the largest group of local endemics, perhaps amounting to 100 species, are essentially restricted to central and southern Coahuila, among them *Dyssodia gypsophila* (Fig. 10), *Euphor-*

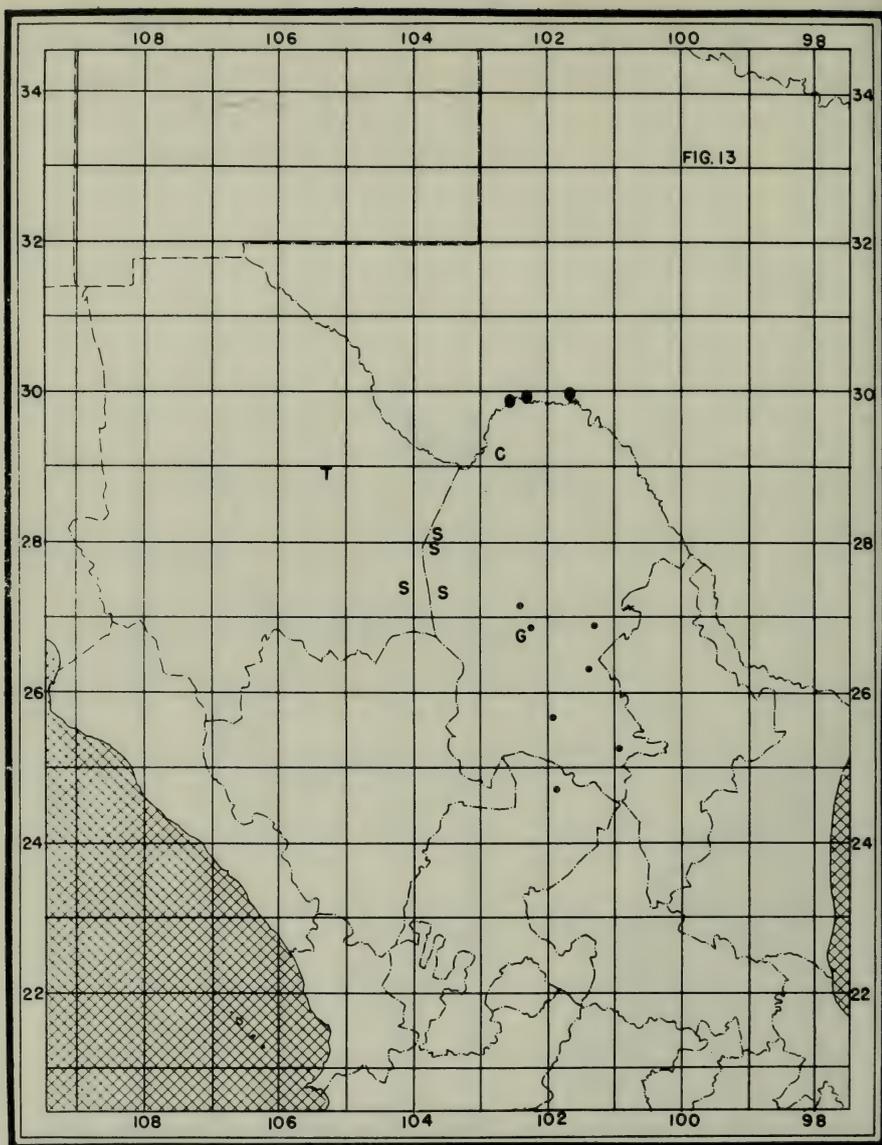


Fig. 13. Map showing distribution of six species of plants endemic to the Chihuahuan Desert region. C, *Galium carmenicola*. G, *Gaillardia gypsophila*. S, *Dasylirion stewartii*. T, *Argemone turnerae*. Ovals, *Galium correllii*. Small circles, *Dasylirion cedrosanum*.

bia fruticulosa (Fig. 11), *Machaeranthera gypsophila* and *M. restiformis* (Fig. 12), *Gaillardia gypsophila* (Fig. 13), *Dasylirion cedrosanum* (Fig. 14), *Breweria multicaulis* (Fig. 14), *Scirpus coahuilensis* (Fig. 14), *Tidestromia rhizomatosa* (Fig. 15), and *Bouteloua johnstonii* (Fig. 16).

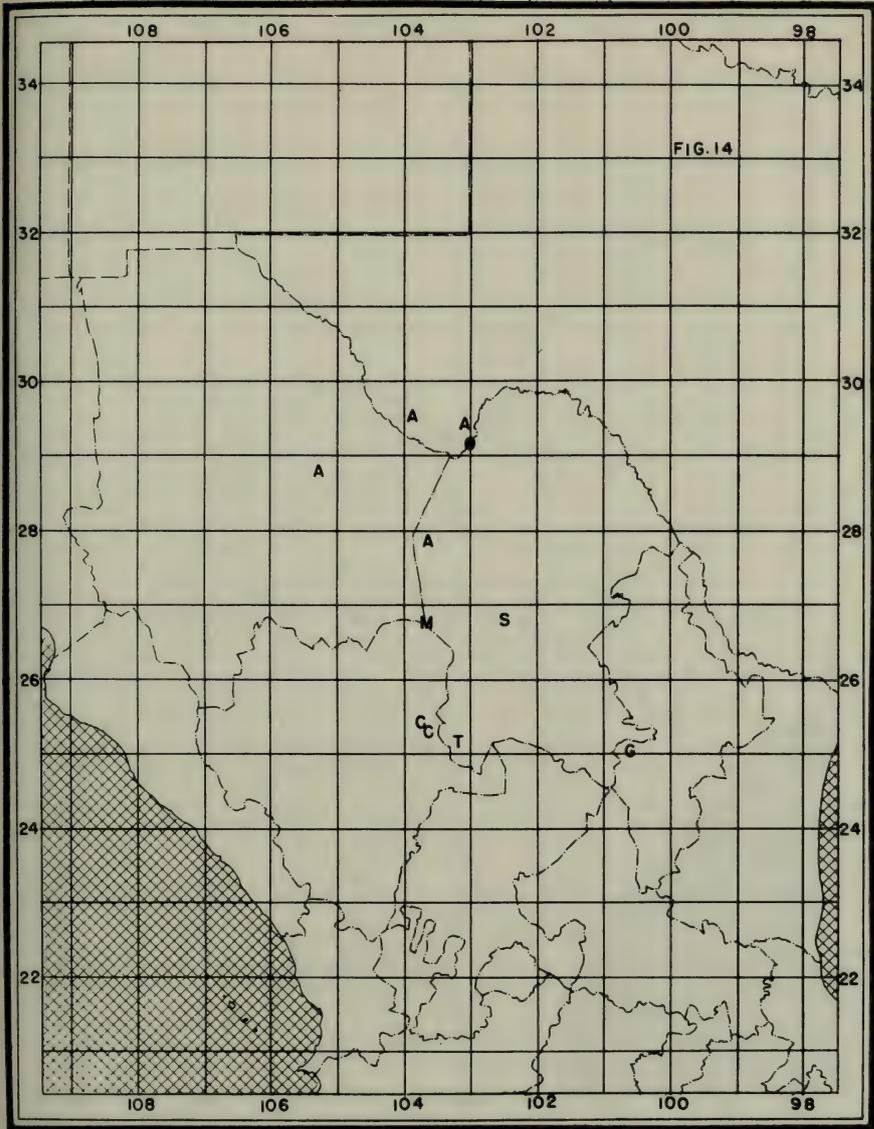


Fig. 14. Map showing distribution of seven species of plants endemic to the Chihuahuan Desert region. A, *Andrachne arida*. C, *Cnidoscolus shrevei*. G, *Aster gypsophilus*. M, *Breweria multicaulis*. S, *Scirpus coahuilensis*. T, *Thamnosma stanfordii*. Oval, *Breweria ovatifolia*.

One of the areas most interesting for its concentration of endemic taxa in a very local area is the San Roberto valley, where the endemic genus *Strotheria gypsophila* occurs as well as a number of endemic species including *Aster gypsophilus* (Fig. 14), *Eriogonum fimbriatum* and *E.*

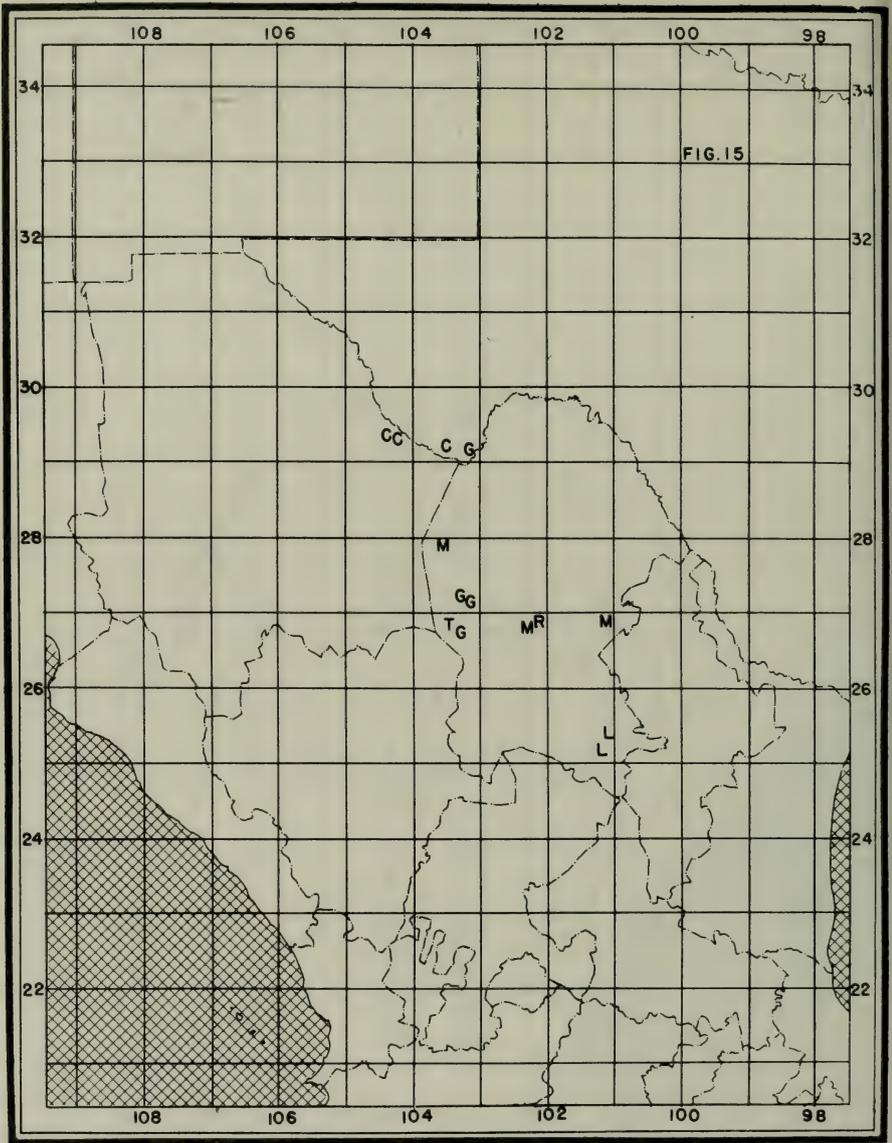


Fig. 15. Map showing distribution of six species of plants endemic to the Chihuahuan Desert region. C, *Tidestromia carnosa*. G, *Tidestromia gemmata*. L, *Aristolochia lassa*. M, *Meiomeria stellata*. R, *Tidestromia rhizomatosa*. T, *Tidestromia tenella*.

turneri (Fig. 16), *Isocoma halophytica*, *Haplopappus rhizomatus*, and *Frankenia margaritae*.

The Jimulco-Chocolate region has its share of highly distinctive en-

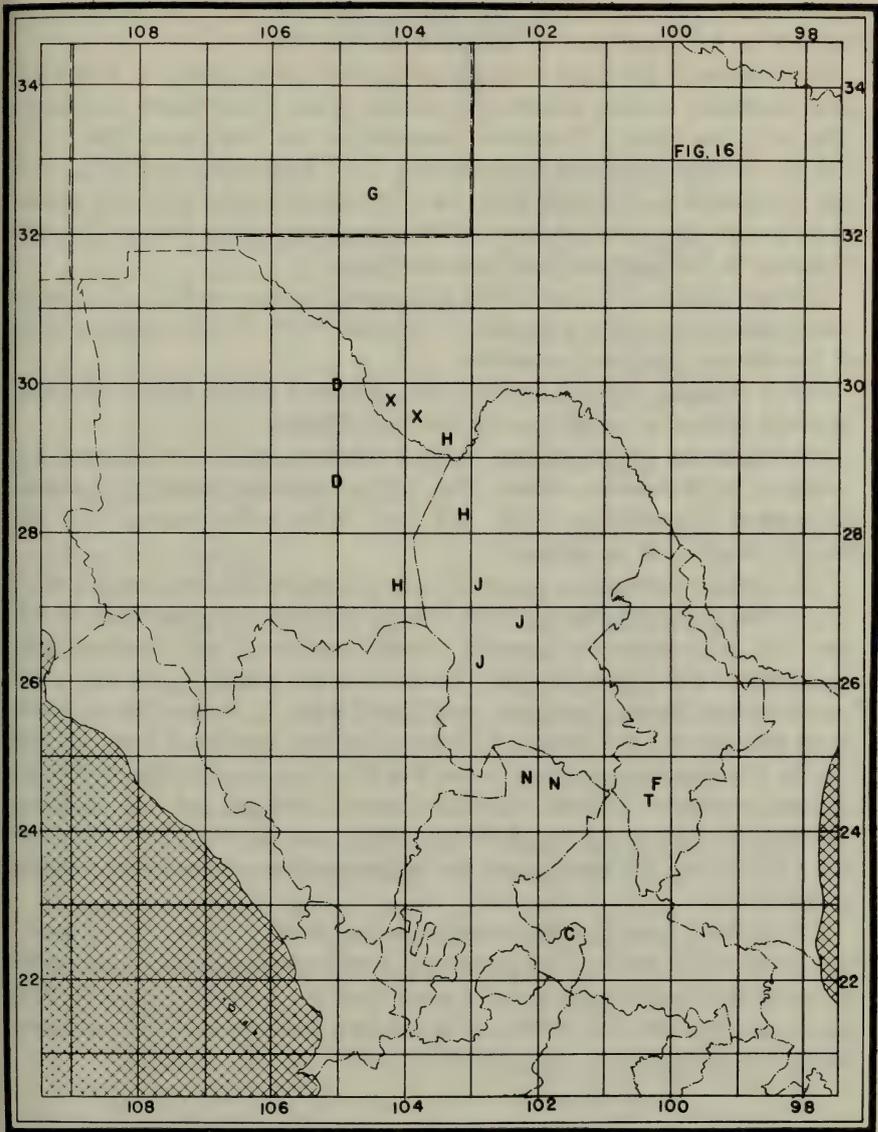


Fig. 16. Map showing distribution of nine species of plants endemic to the Chihuahuan Desert region. C, *Eriogonum clivosum*. D, *Quercus deliquescens*. F, *Eriogonum fimbriatum*. G, *Eriogonum gypsophilum*. H, *Eriogonum hemipterum*. J, *Bouteloua johnstonii*. N, *Eriogonum*, sp. nov. T, *Eriogonum turneri*. X, *Quercus hinckleyi*.

demics including *Thamnosma stanfordii* (Fig. 14) and *Cnidoscolus shrevei* (Fig. 14).

The eastern part of Chihuahua displays local endemics such as

Euphorbia henricksonii (Fig. 7), *Canotia wendtii* (Fig. 7), *Argemone turnerae* (Fig. 13), and *Quercus deliquescens* (Fig. 16).

Northwestern Coahuila and adjacent areas can claim the following local endemics among others: the unique genus *Genistidium dumosum* (Fig. 10), the variety *Euphorbia chaetocalyx* var. *triligulata* (Fig. 11), and the species *Dasyllirion stewartii* (Fig. 13), *Andrachne arida* (Fig. 14), and *Eriogonum hemipterum* (Fig. 16). *Aristolochia lassa* (Fig. 15) seems to be merely the northernmost of the numerous Sierra Madre Oriental endemics in the southeastern Coahuila region.

Machaeranthera johnstonii (Fig. 12) occupies an area of local gypsum outcropping where, for example, *Frankenia leverichii* and a new species of *Tiquilia* are also locally endemic.

Styrax youngae appears to be a rare northern Sierra Madre Oriental endemic related to species on the Edwards Plateau.

Miscellaneous geographically unique distributions seem to appear, for example, in *Meiomeria stellata* (Fig. 15) an endemic halophytic genus. *Eriogonum gypsophilum* (Fig. 16) and *Acleisanthes mana* (Fig. 9) likewise seem to fit no pattern.

"Recurrent distribution patterns" may simply be the result of intuitive (but in this case unfortunate?) tendencies to lump and generalize, in the way the eye tends to connect totally unrelated star-clusters into meaningless but "recognizable" patterns in the night sky. If there are recurrent distribution patterns, and I will leave it to the future when more information is available to form a definite opinion, I believe they can be discerned most clearly in the Big Bend region; the region of central and southern Coahuila between Cuatro Ciénegas and Las Delicias; the Jimulco region; the San Roberto valley; and the Huizache region of San Luis Potosi. All these areas are in the eastern and southern portion of the CDR.

It is in these areas that the uniqueness and enormous biological splendor of the CDR reside. This genetic and evolutionary treasury deserves the most assiduous study and the most dedicated efforts to ensure that future generations will inherit it in all its richness, both the richness known and the richness yet to be discovered.

ACKNOWLEDGMENTS

In addition to the herbarium curators who have aided in my information-gathering, the following persons are among the numerous individuals who provided helpful information of use in this work; I thank them all: Mary Butterwick, Fernando Chiang, Lauramay Dempster, James Henrickson, Emily Lott, Jorge Marroquin, Fernando Medellín Leal, Neil Muller, Don Pinkava, Mike Powell, Jim Reveal, David Riskind, Anders Saustrup, Jackie Smith, Rich Spellenberg, Stuart Strong, John Strother, Bill Turner, Barton Warnock, and Tom Wendt.

Appendix

Key to Taxa

| | |
|--|----------------------------|
| <i>Acacia crassifolia</i> Gray | Thick-leaf Catclaw |
| <i>Acacia neovernicosa</i> Isely | Sticky Catclaw |
| <i>Acleisanthes acutifolia</i> Standley | Sharpleaf Trumpet |
| <i>Acleisanthes nana</i> I. M. Johnst. | Dwarf Trumpet |
| <i>Andrachne arida</i> (Warnock & Johnst.) Webster | Desert Maidenbush |
| <i>Argemone turnerae</i> A. M. Powell | Polly's Pricklypoppy |
| <i>Aristolochia lassa</i> I. M. Johnst. | Tacopate Perezoso |
| <i>Aster gypsophilus</i> B. L. Turner | Gyp Aster |
| <i>Bartlettia scaposa</i> Gray | Bartlett Daisy |
| <i>Bonetiella anomala</i> (I. M. Johnst.) Rzedowski | Correosa del Monte |
| <i>Bouteloua</i> (no need) | Grama |
| <i>Bouteloua johnstonii</i> Swallen | Gyp Grama |
| <i>Breweria multicaulis</i> Brandegee | Stemmy Brewervine |
| <i>Breweria ovalifolia</i> (Torrey) Gray | Eggleaf Brewerrine |
| <i>Canotia wendtii</i> M. C. Johnst. | Conchos Canotia |
| <i>Cnidocolus shrevei</i> I. M. Johnst. | Shreve Bull-nettle |
| <i>Colubrina viridis</i> (M. E. Jones) M. C. Johnst. | Green Snakewood |
| <i>Dasyilirion</i> (no need) | |
| <i>Dasyilirion cedrosanum</i> I. M. Johnst. | Cedros Sotol; Sotol Cenizo |
| <i>Dasyilirion stewartii</i> I. M. Johnst. | Santa Elena Sotol |
| <i>Dyssodia gypsophila</i> B. L. Turner | Gyp Dogweed |
| <i>Eriogonum fimbriatum</i> Hess & Reveal | Fringe Buckwheat |
| <i>Eriogonum gypsophilum</i> Wooton & Standley | Gyp Buckwheat |
| <i>Eriogonum hemipterum</i> (T. & G.) S. Stokes | Halfwing Buckwheat |
| <i>Eriogonum turneri</i> Reveal | Jefe Buckwheat |
| <i>Euphorbia fruticulosa</i> Boissier | Littlebush Spurge |
| <i>Euphorbia fendleri</i> T. & G. var. <i>triligulata</i> (Wheeler) M. C. Johnst. | Finger Spurge |
| <i>Euphorbia henricksonii</i> M. C. Johnst. | Gringo Spurge |
| <i>Euphorbia perennans</i> (Shinners) Warnock & Johnst. | Terlingua Spurge |
| <i>Frankenia leverichii</i> B. L. Turner | Hippy Frankenia |
| <i>Frankenia margaritae</i> Gonzales Medrano | Margarita Frankenia |

- Franseria dumosa* Torrey
Gaillardia gypsophila B. L. Turner
Galium carmenicola L. Dempster
Galium correllii L. Dempster
Genistidium dumosum I. M. Johnst.
Haplopappus rhizomatus M. C. Johnst.
Hechita (no need for author.)
Hilaria mutica (Buckley) Bentham
Isocoma halophytica B. L. Turner
Karwinskia humboldtiana (Schult.)
 Zucc.
Machaeranthera gypsophila
 B. L. Turner
Machaeranthera johnstonii
 (S. F. Blake) B. L. Turner
Machaeranthera restiformis
 B. L. Turner
Meiomeria stellata (Watson)
 Standley
Parthenium incanum H.B.K.
Phyllanthus ericoides Torrey
Polygala maravillasensis Correll
Quercus deliquescens C. H. Muller
Quercus hinckleyi C. H. Muller
Sartwellia mexicana Gray
Sartwellia puberula Rydberg
Scirpus coahuilensis Svenson
Senecio millelobatus Rydb.
Sporobolus airoides (Torrey) Torrey
Strotheria gypsophila B. L. Turner
Styrax youngae Cory
Tetracoccus fasciculatus (Watson)
 Croizat
Thamnosma stanfordii I. M. Johnst.
Tidestromia carnosa I. M. Johnst.
Tidestromia gemmata I. M. Johnst.
Tidestromia rhizomatosa
 I. M. Johnst.
Tiquilia
Varilla mexicana Gray
Viguiera stenoloba S. F. Blake
Yucca carnerosana (Trelease)
 McKelvey
Yucca filifera Chabaud
- Sonoran Spinefruit
 Gyp Firewheel
 Carmen Bedstraw
 Correll Bedstraw
 Falsebroom
 Creeping Falseeaster
 Guapillo
 Tobosa
 Saltflat Rabbitbrush
 Coyotillo
 Gyp Falseeaster
 Ivan's Falseeaster
 Rope Falseeaster
 Mushy Saltwort
 Mariola
 Heather Leafflower
 Maravillas Milkwort
 Chihuahuan Desert Oak
 Hinckley Oak
 Mexican Sartwel
 Dusty Sartwel
 Coahuila Dwarf Bullrush
 Manypart Groundsel
 Sacaton Dropseed
 Gyp Strotherwort
 Young Snowbell
 Closeleaf Fourseed
 Ruda de Jimulco
 Fleshy Tittywort
 Budding Tittywort
 Colonial Tittywort
 Coldenia
 Saladon
 Resinbush
 Palma Zamandoque
 Palma China

Zanthoxylum fagara (L.) Sargent

Zanthoxylum parvum Shinners

Ziziphus lloydii (Standley)

M. C. Johnst.

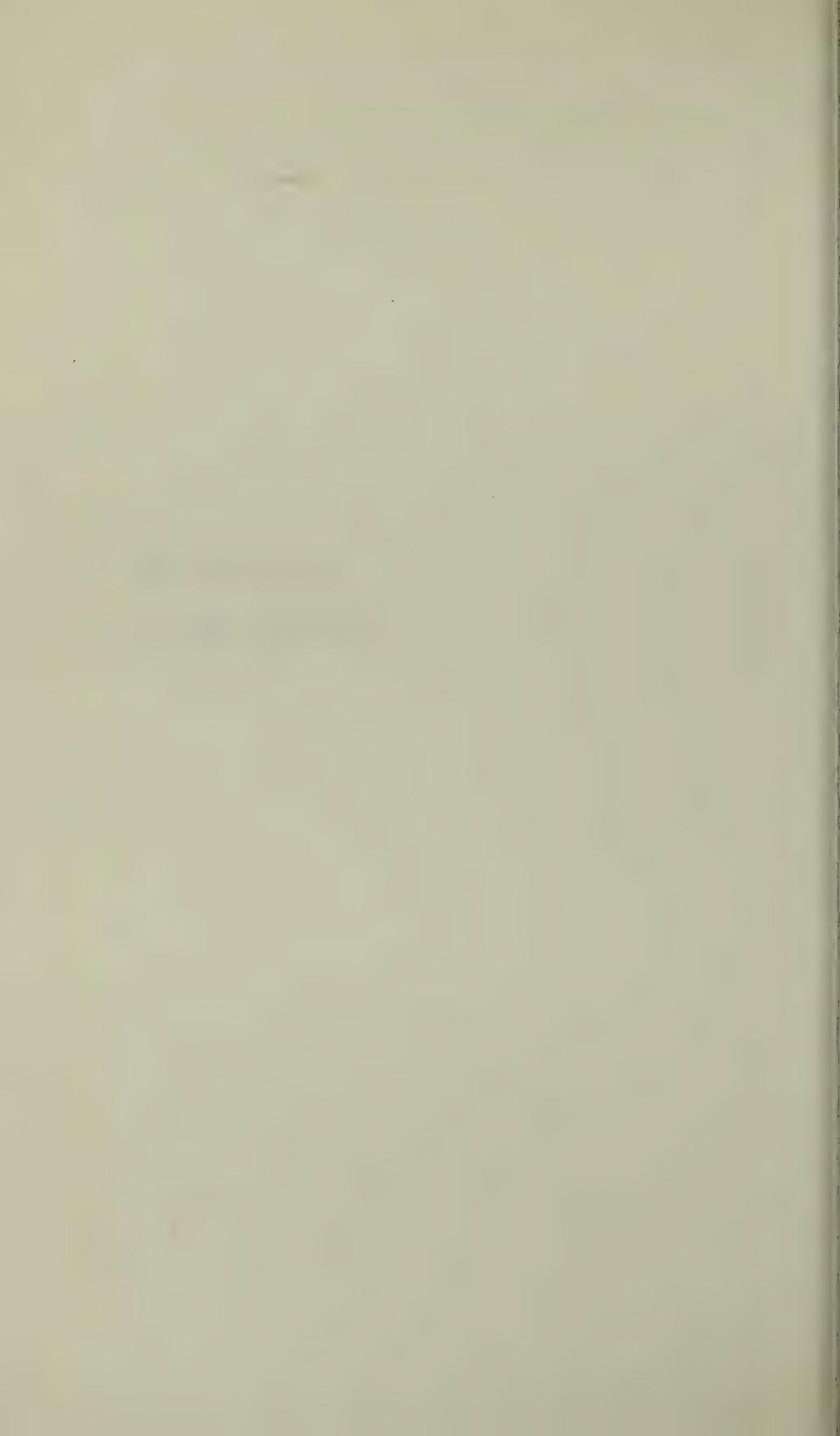
Colima

Mountain Colima; Shinners

Ticketongue

Lloyd Lotebush

Session IV
Ichthyofauna



Introduction

CLARK HUBBS, University of Texas, Austin

Fishes are perhaps the best known group of organisms that are most restricted to water. As water is often a primary limiting force for the Chihuahuan Desert biota, the well being of that fish fauna may provide insight as to the fate of the entire biota.

It is somewhat paradoxical that major increases of available surface water may be as troublesome as major decreases. Cultural and/or industrial development of arid lands is often accompanied by consumptive use of water. If that consumptive use involves ground water, the water table may be lowered. For example, the water level of Well L49-13-612 from the Bolson Deposits in El Paso County has lowered a decimeter per year (steadily) for 20 years (TWDB 1974). More spectacular lowering of the water table may cause surface subsidence, but the effect of gradual decline of available surface waters on fishes has been disastrous (Minckley and Deacon 1968; Hubbs and Echelle 1973). A reasonable rule of thumb is that ground water extracted and evaporated is indirect depletion of surface-water flows at those places where the aquifer surfaces as springs or seeps. Irrigation (and other) diversions may deplete or eliminate surface flows for considerable distances from the removal site. This removal may also involve stranding of fishes in intermittent ditches and/or irrigated fields.

It is obvious that a dry stream bed is detrimental to the survival of the Chihuahuan fishes, but significant depletion of surface-water flows may sufficiently alter the environment so that survival of the indigenous Chihuahuan Desert fishes is unlikely. For example, reduced flows may slow stream flows sufficiently to cause thermal mortalities. This could be exacerbated if overgrazing and erosion have reduced stream-bank cover.

Diversion of surface waters for irrigation also can result in a host of problems associated with removal of geographic barriers that isolate closely related (competing?) species. Minckley will provide details based on his studies in Cuatro Ciénegas.

Although superficially one might consider that the indigenous Chihuahuan Desert fishes might benefit from increases in surface water

following impoundment, the actual circumstances often are the reverse. Many fishes are adapted to specific riverine habitats and are unlikely to survive in reservoirs. All reservoirs on streams in the Chihuahuan Desert lack a large fraction of the indigenous fishes and their elimination may extend far downstream if the hypolimnion release is used exclusively. For example, Jester (1971) showed that the fishes in Elephant Butte Reservoir are a unique subset of the Rio Grande fishes; those fishes listed by Miller (1972) as rare in New Mexico are notably absent in Jester's listing.

The threats to the survival of the native fish fauna are increased by the widespread tendency to import exotic fishes without careful consideration of possible side effects. As most Chihuahuan Desert aquatic ecosystems have few organisms at each trophic level, most are generalists and susceptible to displacement by introduction of competitors which have been subjected to selection in highly competitive ecosystems (Hubbs 1972).

This array of problems suggests that Chihuahuan Desert fishes are in a very precarious situation. The relative health of the indigenous fish fauna to be discussed in the next three papers will suggest the extent of the problems that will occur (or have occurred) in other taxa.

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Composition and Derivation of the Native Fish Fauna of the Chihuahuan Desert Region

ROBERT RUSH MILLER, University of Michigan, Ann Arbor

INTRODUCTION

The Chihuahuan Desert region (Fig. 1) occupies much of the great central tableland of México, originating a short distance north of the U.S.-México boundary and stretching southeastward with gradually increasing elevation for nearly 1400 km to the valley of San Luis Potosí. Its location, size, physiography, and history make it an area of importance for biogeographic studies of the American Southwest. To the northwest, it is rather indefinitely set off from other arid regions that lie between the orogenic break of the Rocky Mountains in New Mexico and the Sierra Nevada Range of California. During the greater rainfall and higher humidity of the Pleistocene, the Chihuahuan Desert served as a dispersal route for aquatic and other organisms; then, as postpluvial aridity set in, isolation, differentiation, and extinction of much of this biota occurred. As a result, it is today an area with numerous relict species (Milstead 1960), some doubtless of pre-Pleistocene origin, thus resembling its more northerly and westerly counterpart, the Great Basin (Hubbs et al. 1974, and references cited).

Although the region is now one of generally scant and highly seasonal rainfall, with numerous endorheic basins, it is crossed by or contains several important stream systems that originate in the elevated, north-south aligned Sierra Madre Occidental that lies to the west of the desert. These river systems harbor an interesting fish fauna rich in material for evolutionary studies but which has not yet received the attention deserved. Not even the rivers themselves have been thoroughly collected, and their continuing modification by man (dam building, irrigation practices, pollution, stocking of exotics) makes it increasingly difficult to gain a complete picture of the aboriginal fauna and of its significance.

In this paper I treat the fishes in broad terms, discussing the general nature of the fauna and its derivation. At least 15% of the known fishes are undescribed. I have field acquaintance with most of the some 100 native species, albeit at least one genus (the remarkable minnow *Stypodon*) and one species (*Cyprinodon*

(1973:Fig. 1). It includes the endorheic basin of La Hediondilla which lies just southeast of Saltillo (mapped on p. 7 in *Caminos de México*, 3rd ed., 1967, *Compañía Hulera Euzkadi*), but excludes Laguna Bustillos and the basin of El Sauz (just W and NNW, respectively, of Ciudad Chihuahua), as well as Laguna de Santiaguillo (N of Ciudad Durango). Although La Media Luna, in the upper Río Verde basin southwest of Río Verde, San Luis Potosí, lies just outside the Chihuahuan Desert region, its aquatic fauna is mentioned because of high endemism, a unique ecosystem, and the current threat to the area.

Most of the drainage of this desert region is interior (Tamayo 1964:Fig. 1), without outlet to the sea and with numerous ephemeral streams that flow through indefinite channels for short periods after heavy summer rains. The Pecos River of New Mexico and Texas and Río Conchos of Chihuahua are, along with the Río Grande, the only important streams whose waters reach the sea (Gulf of Mexico).

The Río Grande (Río Bravo del Norte) is the major through-flowing stream, crossing the region from the vicinity of Albuquerque, New Mexico, to Del Río-Ciudad Acuña, Texas-Coahuila. Studies by geologists and biologists indicate that its upper part has had a history separate from that of the lower portion, but the details of how, when, and just where the integration of these segments took place remains to be determined (Albritton and Smith 1965:98). Although the Río Grande is now essentially dry from El Paso to Ojinaga-Presidio, due to man's activities, the pristine river had sufficiently continuous flow to enable such large fishes as sturgeon, gar (Fig. 2), and blue sucker (*Cycleptus* to move upstream as far as Albuquerque (see below).

The two major tributaries of the Río Grande, Pecos River, and Río Conchos, exhibit significant endemism in their fish faunas and hence I treat them separately from the main river. The Conchos rises on the eastern slopes of the Sierra Madre Occidental and wends its way across the desert to enter the Río Grande well above the Big Bend region. The Pecos, rising in high mountains near Santa Fe, New Mexico (Thomas 1972: Fig. 1), follows a southerly and then easterly course to reach the Río Grande below the Big Bend region; much of the water in a

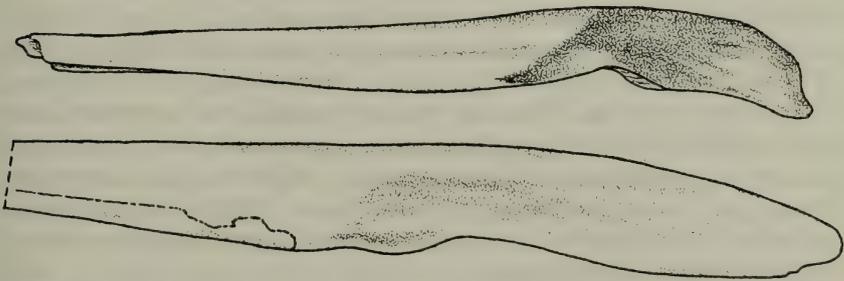


Fig. 2. Ventral views (anterior to left) of left vomers of *Lepisosteus osseus*. Above, from archeological site D770, Pottery Mound, Río Puerco, New Mexico, 59.4 mm; 1325-1490 A.D. Below, Recent specimen.

300-km segment of its lower course is brackish, with salinities locally as high as 25.1 parts per thousand and frequently averaging greater than 10 ppt (Hubbs 1957:99; Hubbs and Echelle 1972:149).

The basis for recognition of the Cuatro Ciénegas basin as a distinct hydrographic unit is fully developed by Minckley (1969 and this volume).

The Tularosa basin in southern New Mexico is a disrupted segment of the Rio Grande, as shown in Hubbs and Miller (1948:117) and discussed further by Miller and Echelle (1974).

Guzmán is the name adopted here for the terminus of the Ríos Mimbres, Casas Grandes, Santa María, and del Carmen, even though they all may not have flowed into Laguna Guzmán (or its expanded version) simultaneously. Brand (1937) referred to this complex of streams as the Guzmán-Santa María Basin, with the following comment: "It is easily conceivable that these lakes [Guzmán, Santa María] may have coalesced in the period when the Rio Grande emptied into this sink. . . ."

The Río Nazas (Conant 1963:Fig. 1) rises north of Ciudad Durango and formerly flowed into the enclosed Laguna de Mayrán which, within historic time, was also joined with Laguna de Viesca (the playa just S of Mayrán on Fig. 1), which is the flood terminus of Río Aguanaval. For this reason, the Aguanaval is treated as part of the Nazas basin (also, its fishes show little differentiation from those in the Nazas).

The region called El Salado comprises the extensive dry plateau of San Luis Potosí and adjacent Zacatecas, extending southward to latitude 22°N (Tamayo 1964, Fig. 2, 116). Thus far only three localities with fish life have been detected in this arid expanse, two (Venados and Moctezuma) between Charcas and Ciudad S. L. Potosí, and the other at Illescas, northwest of Ciudad Zacatecas.

THE FISH FAUNA

Our knowledge of the native fishes of the Chihuahuan Desert region is inadequate. No concerted attempt to sample this fish fauna was made prior to the field work of Meek (1902, 1904), although some important discoveries based on local collecting were reported much earlier (Girard 1856, 1859; Garman 1881; Woolman 1894). Meek's collection stations were confined almost exclusively to points where railroads intersected streams, and much of the subsequent field effort by others (from 1950 to 1974) has been limited to access from highways. Since the trend of the major Mexican streams is mostly at right angles to railroad and highway crossings, only small segments of these streams have, for the most part, been adequately sampled. This is especially true for the Ríos Conchos and Nazas, parts of whose courses are difficult of access. Vast areas of the desert in northern Chihuahua have never been surveyed and the potential for discovery of interesting relicts is great there.

Another factor that has hampered the student of native fishes is the direct modification of the fauna by man. Fish-cultural activities in Texas and New Mexico, dating back at least to the 1930s, and (generally more recently) in

Mexico, have resulted in the spreading of exotic minnows (*Cyprinus*, *Carassius*), suckers (*Ictiobus*), catfishes (especially *Ictalurus punctatus*), poeciliids (*Gambusia*, *Lebistes*, *Xiphophorus*), silversides (*Menidia* in the United States and Mexico, *Chirostoma* in Mexico—Minckley 1965), sunfishes (*Ambloplites*, *Lepomis*, *Micropterus*, etc.), and cichlids (*Tilapia* in Mexico). Establishment of alien species along with direct modification of habitats has resulted in extinction of species (Miller 1961, 1964; Peden 1973) or of populations (Hubbs and Broderick 1963; Hubbs and Wauer 1973; Echelle and Miller 1974; Contreras-Balderas 1969, this volume). This trend must be halted if we are to maximize our knowledge of the biological resources of the Chihuahuan Desert region.

Despite our imperfect knowledge, we know of 107 native species in the area, of which 93 have been described (Table 1). These are distributed among 16 families, of which 6 are primary or strictly fresh-water fishes, 5 are secondary and can tolerate marked salinity, and 5 belong to families that are essentially marine (Clupeidae and Sciaenidae) or regularly spend a large part of their life cycle in fresh water (Anguillidae). The one drum, *Aplodinotus* (Sciaenidae), is confined to fresh water, ranging from Canada to Guatemala. Among the 40 represented genera, 3 comprise 41% of the known fauna: the shiners, *Notropis* (20 species), the pupfishes, *Cyprinodon* (14), and the livebearers of the genus *Gambusia* (10 species). Four of the pupfishes are yet to be described.

For the purposes of this paper, I depart from convention in some scientific names. This is done, in part, to emphasize controversial viewpoints. No subspecies are formally recognized although I believe that their use can be justified. The bases for the names adopted are given below.

(1) *Astyanax mexicanus* (rather than *A. fasciatus mexicanus*) is used in agreement with Bailey et al. (1970:19), based on the premise that it has not been demonstrated that *A. fasciatus* (Cuvier) and *A. mexicanus* (Fillipi) are the same species.

(2) *Codoma ornata*. The cyprinid genus *Codoma* was proposed by Girard (1856:194; redescription in 1859:53-54, Figs. 18-21) on the basis of *C. ornata* from the Río Conchos basin ("Chihuahua River and its tributaries") and *C. vittata* from the Valley of Mexico. The latter was later assigned to the genus *Aztecula* (Jordan and Evermann 1898:2799) and is commonly now called *Notropis aztecus* Woolman, which may be the same species as *Ceraticthys sallei* Günther (pers. observ.). In any event, *C. vittata* is not closely related to *C. ornata*, which is also currently placed in *Notropis*. Gibbs (1957) revised the subgenus *Cyprinella* of *Notropis*, to which he assigned *Notropis ornatus*. That species, however, lacks milky deposition in the fins of nuptial males (Minckley unpubl. data) and is also distinctive in the size, number, and arrangement of breeding tubercles—features that exclude it from *Cyprinella* as diagnosed by Gibbs. A further distinction that I have noted is that the first obvious dorsal ray of adults is well separated by membrane from the first principal ray, much as in *Pimephales* (which *C. ornata* resembles, as pointed out by Girard 1856:195, and by Hubbs and Hubbs 1958:300-301); also the predorsal circumferential scale

TABLE 1. Distribution of native fishes of the Chihuahuan Desert region.

| Taxon | Rio Grande | Cuatro Ciénegas | Pecos | Conchos | Tularosa | Guzmán | Nazas | Hediondilla | El Salado |
|---|----------------|-----------------|-------|---------|----------|----------------|-------|-------------|-----------|
| ACIPENSERIDAE Sturgeons | | | | | | | | | |
| <i>Scaphirhynchus platyrhynchus</i> | X | - | - | - | - | - | - | - | - |
| LEPISOSTEIDAE Gars | | | | | | | | | |
| <i>Lepisosteus oculatus</i> | X | - | X | - | - | - | - | - | - |
| <i>Lepisosteus osseus</i> | X | - | X | X | - | - | - | - | - |
| ANGUILLIDAE Freshwater eels | | | | | | | | | |
| <i>Anguilla rostrata</i> | X | - | X | - | - | - | - | - | - |
| CLUPEIDAE Herrings | | | | | | | | | |
| <i>Dorosoma cepedianum</i> | X | - | X | - | - | - | - | - | - |
| CHARACIDAE Characins | | | | | | | | | |
| <i>Astyanax mexicanus</i> | X | X | X | X | - | - | X | - | - |
| CYPRINIDAE Minnows | | | | | | | | | |
| <i>Camptostoma anomalum</i> | X (L) | - | - | - | - | - | - | - | - |
| <i>Camptostoma ornatum</i> | X (U) | - | - | X | - | CG | X | - | - |
| <i>Codoma ornata</i> | - | - | - | X | - | - | X | - | - |
| <i>Dionda diaboli</i> | X | - | - | - | - | - | - | - | - |
| <i>Dionda episcopa</i> | X | X | X | X | - | - | X | - | - |
| <i>Gila conspersa</i> | - | - | - | - | - | - | X | - | - |
| <i>Gila modesta</i> | X ^a | - | - | - | - | - | - | - | - |
| <i>Gila nigrescens</i> | - | - | - | - | - | - | - | - | - |
| <i>Gila pandora</i> ^c | - | - | X | - | - | X ^b | - | - | - |
| <i>Gila pulchra</i> | - | - | - | - | - | - | - | - | - |
| <i>Hybognathus nuchalis</i> | X | - | - | X | - | - | - | - | - |
| <i>Hybopsis aestivalis</i> | X | - | X | X | - | - | - | - | - |
| <i>Hybopsis gracilis</i> | X (U) | - | X | - | - | - | - | - | - |

TABLE 1. (Continued)

| Taxon | Rio Grande | Cuatro Ciénegas | Pecos | Conchos | Tularosa | Guzmán | Nazas | Hediondilla | El Salado |
|---|----------------|-----------------|----------------|---------|----------|--------|-------|-------------|-----------|
| <i>Notropis amabilis</i> | X | - | X | X | - | - | - | - | - |
| <i>Notropis braytoni</i> | X | - | X | X | - | - | - | - | - |
| <i>Notropis buchmanii</i> | X (L) | - | - | - | - | - | - | - | - |
| <i>Notropis chihuahua</i> | X (U) | - | X | X | - | - | - | - | - |
| <i>Notropis formosus</i> | - | - | - | - | - | X | - | - | - |
| <i>Notropis garmani</i> | - | - | - | - | - | - | X | - | - |
| <i>Notropis jemezianus</i> | X | - | X | X | - | - | - | - | - |
| <i>Notropis lutrensis</i> | X | - | X | X | - | - | X | - | - |
| <i>Notropis nazas</i> | - | - | X | - | - | - | - | - | - |
| <i>Notropis prosperpinus</i> | X | - | X | - | - | - | - | - | - |
| <i>Notropis rutilus</i> | X (L) | - | - | - | - | - | - | - | - |
| <i>Notropis saladonis</i> | X (L) | - | - | - | - | - | - | - | - |
| <i>Notropis simus</i> | X | - | - | - | - | - | - | - | - |
| <i>Notropis stramineus</i> | X (L) | - | - | - | - | - | - | - | - |
| <i>Notropis venustus</i> | X (L) | - | - | - | - | - | - | - | - |
| <i>Notropis xanthicara</i> | - | X | - | - | - | - | - | - | - |
| <i>Pimephales promelas</i> | X | - | X | X | - | X | - | - | - |
| <i>Rhinichthys cataractae</i> | X | - | - ^a | X | - | - | - | - | - |
| <i>Stypodon signifer</i> | - | - | - | - | - | - | X | - | - |
| CATOSTOMIDAE Suckers | | | | | | | | | |
| <i>Carpiodes carpio</i> | X | - | X | X | - | - | X | - | - |
| <i>Catostomus conchos</i> | - | - | - | X | - | - | - | - | - |
| <i>Cycleptus elongatus</i> | - | - | X | X | - | - | - | - | - |
| <i>Ictiobus bubalus</i> | X (L) | - | X | - | - | - | - | - | - |
| <i>Ictiobus niger</i> | X | - | X | X | - | - | X | - | - |
| <i>Moxostoma austrinum</i> | X (U) | - | - | X | - | - | - | - | - |
| <i>Moxostoma congestum</i> | X | - | X | X | - | - | - | - | - |
| <i>Pantosteus plebeius</i> | - ^e | - | - | X | - | X | X | - | - |

TABLE 1. (Continued)

| Taxon | Rio Grande | Cuatro Ciénegas | Pecos | Conchos | Tularosa | Guzmán | Nazas | Hediondilla | El Salado |
|---|------------|-----------------|-------|---------|----------|--------|-------|-------------|-----------|
| POECILIDAE Livebearers | | | | | | | | | |
| <i>Gambusia albarezi</i> | - | - | - | X | - | - | - | - | - |
| <i>Gambusia amisiadensis</i> | X (L) | - | - | - | - | - | - | - | - |
| <i>Gambusia gagei</i> | X (BB) | - | - | - | - | - | - | - | - |
| <i>Gambusia hurtadoi</i> | - | - | - | X | - | - | - | - | - |
| <i>Gambusia krumholzii</i> | X (L) | - | - | - | - | - | - | - | - |
| <i>Gambusia longispinis</i> | - | X | - | - | - | - | - | - | - |
| <i>Gambusia marshi</i> | X (L) | X | - | - | - | - | - | - | - |
| <i>Gambusia nobilis</i> | X (L) | - | X | - | - | - | - | - | - |
| <i>Gambusia senilis</i> | - | - | - | X | - | - | - | - | - |
| <i>Gambusia affinis</i> | X (L) | - | X | - | - | - | - | - | - |
| <i>Xiphophorus gordoni</i> | - | X | - | - | - | - | - | - | - |
| <i>Xiphophorus conchianus</i> | X (L) | - | - | - | - | - | - | - | - |
| PERCICHTHYIDAE Temperate basses | | | | | | | | | |
| <i>Morone chrysops</i> | - | - | X | - | - | - | - | - | - |
| CENTRARCHIDAE Sunfishes | | | | | | | | | |
| <i>Chaenobryttus gulosus</i> | - | - | X | - | - | - | - | - | - |
| <i>Lepomis cyanellus</i> | - | - | X | - | - | - | - | - | - |
| <i>Lepomis megalotis</i> | X (L) | X | X | X | - | - | - | - | - |
| <i>Lepomis macrochirus</i> | X (L) | - | - | - | - | - | - | - | - |
| <i>Micropterus salmoides</i> | X (L) | X | - | - | - | - | - | - | - |
| PERCIDAE Perches | | | | | | | | | |
| <i>Etheostoma australe</i> | - | - | - | X | - | - | - | - | - |
| <i>Etheostoma grahami</i> | X (L) | - | X | - | - | - | - | - | - |
| <i>Etheostoma lepidum</i> | - | - | X | - | - | - | - | - | - |
| <i>Etheostoma pottsi</i> | - | - | - | - | - | - | X | - | - |
| <i>Percina macrolepida</i> ⁵ | X (L) | - | X | - | - | - | - | - | - |

TABLE 1. (Continued)

| Taxon | Rio Grande | Cuatro Ciénegas | Pecos | Conchos | Tularosa | Guzmán | Nazas | Hediondilla | El Salado |
|--|------------|-----------------|-------|---------|----------|--------|-------|-------------|-----------|
| SCIAENIDAE Drums | | | | | | | | | |
| <i>Aplodinotus grunniens</i> | X (L) | - | X | - | - | - | - | - | - |
| CICHLIDAE Mojarras | | | | | | | | | |
| <i>Cichlasoma cyanoguttatum</i> | X (L) | X | X | - | - | - | - | - | - |
| Families: 16 | | | | | | | | | |
| Primary, 6 (57=63 species) | | | | | | | | | |
| Secondary, 5 (31=39 species) | | | | | | | | | |
| Peripheral, 5 (5 species) | | | | | | | | | |
| Genera: 40 | | | | | | | | | |
| <i>Notropis</i> (17=20 species) | | | | | | | | | |
| <i>Cyprinodon</i> (10=14 species) | | | | | | | | | |
| <i>Gambusia</i> (10 species) | | | | | | | | | |
| Species: 93 (107) | | | | | | | | | |
| Undescribed, 16, (5 minnows, 1 sucker, 1 catfish, 4 killifish, 1 darter, 4 cichlids) | | | | | | | | | |

L=lower; U=upper; CG=Casas Grandes ^aRio Salinas nr. Saltillo ^bAlso in Laguna Bustillos ^cSee Miller and Hubbs (1962) ^dIn upper Pecos. ^eIn upper Rio Grande. ^fParras. ^gStevenson 1971.

count below the lateral line varies from 13 to 18 (vs. 9-11). Since there is uncertainty as to just what are the closest relatives of *Codoma ornata*, I retain it for the time being in its own genus as a separate phyletic line that is distributed on both slopes of the Sierra Madre Occidental (Miller 1976a). More than one taxon is evidently included; for example, the samples from the Río Nazas basin are separable in a number of features (fin rays, tubercles, body proportions) from those in the Conchos.

(3) *Notropis formosus* is listed as a binomial rather than as a subspecies of *N. lutrensis* on the basis of the arguments presented by Minckley (1973:139). *N. garmani* is also accorded full species status although it may be aligned soon as a subspecies of *N. lutrensis* (Salvador Contreras-Balderas pers. comm., 1974).

(4) *Moxostoma austrinum*. The inclusion of this species in the Chihuahuan Desert region rests on unpublished research by Robert E. Jenkins. It is known thus far in the United States only from Alamito Creek, Texas (UMMZ 182360, USNM 212109), the mouth of which enters the Rio Grande a short distance below the mouth of the Río Conchos, Chihuahua, where the species also occurs. Formerly, the Conchos records were referred to *M. congestum*.

(5) *Pantosteus plebeius*. Recognition of *Pantosteus* as a full genus has been followed by some (e.g., Minckley 1973) because use of this name immediately communicates a morphological and behavioral type, along with probable habitat predilections. It is here tentatively adopted.

(6) My recent unpublished work indicates that *Ictalurus pricei* is confined to the Pacific slope of northwestern Mexico (*I. meeki* Regan may be a synonym); hence I refer to the Chihuahuan populations formerly identified with this species as *I. "pricei"*.

(7) *Gambusia affinis*. Native populations of this species are referable to *G. a. speciosa* Girard, which I initially was inclined to recognize as a full species until a sample was examined from the basin of the Río Soto la Marina, Tamaulipas (UMMZ 169640), in which the serrae on ray 4p are more posterior and the tip of ray 4a projects posteriorly beyond ray 4p as in southernmost populations of *G. affinis* (compare Figs. A and B in Minckley and Koehn 1966), whereas the dorsal rays number 7 as in *speciosa* (6 in all other forms of *affinis* except *G. a. holbrooki* Girard).

The general configuration of Middle America as we know it today was developed during the Miocene and Pliocene, and the major arrangements of the complex hydrographic systems of Mexico were established during the Pliocene (Maldonado-Koerdell 1964:17, 20). During the Quaternary there were notable stream captures along the Continental Divide in Mexico, integration of the upper and lower parts of the Rio Grande, sea-level changes in the Gulf of Mexico, and some uplift and increasing aridity, but these activities probably did not markedly change the nature of the fish fauna; ranges were extended or contracted, populations were disrupted through isolation of formerly connected waterways, and an unknown amount of extinction undoubtedly took place.

The remnant fish fauna may be assigned to the Chihuahuan Province, which, during its maximum extent (which included all of the basins listed in Table 1 except Hediondilla and El Salado), conformed to my concept of a fish province (Miller 1966:777). Among its distinctive endemics are the genera *Stypodon*, *Codoma*, *Prietella*, and *Megupsilon*, and *Campostoma ornatum* [itself a complex of forms recently considered by Burr (1976)], *Dionda episcopa*, *D. diaboli*, a number of species of *Notropis* (*amabilis*, *braytoni*, *chihuahua*, *jemezianus*, *prosperpinus*, *rutilus*, *saladonis*, *simus*, and *xanthicara*), several species of *Gila*, *Cyprinodon*, and *Gambusia* (Table 1), *Lucania anterioris*, several species of *Etheostoma*, and *Cichlasoma cyanoguttatum*. The province marks the southern limit of sunfishes and darters.

Most of this fish fauna is of Holarctic or Nearctic origin, including the minnows, suckers, catfishes, sunfishes, and darters, which together comprise nearly 60% of the total. Of these, the Ictaluridae, Centrarchidae, and Etheostomatinae (darters, Percidae) are unique North American groups whose entire history is confined to this continent. The Holarctic families are the Cyprinidae and Catostomidae, groups shared with Eurasia.

Since *Cyprinodon* is more diversified in the Chihuahuan Desert region than it is elsewhere, it appears that much of the evolution of this genus has occurred within that area (Miller 1976b). The sturgeon and gars are clearly of northern origin, derived from the rich Mississippi River Province, containing four to five times as many primary fresh-water fishes as does the Chihuahuan Province. When the Rio Grande attained its present configuration, sturgeon, gar, and the blue sucker ascended as far as the vicinity of Albuquerque (Bailey and Cross 1954; Gehlbach and Miller 1961; Fig. 2 herein). The monotypic genus *Megupsilon* (Miller and Walters 1972) is perhaps a pre-Pleistocene relict now restricted to a small spring-fed pond in La Hediondilla. Neotropical elements are represented only by the characin genus *Astyanax*, which is an aggressive predator that invaded the Pecos, Conchos, and Nazas rivers, and by the cichlid genus *Cichlasoma* (subgenera *Herichthys* and *Parapetenia*) which is confined to the lower Rio Grande basin and the bolsón of Cuatro Ciénegas, where it has evolved a small species flock (Minckley, this volume). Distinctly Middle American elements in the Chihuahuan Province are the large number of species of *Gambusia*, belonging to a family that has its center of abundance and diversity between the American Southwest and northern South America.

Also present in the Chihuahuan Desert are elements indicating that there has been multiple invasion of the area. These are members of the autochthonous Mexican family Goodeidae which are abundantly represented in the more southerly Lerma Province, marked by the Pacific-draining Río Lerma basin, which lies across Central Mexico between the transverse Nevolcanic Axis and the Chihuahuan Desert region. Only two genera of this Lerma fauna are known within the Chihuahuan Desert, *Characodon lateralis*, once inhabiting the Parras basin southeast of Laguna Mayrán, and *Xenophorus captivus*, from springs near Venado, Illescas, and Moctezuma in San Luis Potosí. However, it is very likely

that in Plio-Pleistocene times there were other representatives of this family in the Chihuahuan Desert and of another characteristic Lerma fish, the atherine genus *Chirostoma*, which today inhabits the upper Río Mezquital near Ciudad Durango, a stream that formerly flowed into the Río Nazas (Albritton 1958).

La Media Luna (lying just southeast of the area mapped) is the name given to a remarkable aquatic ecosystem about 10 km southwest of Río Verde, San Luis Potosí, at an elevation close to 1000 m. The main laguna, in the form of a half moon, contains several cone-shaped aquifers with a reported maximum depth of 50 m. The water is extraordinarily clear, warm, sulfurish, with an abundance of submerged and floating plants. The waters lead to the Río Verde, part of the great Río Pánuco basin of eastern México. The fish fauna, still not entirely described, includes two endemic genera (*Cualac* of the Cyprinodontidae, and *Ataeniobius* of the Goodeidae) and four other species restricted to the upper Río Verde basin (Miller 1956; Contreras-Balderas and Verduzco-Martinez unpubl. data; Hubbs and Miller unpubl. data). Few studies of other aquatic organisms have been made but among invertebrates sampled thus far are three endemic species of crustaceans (Villalobos and Hobbs 1974). During several visits from 1955 to 1971, I could detect no modification of this unique ecosystem, which also contains valuable Indian artifacts of a now vanished culture (perhaps 1000 years old). However, in 1972, we found introduced fishes in two outflow ditches (water from La Media Luna) south of Río Verde (the Old World cichlid *Tilapia aurea* and the livebearer *Gambusia panuco*) and observed the construction of a major pumping facility on the edge of the main laguna. Such perturbations by man have already affected the aquatic biota of the area which, like the bolsón of Cuatro Ciénegas, is biologically unique and is urgently in need of preservation as a national scientific heritage.

Distributional patterns of Chihuahuan fishes provide evidence of changes in drainage relationships, but the precise geological timing and duration of these shifts are still uncertain.

The failure of such an aggressive fish as *Astyanax mexicanus* to appear in the Guzmán complex supports the view that this genus is a recent (post-Pliocene) invader that arrived after the connection between the upper and lower sections of the Río Grande became established in early Pleistocene times and the Guzmán section had been disrupted, but while the ancestral Río Nazas still reached the through-flowing Río Grande, probably near the Big Bend region. The cyprinid *Dionda episcopa* has very nearly the same distribution as *Astyanax*, with the interesting exception that it also occurs in the upper Río Mezquital, Durango, a former tributary of the Nazas.

Pantosteus or *Catostomus plebeius*, belonging to a phyletic line (*Pantosteus*) largely confined to western United States, gained access to the Chihuahuan Desert region by way of the upper part of the Río Grande (or of connections between what are now the Gila and Mimbres river basins), moving southward from the Guzmán complex presumably by stream captures (see distribution in Smith 1966:Fig. 10). The genus *Gila*, also of western origin, probably moved

into the region similarly, and has since differentiated into a number of taxa (Table 1). One species (*Gila modesta*), now restricted to the headwaters of Río Salinas southeast of Saltillo, plausibly gained access to that stream by a former connection westward with the Nazas basin.

Codoma ornata, present in the Conchos and Nazas basins but not elsewhere in the Chihuahuan Province, also inhabits the upper Río Mezquital, Río Fuerte, and Río Yaqui. It may have evolved in the Nazas basin, suggesting, along with the distribution of *Pantosteus*, that connections between the Nazas and Conchos rivers have allowed fishes to move in both directions.

SURVIVAL AND CONSERVATION

Within the Chihuahuan Desert region we know of one genus, the cyprinid *Stypodon*, and one species, the Parras pupfish *Cyprinodon latifasciatus*, that have been exterminated within the past half century (Miller 1961, 1964). These fishes inhabited the isolated Parras basin of extreme southern Coahuila which, until the 1930s, contained magnificent springs that dwindled when the low mountain south of Parras was tunnelled (Imlay 1936:1097). The only known Chihuahuan population of the northern goodeid, *Characodon lateralis*, also perished there, although the species still survives near Ciudad Durango. The cyprinodontid genus *Megupsilon* (Miller and Walters 1972) is critically endangered by the very recent stocking of largemouth bass in its restricted habitat at Potosí, Nuevo León, and the associated *Cyprinodon* (Miller 1976b) is also threatened. The same spring-fed pond contains an endemic, dwarf crayfish, *Cambarellus alvarezii*.

In that part of the Chihuahuan Desert within the United States, several species are rare and/or endangered. These include the Mexican stoneroller, *Campostoma ornatum*, Devil's River minnow, *Dionda diaboli* (also rare in Mexico), Chichuhua shiner, *Notropis chichuahua*, Prosperine shiner, *Notropis proserpinus*, bluntnose shiner, *Notropis simus* (endangered), Mexican redhorse, *Moxostoma austrinum*, Comanche Springs pupfish, *Cyprinodon elegans* (endangered), Leon Springs pupfish, *Cyprinodon borinus* (endangered), Conchos pupfish, *Cyprinodon eximius*, Big Bend gambusia, *Gambusia gaigei* (endangered), Amistad gambusia, *Gambusia amistadensis* (extinct in nature), and Rio Grande darter, *Etheostoma grahamsi* (rare in México). In México, the Salinas chub, *Gila modesta*, Conchos sucker, *Catostomus conchos*, Mexican blindcat, *Prietella phreatophila* (endangered), Monterrey platyfish, *Xiphophorus couchianus* (endangered), and northern platyfish, *Xiphophorus gordonii*, all need help if they are to survive.

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Endemic Fishes of the Cuatro Ciénegas Basin, Northern Coahuila, Mexico

W. L. MINCKLEY, Arizona State University, Tempe

The basin of Cuatro Ciénegas, Mexico, has been described in considerable detail in a number of publications, and a review of literature on the aquatic and semi-aquatic environments and biota was provided by Minckley (1969). Subsequent work, published and unpublished, continues to emphasize the uniqueness of the overall biota. In fact, the degree of reliction and endemism in such a small area, and the biogeographic implications of some of the living flora and fauna, make this *bol-són* one of the most important areas yet discovered in the Western Hemisphere.

The present paper deals with the fishes of the basin, which although spectacular in their own right, now are far exceeded in importance by a number of invertebrate groups, and tremendously exceeded by diversity and perhaps endemism in higher vascular plants. A number of other papers in the present symposium volume refer specifically to Cuatro Ciénegas, especially those of D. J. Pinkava and E. R. Meyer.

ZOOGEOGRAPHIC RELATIONS OF THE ICHTHYOFAUNA

Intrabasin Distributions

Within the Cuatro Ciénegas basin a number of surficial drainage patterns exist, which apparently were distinct until recently interconnected by man (Minckley 1969). Nevertheless, actual dispersion of the fishes present seems to be dictated more by ecological preferences and/or tolerances. The basin includes all known types of desert aquatic habitats, with the exception of a large, erosive river. In Fig. 1 (from Deacon and Minckley 1974) a breakdown of the various habitats and their fish inhabitants is attempted.

Eight fish families are represented. Four of these, the ictalurids, cyprinids, centrarchids, and percids, are northern and eastern in their affinities. It is notable that species of these families tend to live in larger warm or cool springs and especially in their outflows, with a pattern of

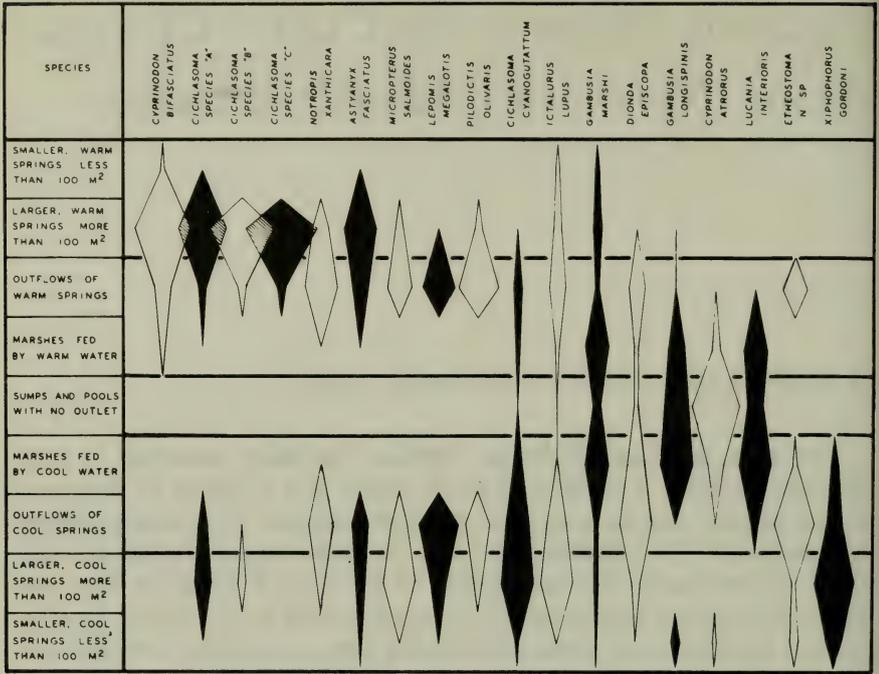
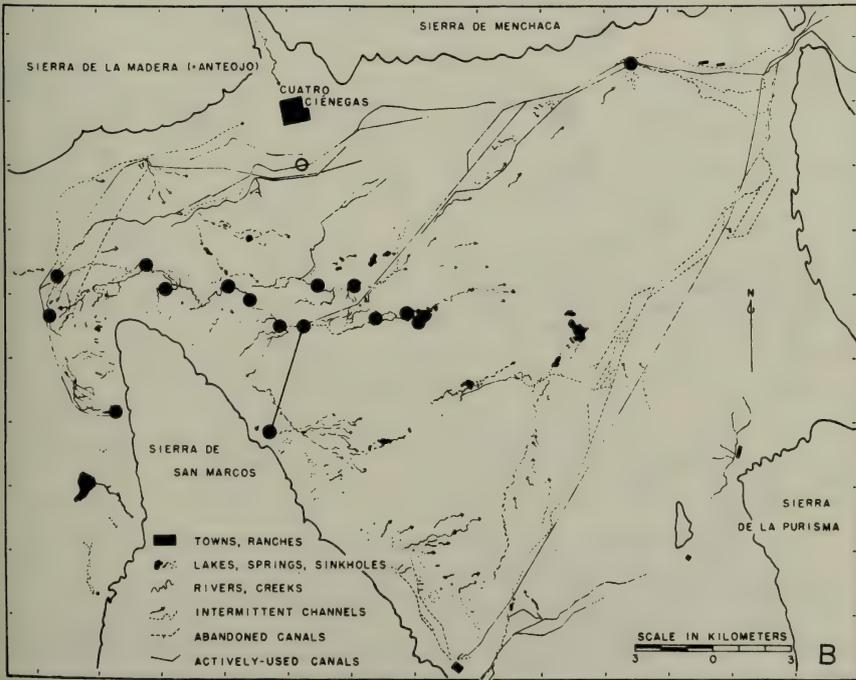
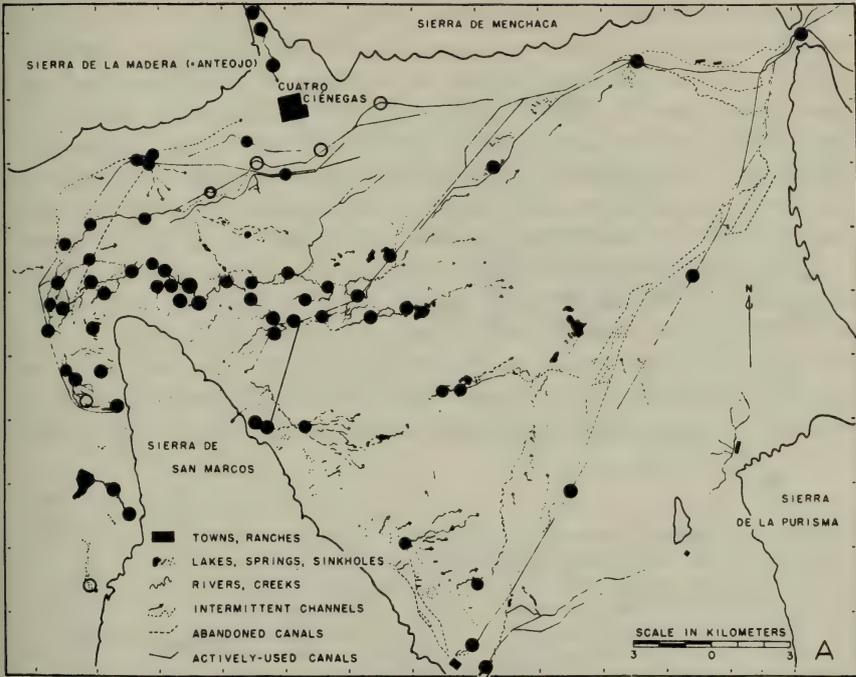


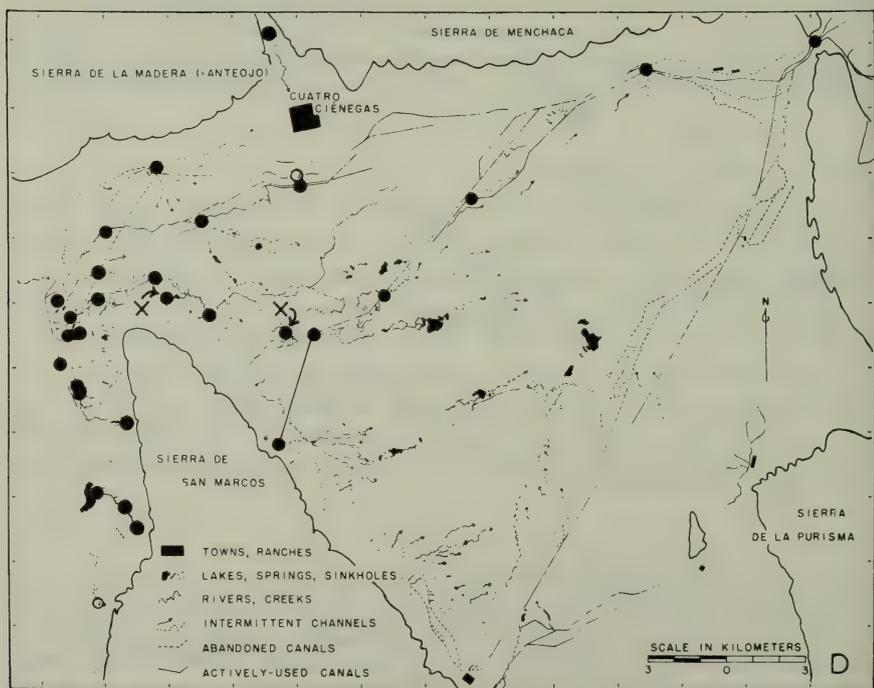
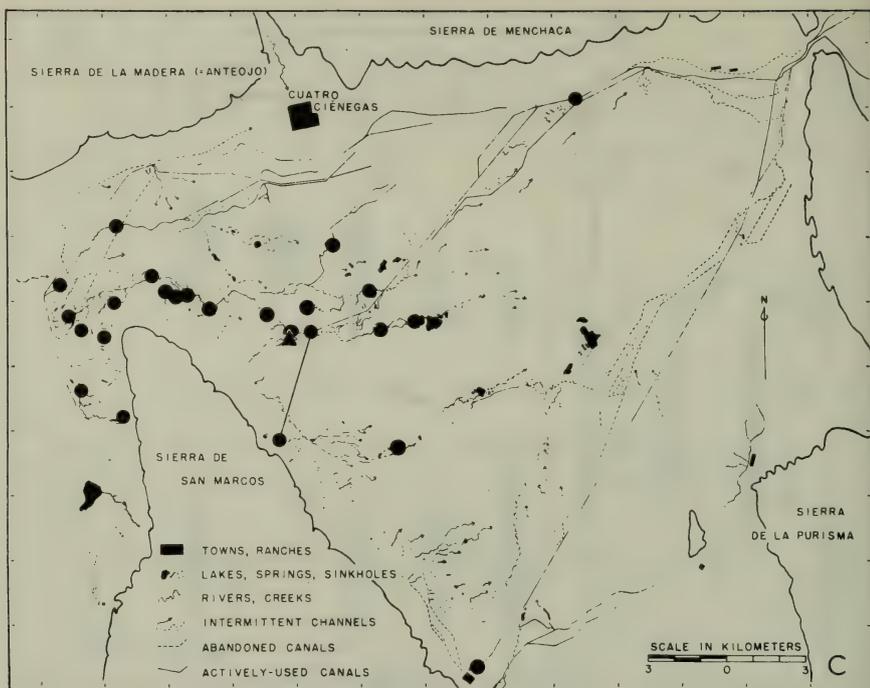
Fig. 1. Generalized habitat preferences and relative abundances of fishes of the Cuatro Ciénegas basin, Coahuila, northern Mexico. No comparisons among species, other than individual species' habitat dispersion relative to those habitats and associated species present, are intended. The two piscivorous cichlid species of the basin are combined as "species C"; see text and Fig. 6 for further explanation.

being more prevalent in the larger, cooler environments (note the genera *Notropis*, *Micropterus*, *Lepomis*, *Pilodictis*, *Ictalurus*, *Dionda*, and *Etheostoma*; Fig. 1). The pattern of these genera living in larger habitats of the basin also is borne out by their spatial distributions (Figs. 2-6).

The remaining four families consist of the cyprinodontids, with their most intimate connections to the coastal fauna of eastern North America and further south, and the characids, poeciliids, and cichlids, with affinities in Middle America and further south. Again, it is notable that the genera with the most southern affinities (*Cichlasoma* and *Astyanax*)

Fig. 2. Distributions of fishes within the Cuatro Ciénegas basin, Coahuila, northern Mexico. A = *Astyanax fasciatus mexicanus*, with open circles indicating extinct populations and dots indicating viable populations. B = *Dionda episcopa* subsp., with symbols as for A. C = *Notropis xanthicara*, symbols as for A except a triangle denotes the type locality. D = *Ictalurus lupus* subsp. and *Pilodictis olivaris*, with symbols the same as for A excepting X denoting points of occurrence of *Pilodictis*. →





tend to favor larger warm springs, while genera with coastal relatives (with two exceptions) are either widespread through various habitats of the basin or occur in marshes or sumps and pools with no outlets (*Gambusia*, *Lucania*, and one *Cyprinodon*; Fig. 1). The two exceptions, *Cyprinodon bifasciatus* Miller and *Xiphophorus gordonii* Miller and Minckley, are thermal endemic and highly noncompetitive, respectively, thus restricting them in general to their indicated habitats and relative abundances (Fig. 1). The spatial distributions of fishes of these last four families also are provided in the array of distribution maps (Figs. 2-6).

Dispersion patterns of fishes in the Cuatro Ciénegas basin present some exceedingly interesting problems, especially in the cyprinodontids, poeciliids, and cichlids. The two pupfishes, *Cyprinodon bifasciatus* and *C. atrorus* Miller, hybridize in areas where they are artificially brought into contact by the construction of interconnecting waterways, and, in

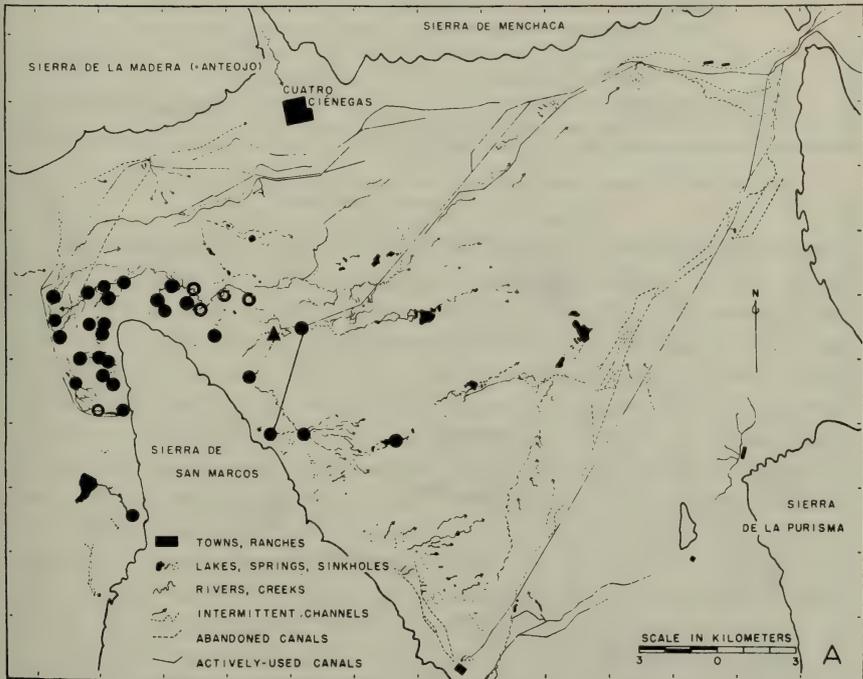
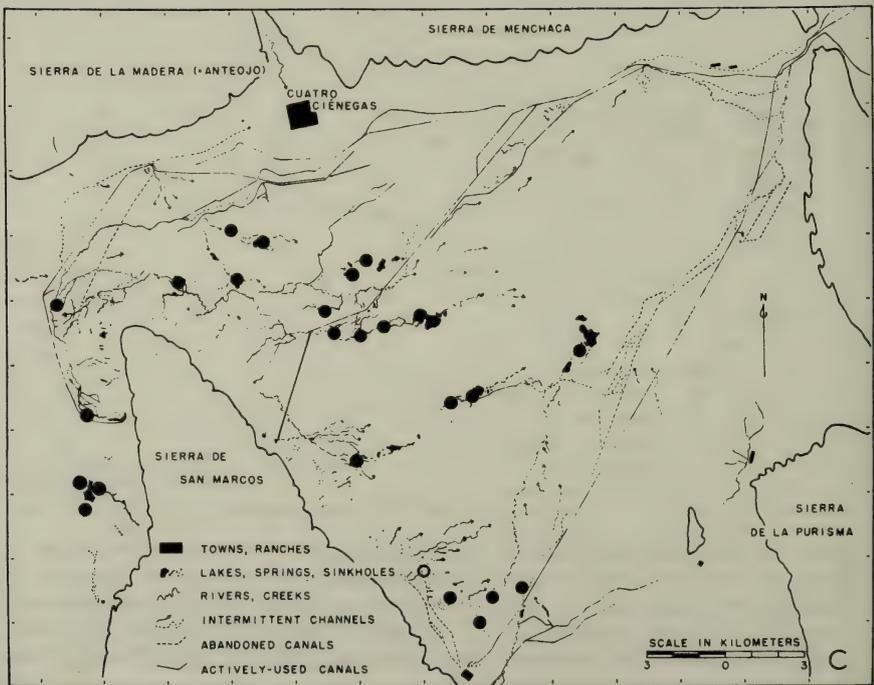
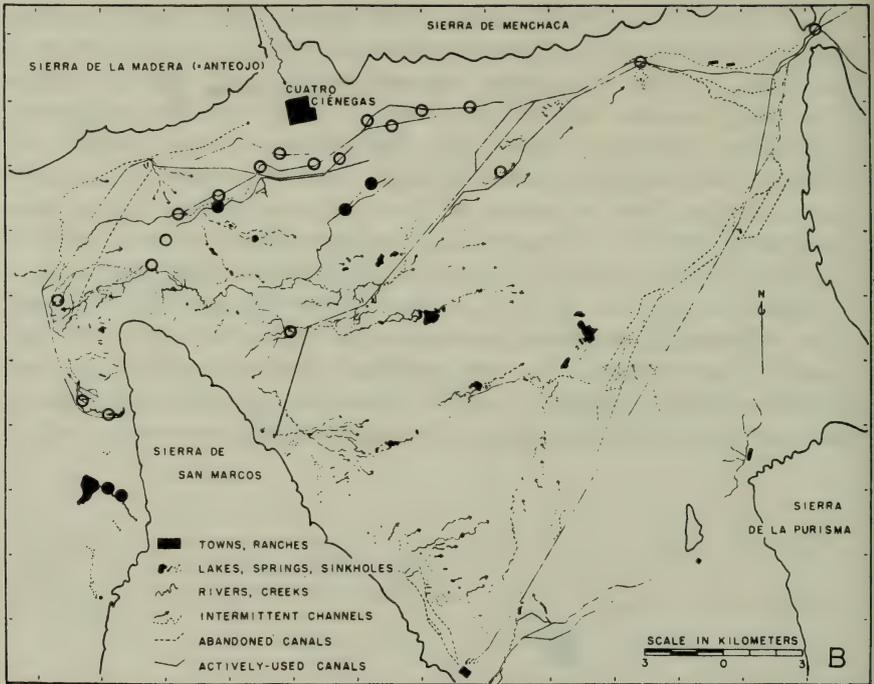
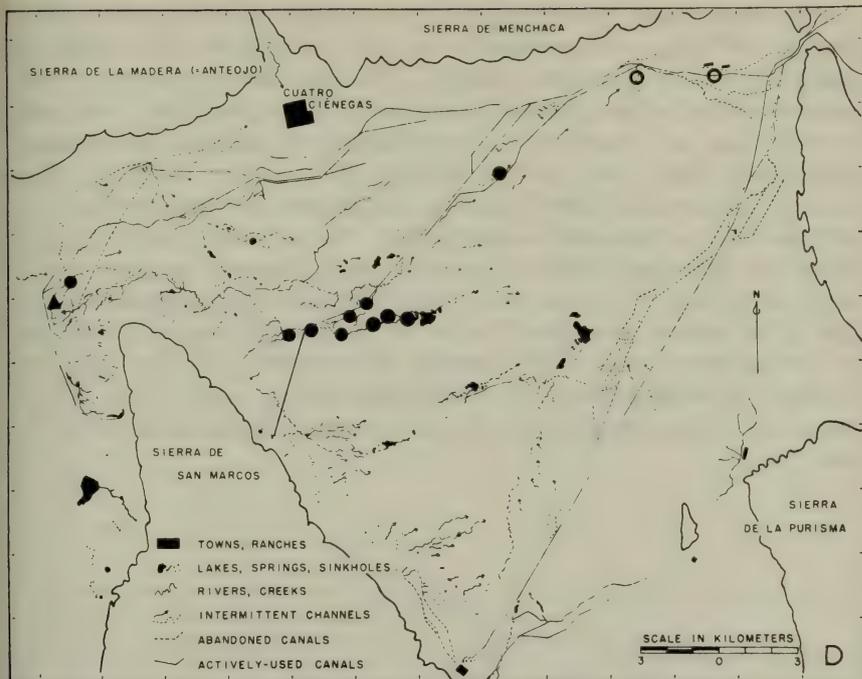


Fig. 3. Distributions of fishes within the Cuatro Ciénegas basin, Coahuila, northern Mexico. A = *Cyprinodon bifasciatus*, with open circles indicating extinct or seasonal (summer) populations, dots indicating viable populations and a triangle denoting the type locality. B = *Cyprinodon bifasciatus* × *C. atrorus* hybrids, with symbols as for A. C = *Cyprinodon atrorus*, with symbols as for A and the type locality not marked, but likely on the of the major canals immediately south of Cuatro Ciénegas. D = *Lucania interioris*, with symbols as for B. →





two instances, under apparently natural situations. Note in Figs. 3A-C that the distribution of *C. bifasciatus* is linked intimately to the tip of Sierra de San Marcos and thermal waters emerging from springs adjacent to bajada slopes of that mountain. Hybrid pupfish have been taken generally outside the arc of thermal springs, on the basin floor, and generally toward (or within) the range of *C. atrorus*. And, *C. atrorus* persists in a relatively pure or pure form on the *barrial*, or basin floor, and into the southeastern lobe where thermal springs are rare or nonexistent. One population referable to *C. bifasciatus*, that indicated by the most easterly dot on Fig. 3A, almost certainly represents an ancient, introgressed, hybrid population (unpublished data). The other natural incident, which has been under scrutiny since 1960, is a population which inhabits an ever-enlarging sink in the Río Churince, the small stream that feeds the large lake to the south and immediately west of Sierra de San Marcos. Until perhaps 1963 few pupfishes of either species were taken from this stream. As the pool enlarged, however, putative hybrids were found, and a major swarm has developed over the years as the pool increased to perhaps a hectare in surface area by 1973. Arnold (1970 and subsequent pers. comm.) has established physico-chemical intermediacy of the waters of this forming habitat, and is studying the development of the hybrid population.

Note that many hybrid populations studied in the period 1960 through 1973 have disappeared (Fig. 3B), principally as a result of changes in man's water-use patterns. Also, the intimate nature of the zone of contact of the parental species makes it highly likely that such hybridization and destruction of intermediate or possible introgressed populations have gone on for millenia in transitory habitats, thus strongly supporting Hubbs' (1955) discussions and explanations for hybridization in fishes and its significance. The referred population of *C. bifasciatus*, discussed before as probably arising through introgression of some genes from *C. atrorus* into a downflow, perhaps marginal population of the former, now lives in a series of deep pits, larger, but similar in configuration to the newly forming pit along the Río Churince. On the basis of aerial photographs and ground survey, water levels in that system are failing rapidly, and the fishes seem doomed in the near future.

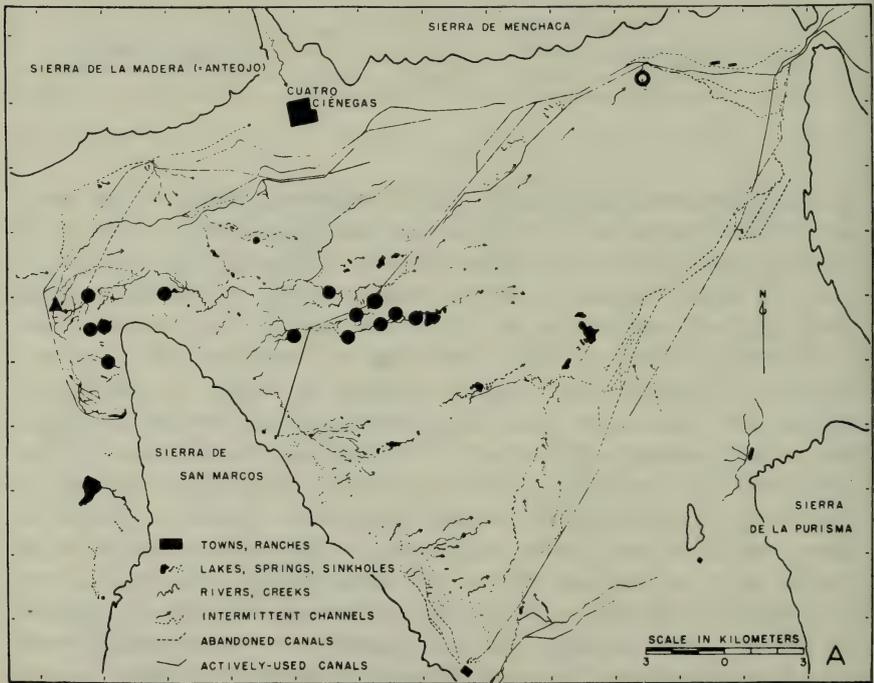
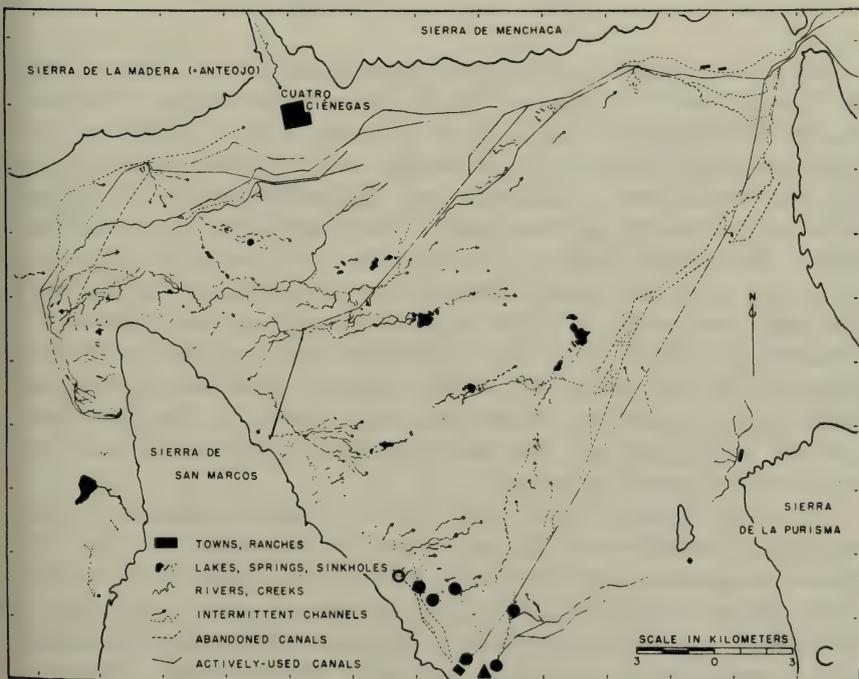
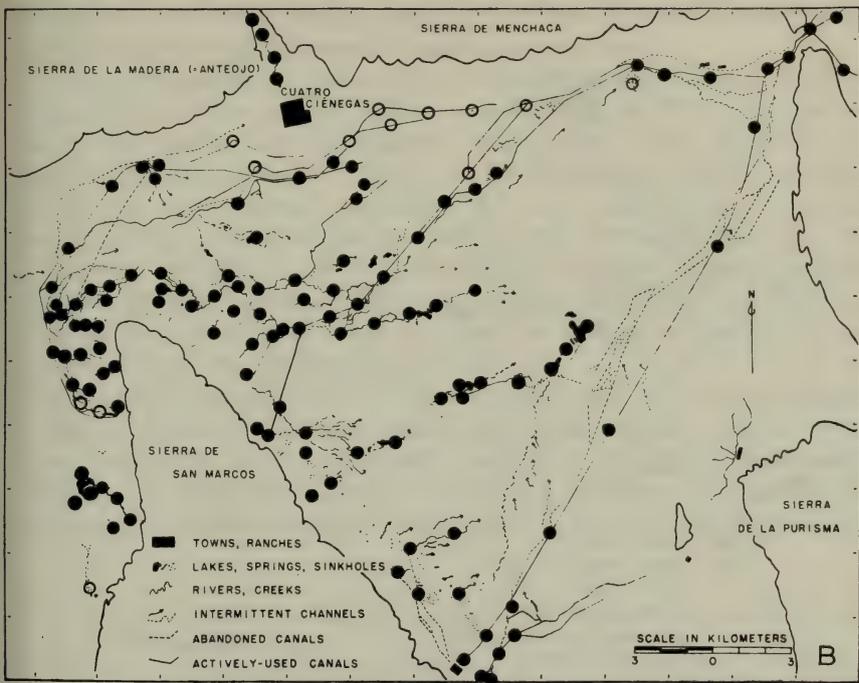
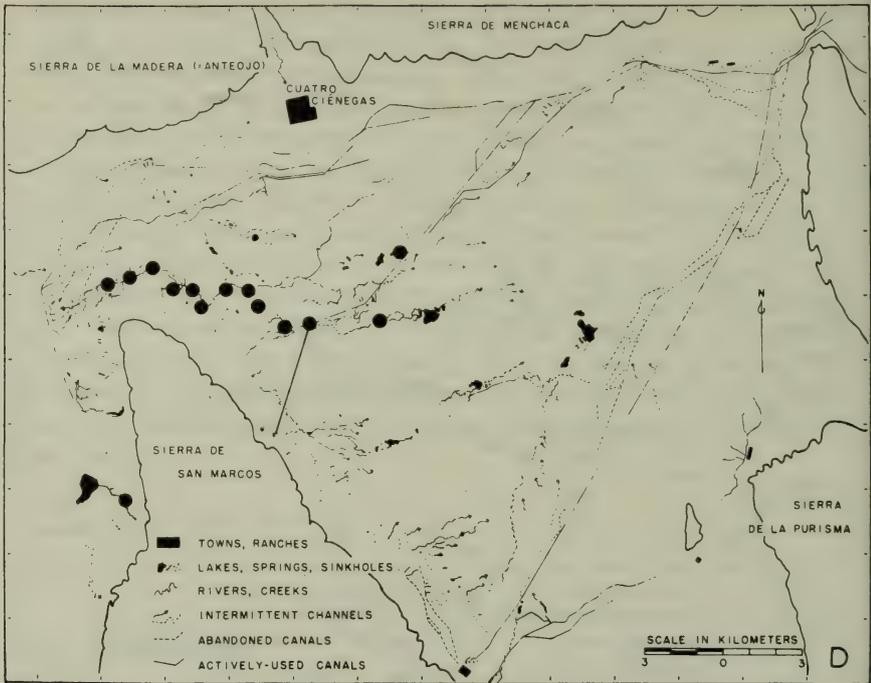


Fig. 4. Distributions of fishes within the Cuatro Ciénegas basin, Coahuila, northern Mexico. A = *Gambusia longispinis*, with open circles indicating extinct populations, dots indicating viable populations (although sometimes seasonal), and a triangle denoting the type locality. B = *Gambusia marshi*, with symbols as for A. C = *Xiphophorus gordonii*, with symbols as for A. D = *Lepomis megalotis* subsp., with symbols as for A. →





Among the poeciliids of the basin, three major points of interest may be brought out. As discussed in the original description, *Gambusia marshi* Minckley and Craddock (in Minckley 1962) persists as two-color phases in Cuatro Ciénegas waters, and elsewhere in its range in the Río Salado basin of Coahuila and adjacent states. A dark-striped form, with distinctly outlined scales, tends to inhabit thermal springs, with a distribution roughly paralleling that of *Cyprinodon bifasciatus* (Fig. 3A). A spotted phase, with very little indication of a lateral band and only weak outlining of the scales with scattered melanophores, is present on the basin floor and in downflow habitats (this last form is dominant in most of the Río Salado system). These two color phases show strong tendencies toward homotypic mating in the laboratory (Arnold 1966), and very few wild populations tend toward what one might call intergrades or hybrids.

A second problem under study is a very obvious allopatry, in the ecological sense, between *G. marshi* and *G. longispinis* Minckley. The former is aggressive and widespread, moving into open water at will and living side-by-side with a number of potential predators. *G. longispinis* is exceedingly secretive and difficult to collect, usually occurring in dense marsh vegetation or in clumps of riparian grasses. Under laboratory

conditions, no forced mating between these two species has ever been accomplished despite repeated attempts (unpubl. data).

The third interesting phenomenon is the geographic allopatry of *G. longispinis* and *Xiphophorus gordonii* (see Figs. 4A and 4C). Females of these two species are superficially very similar, their habitats and general behavior in nature and in the laboratory are almost identical. Males of *Xiphophorus* generally did not discriminate between homospecific and heterospecific females, but the reciprocal, with *G. longispinis*, resulted in total discrimination by males against platyfish females. Perhaps actions of this sort, or some competitive interaction, preclude cohabitation by these two species—one more question to be answered about the fishes of Cuatro Ciénegas.

The most pressing and most complex problem at the intrabasin level in fishes of Cuatro Ciénegas centers about the cichlids. These fishes have been under study by myself, and more recently by LaBounty (1974), and continue to present a perplexing situation. A species-flock of cichlids was first announced as present in the basin by Taylor and

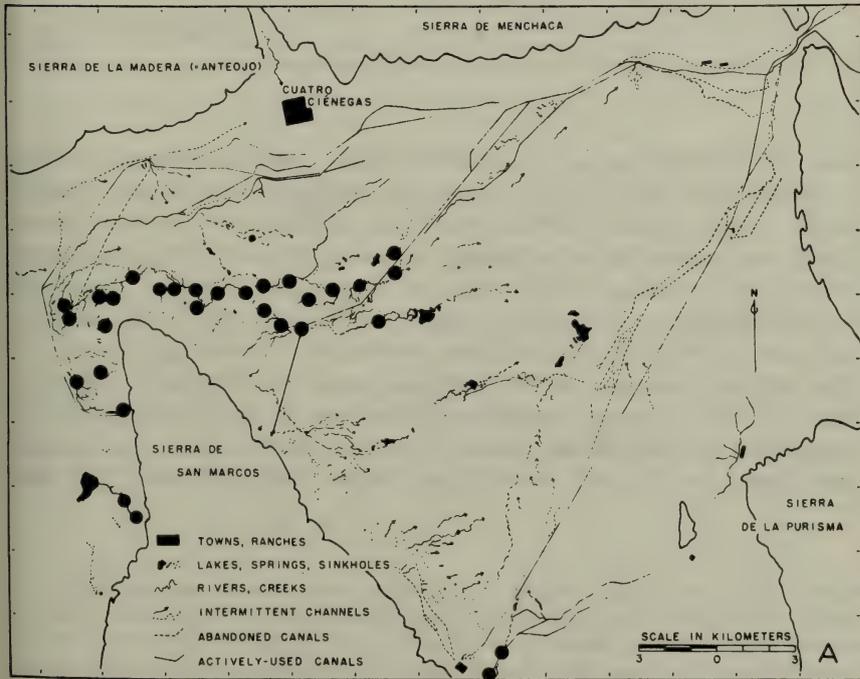
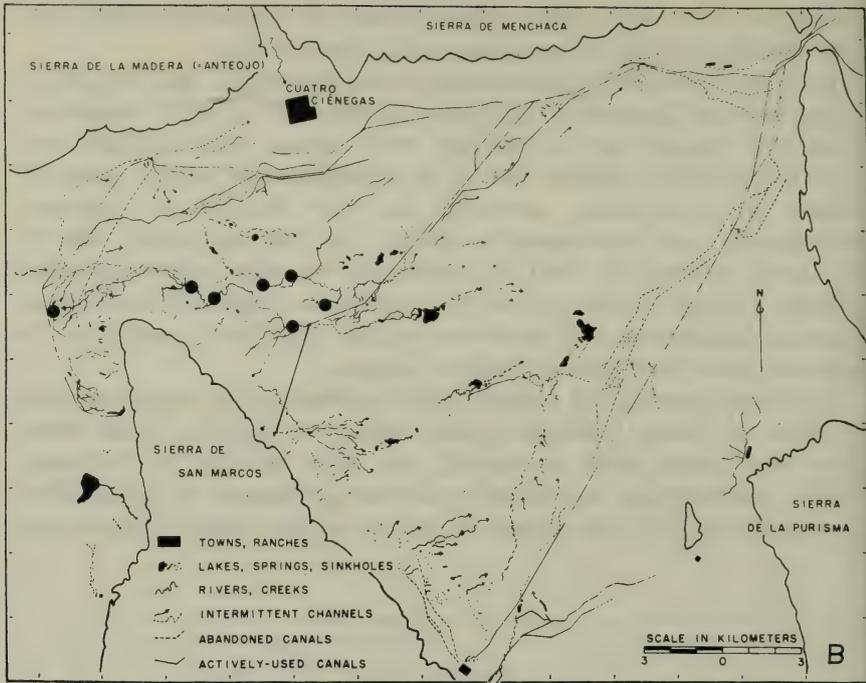
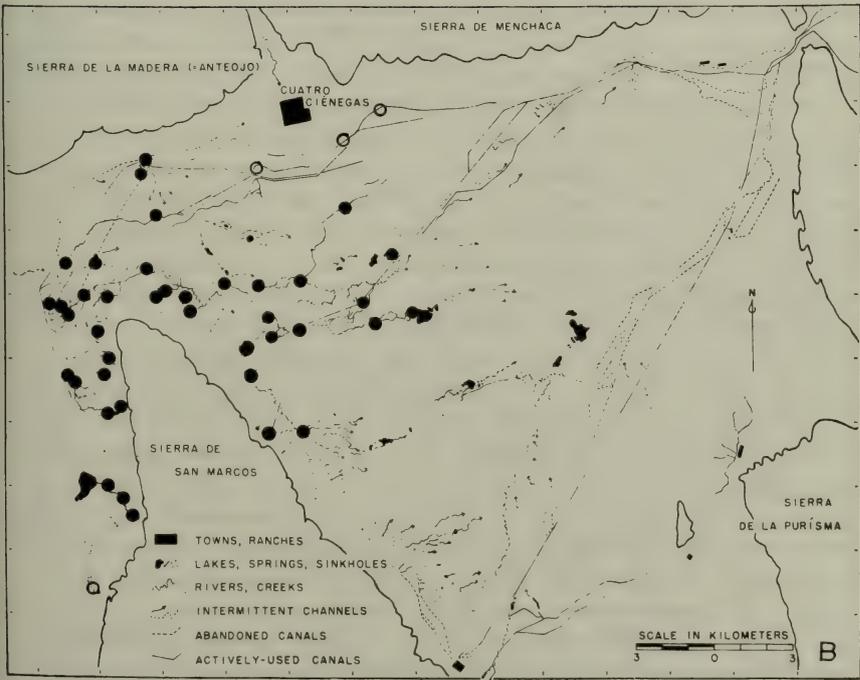
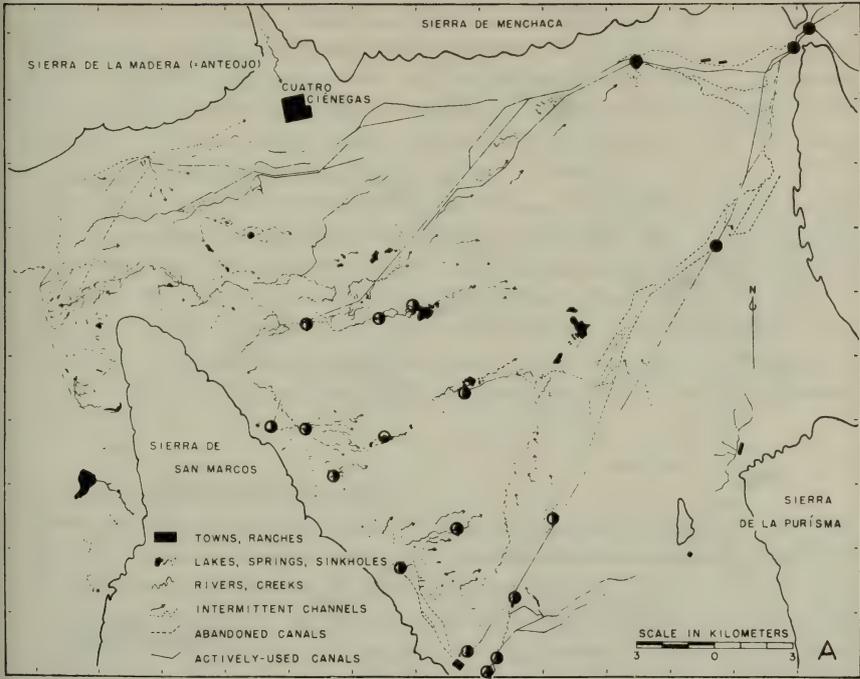


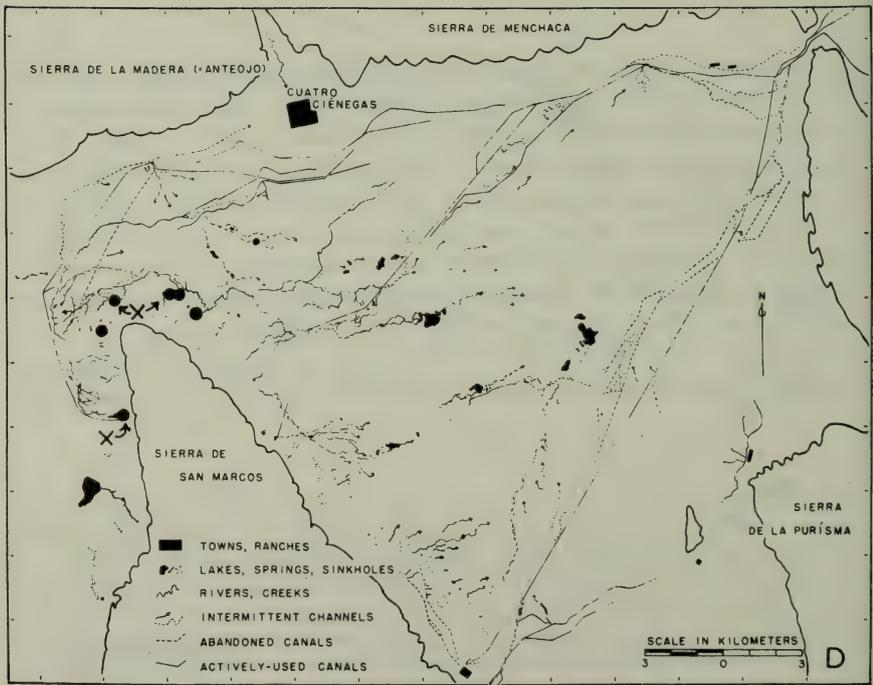
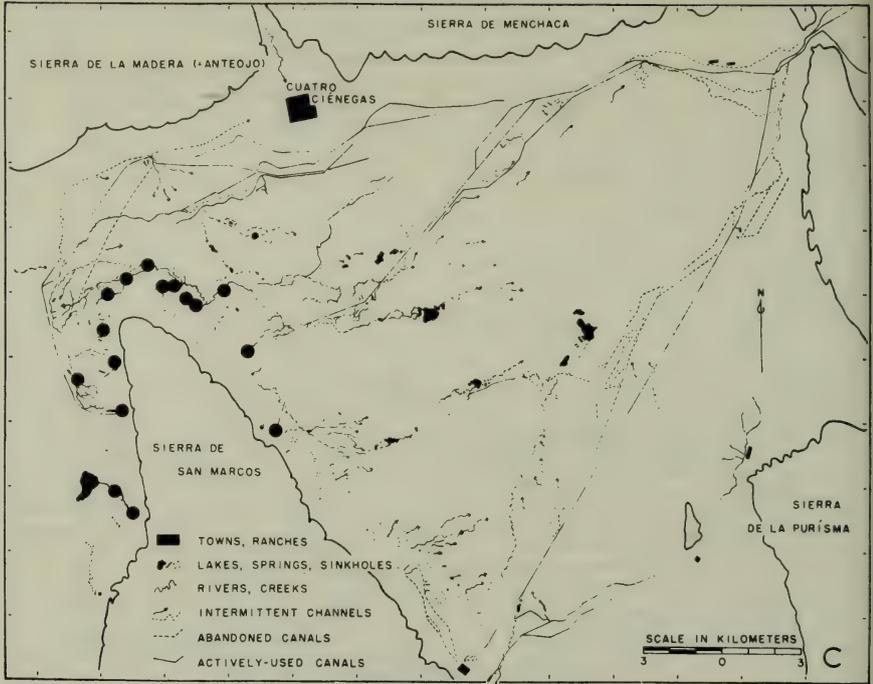
Fig. 5. Distributions of fishes within the Cuatro Ciénegas basin, Coahuila, northern Mexico. A = *Micropterus salmoides* subsp., dots indicating viable populations. B = *Etheostoma* sp., with symbols as for A.



Minckley (1966), consisting of three species—one a detritivore, another a molluscivore, and a third piscivorous. LaBounty, in a more detailed study, found a fourth distinct form and determined that the species-flock was related far more closely to more southern forms (subgenus *Parapetenia* [(Regan 1905)] than to the coastal and Río Grandean cichlids (subgenus *Herichthys* [Baird and Girard 1854]). In addition, LaBounty (1974) determined that two kinds of *Herichthys* inhabit the Río Grande drainage, and that both are present in the Cuatro Ciénegas basin (or that another *Herichthys*, other than the form identified from the middle Río Grande as distinct from *Cichlasoma* [H.] *c. cyanoquttatum* [Baird and Girard], exists in the Cuatro Ciénegas basin). The four

Fig. 6. Distributions of fishes within the Cuatro Ciénegas basin, Coahuila, northern Mexico: A = *Cichlasoma* (*Herichthys*) spp., with dots indicating definite *C. (H.) c. cyanoquttatum*, and half-darkened circles indicating populations where another form of *Cichlasoma* (*Herichthys*) occurs, sympatrically with the former, alone, or perhaps with one of the species of *Cichlasoma* (*Parapetenia*) spp. of the system. B = *Cichlasoma* (*P.*) species A, the detritivorous form, with dots indicating viable populations and open circles for extinct populations. C = *Cichlasoma* (*P.*) species B, the molluscivore, with symbols as for B. D = *Cichlasoma* (*P.*) C and D, with record localities for the last, commonly known as the unexpected cichlid, indicated by an X. Both the last fishes appear to be piscivorous; see text for further explanation. →





kinds of *Parapetenia* are widely sympatric in the basin (Figs. 6B-D), with the detritivore being most widely distributed, the molluscivore being less so, and the two piscivores rare and restricted to headspring situations. There is substantial evidence for recent and progressive invasion of the basin by *C. (H.) c. cyaguttatum*, and for hybridization of that form with the local *Herichthys* as is explained below.

The *Parapetenia* of Cuatro Ciénegas exist as two pair of sibling species, externally indistinguishable between siblings, but distinctly different when the pairs are compared. The same situation obtains for the two kinds of *Herichthys*. With all these fishes, pharyngeal dentition is diagnostic at the specific level, and oral dentition distinguishes the two subgenera. This condition parallels many such situations in groups of African Cichlidae, as reviewed by Fryer and Iles (1972) and Greenwood (1974).

External Zoogeographic Relations

A recapitulation of the status of the various components of the fish fauna of Cuatro Ciénegas and some additional information on levels of differentiation of the various kinds are provided in Table 1. Of the total of 20 kinds known to be present, 15 are differentiated to at least the subspecific level, and 11 are endemic. Only 2 of the 11 endemic species, *Notropis xanthicara* (Minckley and Lytle) and the undescribed *Etheostoma*, have affinities to the north and east, to the middle Rio Grande fauna of Lytle (1972), a fauna derived with few exceptions from the rich Mississippi River biota. Of the remaining nine endemic species, *Xiphophorus gordonii* and the species-flock of four cichlids (subgenus *Parapetenia*) have strong affinities to the south and east, which is substantiated by the presence of *Gambusia marshi*, endemic to the Río Salado system and the northernmost member of the subgenus *Heterophallina* Hubbs (1926). *Lucania interioris* (Hubbs and Miller) and the two *Cyprinodon* may be considered as coastal derivatives, yet the first is highly differentiated and exhibits many primitive traits (Hubbs and Miller 1965). There can be little doubt on the basis of morphology and male breeding coloration that *Cyprinodon atrorus* shows a strong resemblance to certain species related to *C. eximius* Girard (Miller 1968), which hold forth on the Mexican Plateau and in fact in tributary mouths along the Rio Grande as far downstream as the Devil's River, Val Verde County, Texas. (I have not studied the population of pupfishes at the headspring of the Devil's River, and can therefore not evaluate the possible relationship to that form.) It seems safe, however, to assume relationships of *C. atrorus* to the south and east, a connection possibly shared with the undescribed *Etheostoma* (toward *E. pottsi* [Girard] of the central plateau) and the Cuatro Ciénegas form of *Ictiurus lupus* (Girard), notwithstanding their original derivation from the

east. *Cyprinodon bifasciatus* presents somewhat of an enigma. Miller (1968) considered it an ancient derivative of the coastal *C. variegatus* Lacépède, yet stressed its many unique features and its substantial divergence from the general *Cyprinodon* morphology. In many ways *C. bifasciatus* superficially bears strong resemblance to another unique cyprinodont, *Cualac tessellatus* Miller (1956) from La Media Luna, San Luis Potosí, in the Río Panuco Drainage. With the strong affinities of the Cuatro Ciénegas fauna to the southeast, a relationship between *C. bifasciatus* and *Cualac* seems feasible.

TABLE 1. Ichthyofauna of the Cuatro Ciénegas Basin, Coahuila, northern Mexico, with notes on probable evolutionary and geographic relations; see text for literature and for further explanation.

| Taxon ^a | Probable Evolutionary Relationships | Geographic Relationships |
|---|---|---|
| <i>Astyanax fasciatus mexicanus</i> (Fillipi) | <i>A. fasciatus</i> subsp. | South Texas, Mexico, Middle and South America |
| * <i>Notropis xanthicara</i> Minckley and Lytle | "N. proserpinus group" subgenus <i>Cyprinella</i> | Middle Rio Grande Fauna |
| ** <i>Dionda episcopa</i> subsp. | <i>D. episcopa</i> - <i>D. diaboli</i> complex | Middle Rio Grande and northeastern Mexico |
| ** <i>Ictalurus lupus</i> subsp. | "I. lupus group" subgenus <i>Ictalurus</i> | Edwards Plateau, Middle Rio Grande, eastern Mexico and Mexican Plateau |
| <i>Pilodictis olivaris</i> (Rafinesque) | monotypic | Mississippi-Rio Grande mainstream fauna |
| * <i>Lucania interioris</i> Hubbs and Miller | <i>L. parva</i> (Baird and Girard) | Coastal eastern United States and Mexico, Rio Grande (especially Pecos River) |
| * <i>Cyprinodon bifasciatus</i> Miller | <i>C. variegatus</i> subsp. complex (?) and related species | As for <i>L. parva</i> , but including insular Caribbean species |
| * <i>C. atrorus</i> Miller | <i>C. eximius</i> subsp. complex and related species | North Central Mexican Plateau |
| * <i>Gambusia longispinis</i> Minckley | Some species of "G. nobilis group" of Hubbs and Springer subgenus <i>Gambusia</i> | As for <i>I. lupus</i> given above excepting Pacific drainages of Mexican Plateau |
| <i>G. marshi</i> Minckley and Craddock | Subgenus <i>Heterophalina</i> | Principally Río Soto la Marina and Panuco northeastern Mexico |

TABLE 1. (Continued)

| Taxon ^a | Probable Evolutionary Relationships | Geographic Relationships |
|--|---|---|
| * <i>Xiphophorus gordonii</i> Miller and Minckley | <i>X. couchianus</i> (Girard) or possibly <i>X. variatus xiphidium</i> (Gordon) | If the former, Río San Juan, Nuevo Leon, Mexico; if the latter as for <i>G. marshi</i> (part, Río Soto la Marina) |
| ** <i>Lepomis megalotis</i> subsp. | <i>L. megalotis</i> subsp. | Mississippi-Río Grande tributaries and eastward |
| ** <i>Micropterus salmoides</i> subsp. | <i>M. salmoides</i> subsp. | As for <i>L. megalotis</i> |
| * <i>Etheostoma</i> sp. | <i>E. grahami</i> - <i>E. lepidum</i> complex, and <i>E. pottsi</i> (Girard) | As for <i>G. longispinis</i> |
| <i>Cichlasoma (Herichthys) c. cyanoguttatum</i> (Baird and Girard) | <i>C. (H.) cyanoguttatum</i> subsp. | Coastal streams of north-eastern Mexico |
| <i>C. (H.)</i> sp. | <i>C. (H.) c. cyanoguttatum</i> | Middle Río Grande |
| * <i>C. (Parapetenia)</i> sp. "A" "Lugo's cichlid" | <i>C. (P.)</i> sp. unknown | Río Panuco system and south to Middle America |
| * <i>C. (P.)</i> sp. "B" "Caracole cichlid" | " | " |
| * <i>C. (P.)</i> sp. "C" "Longheaded cichlid" | " | " |
| * <i>C. (P.)</i> sp. "D" "Unexpected cichlid" | " | " |

^aThose species marked by a single asterisk (*) are known only from the basin of Cuatro Ciénegas; those marked by double asterisks (**) are differentiated to at least the subspecific level within the basin when compared to material from the Río Salado and its tributaries, into which Cuatro Ciénegas waters now flow as a result of canal connections.

Of the fishes remaining to be discussed, *Astyanax fasciatus mexicanus* (Fillipi) is widespread and quite uniform in its morphology throughout northern Mexico, and material from within the basin is identical to specimens taken from the Río Salado and its tributaries. *Dionda episcopa* (Girard) of the basin is quite distinct from other Río Salado populations, but as pointed out by Hubbs and Ortenburger (1929), Hubbs and Brown (1956), and Minckley (1969), the subspecies of this form are in dire need of definition. Perhaps this will soon be accomplished since I find the formidable team of Hubbs and Miller are actively working with the genus (Hubbs and Miller 1974; C. L. Hubbs pers. comm.). The flathead catfish of Cuatro Ciénegas is known from only two specimens, both young, and from visual observation of three subadults;

the two juveniles appear typical in all respects to specimens of *Pilodictis* from elsewhere. The secretive *Gambusia longispinis*, as noted in Table 1, seems intimately related to certain species of the "*Gambusia nobilis* group" of Hubbs and Springer (1957), especially to *Gambusia gaigei* Hubbs, which occurs in the Big Bend National Park, Texas (Hubbs and Broderick 1963). I reject the suggested relationship between *G. longispinis* and *G. atrora* Rosen and Bailey (1963) despite similarities in the gonopodia of males of the two species. On the basis of morphology of the pectoral fin, *G. atrora* seems far closer to the subgenus *Heterophalina* and occurs too far south to be more than remotely related to species of the Rio Grande gambusiin fauna. The body shape, slimness, and pigmentation of *G. atrora* also are unique, and bear little resemblance to more northern gambusiin fishes.

The sunfishes of Cuatro Ciénegas, *Lepomis megalotis* (Rafinesque) and *Micropterus salmoides* (Lacépède), are distinctive when compared with their counterparts from other parts of the Río Salado system, yet do not appear differentiated to the level of species. There is some evidence that within the last few years (since 1968) some importation of *M. salmoides* may have occurred, and the blackened, elongate largemouth of Cuatro Ciénegas, with an extremely produced lower jaw, has been replaced in some less isolated habitats by a more typical, heavy bodied, differently pigmented form.

The *Cichlasoma* (*Herichthys*) fishes of the Cuatro Ciénegas basin continue to present a major problem. LaBounty (1974) presented various alternative explanations for the situation as follows:

Herichthys is present . . . , some of which are obviously *H. c. cyanoguttatus*, but others which represent one of three alternatives: (1) an undescribed *Herichthys* likely derived from the Texas cichlid (a new form discovered in the middle Rio Grande region) and now in secondary contact and sympatry, or hybridizing, with the Rio Grande cichlid that invaded the basin through canal connection; (2) Rio Grande cichlids participating in miscegenation with caracole cichlids (*C. Parapetenia* sp. "B") to produce a hybrid swarm . . . , or (3) a combination of primary hybridization and some introgression among Texas, Rio Grande, and caracole cichlids.

Figure 6A summarizes the known distribution of these fishes as of 1973. It is apparent that *C. (H.) c. cyanoguttatum* is invading the basin through canal connections, and on the basis of data available to date, it appears that LaBounty's alternative 3 is most acceptable; this problem is still under intensive study.

SUMMARY AND DISCUSSION

Considering degrees of differentiation at the specific and subspecific level, the endemic fish fauna of the Cuatro Ciénegas basin has its affinities strongly weighted toward the south coastal fauna of Mexico. Only two full species endemic to the area are of northern derivation, plus

four forms considered as sharing that affinity which are seemingly differentiated to the subspecific level. Thus, 9 of the 15 endemic forms within the basin, plus *Gambusia marshi*, present in the basin and outside in the Río Salado system, dominate the fauna, and all are differentiated to the specific level. Multiple invasions of the area obviously have occurred, as pointed out by Minckley (1969) and others. The highly differentiated *Cyprinodon bifasciatus*, *Gambusia marshi*, and the likely autochthonous species-flock of cichlids (*Cichlasoma* [*Parapetenia*] spp.) perhaps represent an ancient component of the extant fauna. Also included here may be *Xiphophorus gordonii*, if its true relationships are nearer *X. variatus xiphidium* (Gordon) rather than *X. couchianus* (Girard); (see Miller and Minckley 1963; for a review of the groups see Rosen 1960; and for opposing views see Rosen and Bailey 1963). A secondary invasion may be represented by some of the species related to the middle Rio Grande fauna, such as *Notropis xanthicara*, *Ictalurus lupus*, *Gambusia longispinis*, the undescribed *Etheostoma*, and perhaps the undescribed form of the subgenus *Herichthys*, genus *Cichlasoma*. *Lucania interioris* might be quite ancient in derivation, or secondary in its differentiation within the system. It is difficult to speculate upon the origins of *Dionda episcopa* subsp., *Cyprinodon atorus*, and (as noted in Table 1) even perhaps upon the *Etheostoma*, *G. longispinis*, and *I. lupus*. All these animals have relatives or share numerous morphological features with species of the north central Mexican Plateau, and may well represent derivatives of another movement of fishes from the west into the area. The sunfishes, *Micropterus* and *Lepomis*, must have moved to Cuatro Ciénegas basin relatively late, and *Cichlasoma c. cyanoguttatum* is known to be a recent invader. The times of origin of the local populations of *Astyanax f. mexicanus* and *Pilodictis olivaris* (Rafinesque) are indiscernible at present.

I am fully aware of the dangers in interpretation of invasions, or times of reliction and differentiation, based upon the degrees of differences among families, genera, species, or even subspecies. In fact, I propose that this concept has been misused by ichthyologists and others and firmly believe that a given isolate need not differentiate morphologically, physiologically, biochemically, or any other way if selective pressures remain commensurate with the population's genetic capabilities. However, overwhelming evidence exists that the concept may be applied when one considers the overall biota of Cuatro Ciénegas, for example, with the invertebrates as mentioned in the introduction. Holsinger and Minckley (1971) summarized the numbers of families, genera, and known species of these groups and provided the approximate percentages of endemism of some categories. The breakdown for crustaceans and mollusks is as follows (percentages are in parentheses): Crustacea—7, 8(50), and 10(60); Mollusca—7, 22(27), and 34(50)

(families, genera, and species, respectively). As with the fishes, species of these two groups of invertebrates show highly varied regional affinities, ranging from the widespread amphipod *Hyaella azteca* (Suassure), which occurs essentially throughout North and Middle America, to *Mexistenasellus coahuila* (Cole and Minckley 1972), which represented at the time of its discovery the first record of the family Stenasellidae in the Western Hemisphere. The identical situation exists in molluscs, with the aquatic species of the basin ranging from widespread, common forms, through endemic subfamilies. Antiquity of the molluscan fauna of the region, corresponding to that of crustacea has been further bolstered by discovery of a "tertiary gastropod" living in Texas (Taylor 1974a,b). There are suggestions that the origins of portions of this unique assemblage are from totally different lines of gastropod evolution than others, and, further, that these different lines exhibit convergent evolution. However, some genera (along with some other molluscs of Texas) have their closest apparent relationships to animals of the peri-Mediterranean region (Taylor 1966, in Holsinger and Minckley 1971, and pers. comm.). Recent work in the Cuatro Ciénegas basin has revealed several additional molluscan species seemingly restricted to the basin (J. J. Landye pers. comm.). Summaries of some of the zoogeographic implications of the invertebrate fauna of the region are provided by Bowman (1964), Taylor (1966), Holsinger and Peck (1968), Staroboytsov (1970), Holsinger and Minckley (1971), Cole and Minckley (1972), Magniez (1972), and Argano (1973).

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Speciation Aspects and Man-Made Community Composition Changes in Chihuahuan Desert Fishes

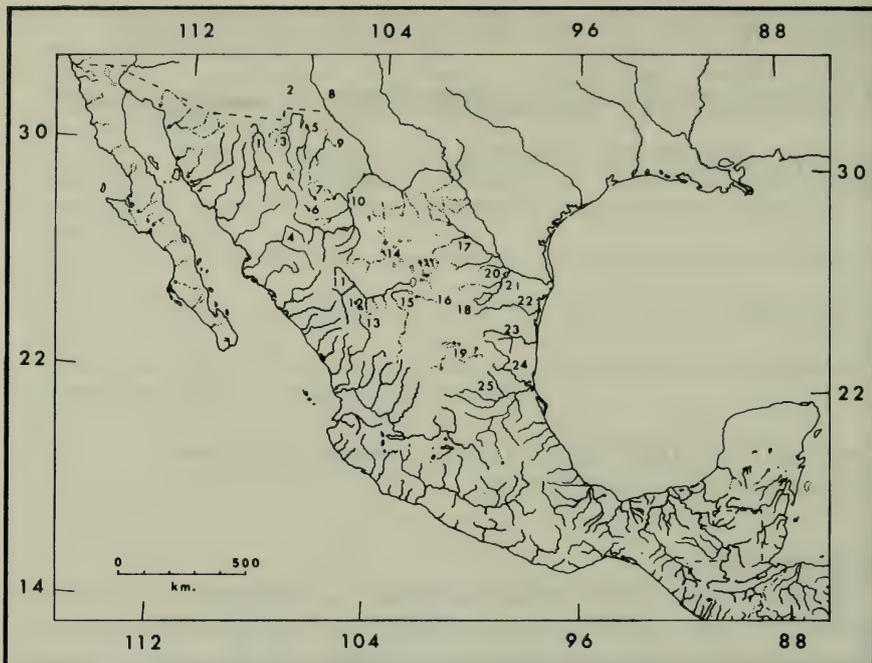
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INTRODUCTION

The fish fauna of the Chihuahuan Desert is composed of 107 native species, according to Miller (this volume), and is of Northern origin for the most part, as demonstrated by the presence of the same or closely related species. This fauna includes the fishes of most interior drainages that once were part of the Rio Bravo (Meek 1903, 1904; Tafall 1946 cited by Tamayo 1962). These interior drainages are the rivers Mimbres, Casas Grandes, Santa María, Carmen, Nazas, Aguanaval, Palomas, Parras, Illescas-Moctezuma, and Hediondilla that lie entirely or mostly within the Chihuahuan Desert; other related interior drainages are the Lagunas Encinillas (=Sauz), Bustillos, and Santiaguillo (Map 1).

SPECIATION ASPECTS

The Chihuahuan isolated basins have an impoverished fauna, usually composed of from one-half to one-fourth the number of fish species found in similar but exterior rivers that have an outlet to the sea or are parts of major drainages. This is demonstrated in Fig. 1, where correlations are found between basin surfaces and species number, also demonstrable for number of genera and families. Similar correlations of area/species number have been studied in plants of the California islands (Johnson et al. 1968), British Isles (Johnson and Raven 1970; Johnson and Simberloff unpubl. data), Galápagos Archipelago (Johnson and Raven 1973), and in fishes of world lakes (Barbour and Brown 1974), either with emphasis on endemics or total species. Such fish-species number is probably a function of habitat diversity, higher in large rivers, although this relation might be modified by the diversity of the regions traversed by the rivers, such as in the Rfo Salado (66,050 km²,



Map 1. Basins mentioned in the text: 1. Río Yaqui, 2. Río Mimbres, 3. Río Casas Grandes, 4. Río del Fuerte, 5. Río Santa María, 6. Laguna Bustillos, 7. Encinillas, 8. Upper Rio Grande, 9. Río Carmen, 10. Río Conchos, 11. Río Nazas, 12. Laguna Santiaguillo, 13. Río Mezquital, 14. Río Cadena, 15. Río Aguanaval, 16. Parras, 17. Río Salado, 18. Hediondilla, 19. Moctezuma-Illescas, 20. Río Alamo, 21. Río San Juan, 22. Río San Fernando, 23. Río Soto la Marina, 24. Río Tamesí, 25. Río Pánuco.

35 spp.) and the Río Pánuco (66,300 km², 43 spp.). Also correlated to the basin area is the number of endemic species, negatively for the smaller basins and changing to positive correlation as the streams get larger, forming a U-shaped line; exterior drainages show positive correlation between size and endemic species number. The high endemism of interior drainages is demonstrable at the species or forms levels, the latter including the sum of species and subspecies and their respective percentages.

Endemic genera are known from very small drainages or springs, probably due to divergence through genetic drift. If a score of endemic points is made, with 3 for genera, 2 for species, and 1 for subspecies, the result is another U-shaped line. The raw data of this correlation appear in Table 1. The endemic genera referred to are: a *Cyprinodon*-like form from Baños de San Diego, Chihuahua (Minckley pers. comm.); *Stypodon* Garman (1881) from Parras, Coahuila; *Megupsilon* Miller and

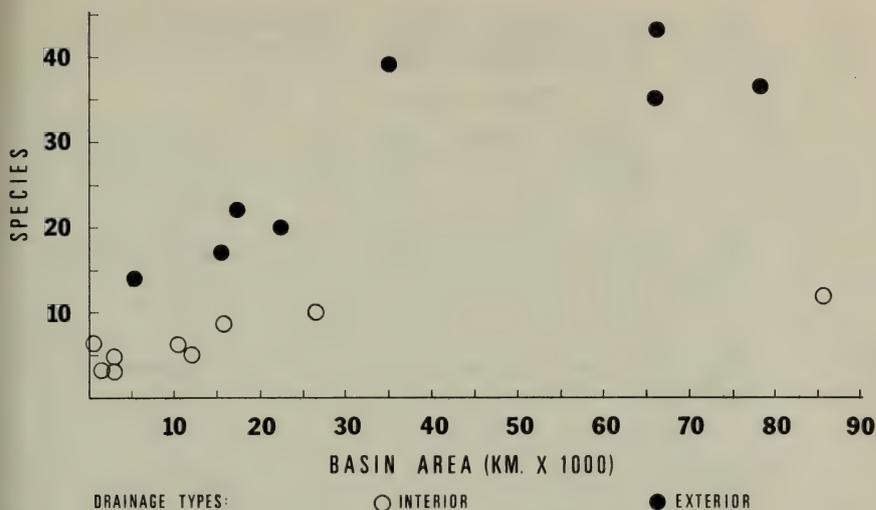


Fig. 1. Correlation diagram of basin area and species number for interior and exterior drainages of the Chihuahuan Desert.

Walters (1972) from Potosí or Hediondilla, Nuevo León; *Xenophorus* Hubbs and Turner (1939) from the Illescas-Moctezuma area, San Luis Potosí; *Cualac* Miller (1956) and *Ataeniobius* Hubbs and Turner (1939) both from La Media Luna-Río Verde region, San Luis Potosí (Map 2). They are distinctive forms from springs or basins that are small, old, or both.

The infraspecific variation in Chihuahuan Desert fishes is not well known, except for a few detailed studies, mostly unpublished. One of them is the case of *Notropis lutrensis sensu lato*, with interesting geographic variation, exemplified by lateral-line scale count (Table 2). There are several of its subspecies and races in almost all of the former Río Bravo streams, its characters varying widely (Map 3). Percent divergence between the means for 13 characters in 13 populations has been studied, considering the Río San Juan race as the value 0 or as the nearest to the ancestral stock. The mean divergence for races of the Samalayuca complex (Casas Grandes, Carmen, North and South Yaqui, and Saúz, but not the Santa María) is from 42.4 to 83.8%. They share eight anal rays, greenish and yellow breeding males, small breeding tubercles, and high scale counts. The Santa María form, *N. l. santamariae*, diverges 51.0%, and is distinguished by its all-yellow breeding males. The Nazas-Aguanaval races, *N. l. garmani*, diverge 46.2%. The Conchos undescribed subspecies has diverged relatively little, 26.4%. Finally, the Upper Rio Grande and the Pecos races are the least divergent, with 13.0

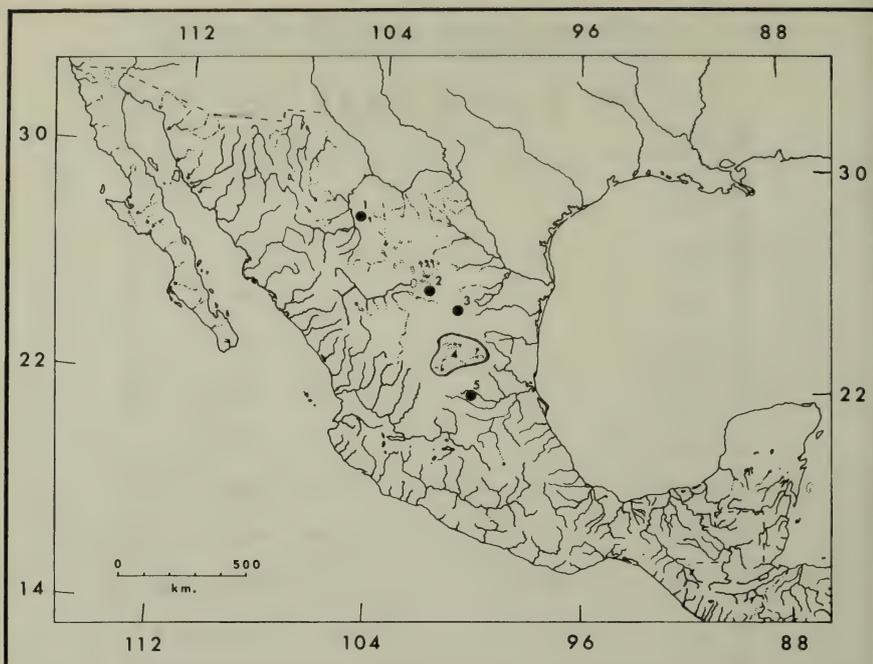
TABLE 1. Correlation between drainage surface, fish richness, and endemism at Chihuahuan and non-Chihuahuan basins.

| Type Basin | Surface km ² | Fish Fauna | | | | | | Endemism | | | | |
|----------------------|----------------------------|------------|------|----------|------|--------------|---------------|------------|-------|-------|--|--|
| | | Total | | Endemics | | Forms (1) | Points (2) | Percentage | | | | |
| | | Fam. | Gen. | Fam. | Gen. | | | spp. | Forms | | | |
| Springs | | | | | | | | | | | | |
| Hediondilla (Potosi) | 5.5 | 1 | 2 | 1 | 2 | - | 2 | 7 | 100.0 | 100.0 | | |
| Media Luna | 50 | 6 | 10 | 2 | 6 | 1 | 7 | 19 | 60.0 | 70.0 | | |
| Cuatro Ciénegas | 600 | 8 | 13 | - | 9 | 4? | 13 | 22 | 50.0 | 72.2 | | |
| Interior | | | | | | | | | | | | |
| Parras | 400 | 4 | 6 | 1 | 5 | 1 | 6 | 14 | 71.4 | 85.7 | | |
| Santiagoillo | 1790 | 3 | 3 | - | 2 | - | 2 | 4 | 66.6 | 66.6 | | |
| Encinillas (Sauz) | 2700 | 4 | 5 | - | 2 | 2 | 4 | 6 | 40.0 | 80.0 | | |
| Bustillos | 2720 | 2 | 3 | - | - | 2 | 2 | 2 | 0 | 66.6 | | |
| Santa Maria | 10680 | 3 | 6 | - | 1 | 3 | 4 | 5 | 16.6 | 66.6 | | |
| Carmen (Patos) | 11880 | 3 | 5 | - | 1 | 1 | 2 | 3 | 20.0 | 40.0 | | |
| Casas Grandes | 16600 | 4 | 8 | - | 2 | 1 | 3 | 5 | 25.0 | 37.5 | | |
| Aguanaval | 26560 | 5 | 7 | - | 4 | 2 | 6 | 10 | 40.0 | 60.0 | | |
| Nazas | 85530 | 6 | 9 | - | 3 | 5 | 8 | 11 | 25.0 | 66.6 | | |
| Exterior | | | | | | | | | | | | |
| Alamo | 4381 | 10 | 12 | - | - | - | - | - | 0 | 0 | | |
| San Fernando | 15640 | 9 | 13 | - | - | 1 | 1 | 1 | 0 | 5.9 | | |
| Tamesi | 17690 | 9 | 14 | - | 1 | 4 | 5 | 6 | 4.3 | 21.7 | | |
| Soto la Marina | 22600 | 14 | 16 | - | 1 | 4 | 5 | 6 | 5.0 | 25.0 | | |
| San Juan | 35226 | 12 | 25 | - | 2 | 2 | 4 | 6 | 5.1 | 10.3 | | |
| Salado | 66050 | 11 | 20 | - | 2 | 2 | 4 | 6 | 8.8 | 11.4 | | |
| Panuco | 66300 | 16 | 23 | 1 | 10 | 7 | 17 | 27 | 23.3 | 39.5 | | |
| Conchos | 77090 | 10 | 23 | 1? | 9 | 6 | 15 | 26 | 25.0 | 41.7 | | |

(1) Sum of species and subspecies. (2) Values: genus 3, species 2, subspecies 1.

TABLE 2. Frequency distribution of lateral line scales in subspecies and races of *Notropis lutrensis* from the Rio Grande basin and range.

| ssp. or race; river | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | n | x |
|----------------------------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|-----|------|
| <i>forlonensis</i> ; Pánuco | 1 | | 1 | 5 | 20 | 56 | 61 | 8 | 2 | | | | | | | | | | | | 154 | 33.3 |
| intergrades; Soto la M. | | | | 1 | 11 | 22 | 5 | 1 | | | | | | | | | | | | | 40 | 32.8 |
| <i>lutrensis</i> : | | | | | | | | | | | | | | | | | | | | | | |
| San Fernando | | | 1 | 2 | 8 | 31 | 56 | 37 | 24 | 8 | 2 | | | | | | | | | | 169 | 34.1 |
| Rio Grande | | | | | | | | | | | | | | | | | | | | | | |
| San Juan | | 2 | 2 | 2 | 9 | 22 | 40 | 6 | | | | | | | | | | | | | 81 | 33.2 |
| NE Coahuila | | | 2 | 6 | 13 | 18 | 8 | 1 | | | | | | | | | | | | | 48 | 33.3 |
| Pecos | | | | 9 | 22 | 26 | 6 | 1 | | | | | | | | | | | | | 64 | 33.3 |
| Big Bend | | | | | | | 3 | 4 | | | | | | | | | | | | | 7 | |
| Upper Rio Grande | | | | 1 | 5 | 20 | 19 | 7 | 1 | | | | | | | | | | | | 53 | 34.3 |
| ssp.; Conchos | | | | 4 | 21 | 34 | 25 | 14 | 1 | | | | | | | | | | | | 115 | 34.1 |
| <i>garrmani</i> ; Nazas | | | | 2 | 9 | 49 | 34 | 25 | 11 | 3 | 1 | | | | | | | | | | 134 | 35.8 |
| ssp.; Encinillas | | | | | | | 3 | 8 | 4 | 11 | 9 | 7 | 3 | 2 | 2 | 1 | | | | | 50 | 38.3 |
| <i>formosus</i> : | | | | | | | | | | | | | | | | | | | | | | |
| Carmen | | | | | | | 1 | 16 | 11 | 9 | 6 | 3 | | | | | | | | | 53 | 36.9 |
| Casas Grandes | | | | | | | 4 | 6 | 9 | 10 | 14 | 14 | 10 | 10 | 12 | 6 | 2 | 3 | 3 | | 103 | 40.1 |
| North Yaqui | | | | | | | 3 | 9 | 10 | 10 | 6 | 4 | 5 | 2 | 1 | | | | | | 50 | 38.0 |
| South Yaqui | | | | | | | 4 | 8 | 12 | 5 | 1 | | | | | | | | | | 30 | 35.5 |
| <i>santamariae</i> ; Santa María | | | | | | | 11 | 36 | 48 | 30 | 20 | 6 | 3 | | | | | | | 1 | 158 | 36.1 |

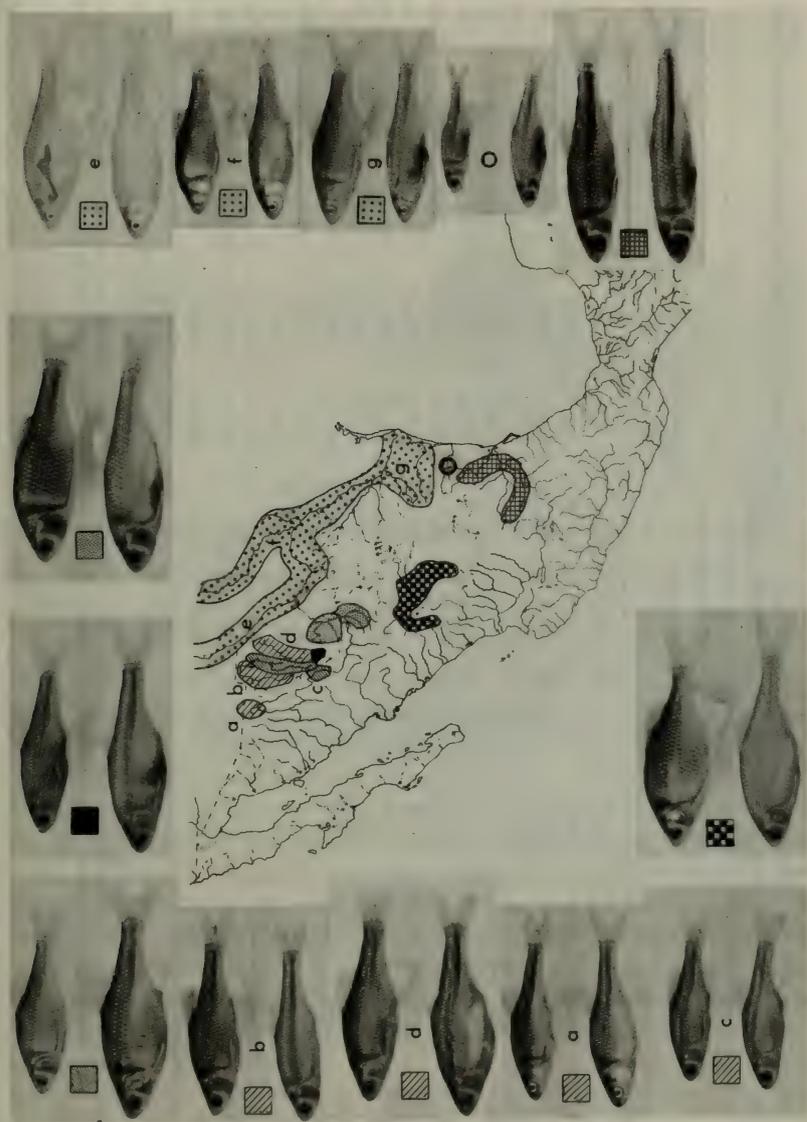


Map 2. Localities of the Chihuahuan Desert with endemic fish genera and their survival status: 1. *Cyprinodon*-like sp., undescribed, San Diego, Chihuahua; 2. *Stypodon*, Parras, extinct; 3. *Megupsilon*, Hediondilla, endangered; 4. *Xenophorus*, Illescas-Moctezuma; 5. *Cualac* and *Ataeniobius*, La Media Luna, endangered.

and 10.2%, respectively. The character matrix of the data given appears in Table 3.

If we assume such values are a function of time, and represent a level of separation from the main river, then the Upper Rio Grande and Pecos races are the most recent and keep their link to the main populations downstream. The Conchos form differs little more, inhabiting a sub-basin intermittently connected to the main Rio Bravo, a condition that allows divergence to arise, but not to proceed too far, subject to the mobility of the species. Next and older, comes the Nazas-Aguanaval complex, and the oldest is the Samalayuca complex. Thus, the desert advance in Mexico is from north and west to south and east. The former connections of the basins, flow direction, and desert advance appear on Map 4. Species-groups that seem worth studying to test this scheme are the *Gila nigrescens* complex and the *Cyprinodon eximius* complex, widely represented in the region.

Another case studied that points to a complementary scheme of stream captures, rather than former river connections, is *Codoma or-*

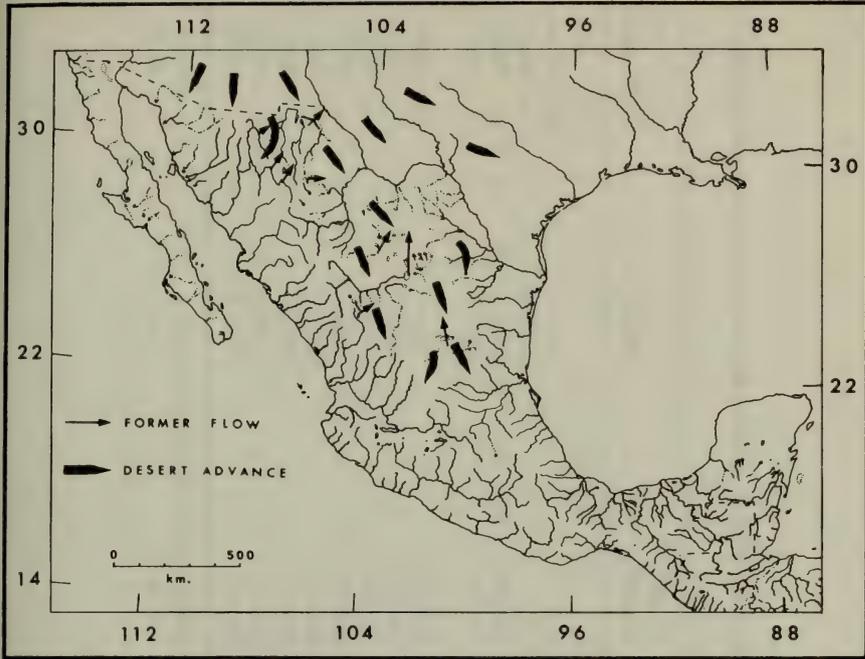


Map 3. *Notropis lutrensis* ssp. and races in the Rio Bravo Basin and Range, showing physiognomy and distribution.

TABLE 3. Character matrix of percentage divergence between means of different populations from the presumed ancestral stock in *Notropis luteus* from the Rio Grande basin and range to the Rio Panuco, Mexico: Meristics.

| | Populations | | | | | | | | | | | | |
|-----------|-------------|-------|-------|-------|-------|-------|-------|-------|-------|--------|-------|-------|-------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
| A | 0 | 0 | 0 | 0 | 0 | 0 | 100.0 | 0 | 0 | 0 | 0 | 0 | 0 |
| B | 9.1 | 0 | 9.1 | 18.2 | 0 | 9.1 | 100.0 | 90.9 | 63.6 | 72.7 | 90.9 | 90.9 | 81.8 |
| C | 0 | 54.0 | 20.0 | 0 | 13.3 | 46.7 | 66.7 | 13.3 | 54.0 | 100.0 | 80.2 | 46.7 | 73.4 |
| D | 100.0 | 66.7 | 33.3 | 66.7 | 33.3 | 66.7 | 66.7 | 33.3 | 0 | 66.7 | 0 | 66.7 | 66.7 |
| E | 1.5 | 7.3 | 13.1 | 1.5 | 1.5 | 13.1 | 37.7 | 74.0 | 53.7 | 100.0 | 69.6 | 33.4 | 42.1 |
| F | 1.5 | 1.5 | 16.2 | 4.4 | 11.8 | 30.9 | 66.2 | 76.4 | 45.6 | 100.0 | 41.2 | 36.8 | 39.7 |
| G | 15.8 | 11.9 | 14.9 | 0 | 14.9 | 28.5 | 33.7 | 59.4 | 55.4 | 100.0 | 39.6 | 45.5 | 45.5 |
| H | 21.4 | 16.7 | 14.3 | 2.4 | 19.0 | 26.2 | 40.5 | 57.1 | 71.4 | 100.0 | 52.4 | 28.6 | 42.8 |
| I | 11.6 | 6.7 | 15.0 | 6.7 | 11.6 | 30.7 | 32.4 | 73.5 | 43.4 | 100.0 | 31.7 | 58.4 | 47.4 |
| J | 21.1 | 21.1 | 9.6 | 13.4 | 21.1 | 28.8 | 17.3 | 67.2 | 46.1 | 100.0 | 32.6 | 36.5 | 38.4 |
| K | 16.7 | 20.9 | 8.3 | 4.2 | 20.9 | 25.0 | 16.7 | 62.6 | 41.7 | 100.0 | 33.4 | 25.0 | 41.7 |
| L | 22.2 | 25.9 | 11.1 | 14.8 | 27.2 | 37.0 | 22.2 | 74.0 | 51.8 | 100.0 | 29.6 | 44.4 | 44.4 |
| M | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 50.0 | 50.0 | 50.0 | 50.0 | 50.0 | 100.0 |
| Sum | 220.9 | 232.7 | 164.9 | 132.3 | 169.6 | 342.7 | 601.1 | 731.7 | 576.7 | 1089.4 | 551.2 | 562.9 | 663.9 |
| \bar{x} | 17.0 | 17.9 | 12.7 | 10.2 | 13.0 | 26.4 | 46.2 | 56.3 | 44.4 | 83.8 | 42.4 | 43.3 | 51.1 |

Populations: 1 Panuco, 2 Soto la Marina, 3 San Fernando, 4 Pecos, 5 Upper Rio Grande, 6 Conchos, 7 Nazas 8 Encinillas, 9 Carmen, 10 Casas Grandes, 11 North Yaqui, 12 South Yaqui, 13 Santa Maria.
 Characters: A Dorsal, B Anal, C Pectoral, D Pelvic, E Lateral Line, F Predorsals, G Total Circumcorporal, H Dorsal Circumcorporal, I Ventral Circumcorporal, J Total Circumpeduncular, K Dorsal Circumpeduncular, L Ventral Circumpeduncular, M Color. Values are percent difference of the mean from 0 (for San Juan stock).



Map 4. Former flow of rivers and direction of desert advance in the Chihuahuan Province.

nata. Pending a report on the validity of the genus (Contreras and Minckley unpubl. data), the most appropriate name of the species is used here. This species is known from six basin populations: the Upper Yaqui, the Upper and a Lower Conchos races, Nazas, Mezquital, and a few specimens are known from the Upper Río del Fuerte but they have not been analyzed. The Lower Conchos race seems to be the ancestral form, the Yaqui, Nazas, and Upper Conchos (and maybe the del Fuerte also) depart from it respectively 24.8, 51.6, and 81.3%. The Mezquital race diverges 86.9% in the same direction as the Nazas form, but more extremely, as shown by the signs of divergence (Table 4). Most characters analyzed, exemplified by lateral line and total circumcorporal scale counts, show a Y-shaped cline, with the Lower Conchos race at the angle of the Y (Table 5). This scheme seems possible only through stream captures, of which only one has been documented, the loss of the Guadiana Valley from the Río Nazas to the Río Mezquital (Albritton 1958). This same pattern and the characteristic one of relict distributions modeled by Darlington (1957:485) caused by differential survival should not be confused. Any one of them should be looked for in *Pimephales promelas* and *Dionda episcopa* races and in several others.

TABLE 4. Character matrix of differences between means of meristic characters for different populations from the presumed ancestral stock in *Codoma ornata* from the Rio Grande basin and range, northern Mexico.

| | Yaqui | Upper Conchos | Nazas | Mezquital |
|---------------------------|--------|------------------|---------|-----------|
| Rays: | | | | |
| Dorsal | 0. = | 0 = | 0 = | 100.0 - |
| Anal | 83.3 + | 83.3 + | 100.0 + | 91.7 - |
| Pectorals | 10.0 + | 100.0 + | 40.0 + | 90.0 - |
| Pelvics | 36.4 + | 54.5 + | 45.5 + | 100.0 + |
| Scales: | | | | |
| Lateral line | 26.8 - | 100.0 + | 19.5 - | 24.4 - |
| Predorsal | 87.3 - | 50.0 + | 72.7 - | 100.0 - |
| Total circumcorporal | 21.2 - | 100.0 + | 51.5 - | 84.8 - |
| Predorsal circumcorporal | 38.9 - | 100.0 + | 50.0 - | 88.9 - |
| Ventral circumcorporal | 5.9 - | 100.0 + | 52.9 - | 70.6 - |
| Total circumpeduncular | 6.7 + | 100.0 + | 53.3 - | 93.3 - |
| Dorsal circumpenduncular | 0 = | 87.5 + | 62.5 - | 100.0 - |
| Ventral circumpenduncular | 0 = | 100.0 + | 71.4 = | 100.0 - |
| Sum | 297.5 | 975.3 | 619.3 | 1043.7 |
| \bar{x} | 24.79 | 81.28 | 51.61 | 86.90 |

TABLE 5. Frequency distribution of scale counts in five races of *Codoma ornata* from northwestern Mexico.

| | | Lateral line scales | | | | | | | | | | | | | | | n | \bar{x} | |
|---------------|---|-----------------------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|-----------|-----------|
| | | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | n | \bar{x} |
| Yaqui | 1 | | | 3 | 7 | 41 | 51 | 22 | 10 | 5 | | | | | | | | 140 | 36.8 |
| Upper Conchos | | | | | | | 1 | 2 | 9 | 11 | 22 | 14 | 17 | 11 | 9 | 3 | 2 | 101 | 42.0 |
| Lower Conchos | 1 | | | | 8 | 8 | 21 | 23 | 14 | 6 | 4 | 3 | 2 | | | | | 90 | 37.9 |
| Nazas | | | | | 4 | 33 | 47 | 20 | 6 | 3 | 1 | 1 | | | | | | 115 | 37.1 |
| Mezquital | | | | 3 | 11 | 36 | 37 | 31 | 8 | 2 | | | | | | | | 128 | 36.9 |
| | | Total circumcorporal scales | | | | | | | | | | | | | | | | | |
| | | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | n | \bar{x} |
| Yaqui | 1 | | | 3 | 11 | 21 | 25 | 22 | 24 | 17 | 8 | 7 | 1 | | | | | 140 | 31.0 |
| Upper Conchos | | | | | | | | | 7 | 11 | 18 | 20 | 21 | 17 | 4 | 1 | 2 | 101 | 35.0 |
| Lower Conchos | | | | 1 | 4 | 3 | 11 | 22 | 21 | 16 | 6 | 3 | 2 | | 1 | | | 90 | 31.7 |
| Nazas | | | | 4 | 16 | 22 | 28 | 27 | 2 | 5 | 1 | | | | | | | 115 | 30.0 |
| Mezquital | 2 | | | 9 | 22 | 30 | 24 | 13 | 11 | 10 | 5 | 2 | | | | | | 128 | 28.9 |

Dealing with the Great Basin, Hubbs and Miller (1948) confirmed the paleohydrological data with fish zoogeography. In the Chihuahuan Desert, the ichthyological evidence is used almost exclusively because of the scarcity of Pleistocene studies. Care should be taken in drawing conclusions from variational data, because variation in fishes may be modified by basin size (the extreme development of endemic genera), age (the probable time levels in speciation of *N. lutrensis*), and community size (unpublished data on one extralimital species pair shows to high variability in one form living in a 5-species community, and consistency for the other one living in a 12-species group). From the data available, small, old basins and simple communities favor stronger differences, and large, young basins and complex communities favor smaller divergences. These inductive statements need ample support before firm conclusions may be reached.

After the work of Miller (1977) and personal estimates, there are 17 species and at least 20 subspecies still undescribed in Chihuahuan fishes. The only published zoogeographical study is that of Smith (1966) on *Pantosteus plebeius*. Only those species described after 1957 are



Map 5. Localities of the Chihuahuan Desert where fish community composition changes have been detected in the last 25-100 years: 1. Chihuahua City, 2. Delicias, 3. Jiménez, 4. Parras, 5. Hediondilla, 6. Monterrey, and 7. La Media Luna.

TABLE 6. Vanishing fish fauna of the Rio Chihuahua, Chihuahua City, Mexico, between 1856 and 1968.

| | 1856 | 1892 | 1901 | 1964 | 1968 |
|--------------------------------|------|------|------|------|------|
| | 1859 | 1894 | | | |
| Native Species | | | | | |
| <i>Asyanax mexicanus</i> | = | X | X | = | R |
| <i>Campostoma ornatum</i> | X | X | X | | |
| <i>Gila pulchra</i> | X | X | X | X | X |
| <i>Pimephales promelas</i> | = | X | X | X | |
| <i>Codoma ornata</i> | X | = | X | | |
| <i>Notropis chihuahua</i> | = | X | X | | |
| <i>Notropis lutrensis</i> ssp. | = | X | X | | |
| <i>Dionda episcopa</i> ssp. | = | X | X | | |
| <i>Cyprinodon eximius</i> | X | X | X | X | X |
| <i>Gambusia senilis</i> | X | X | X | | |
| <i>Etheostoma australe</i> | X | X | X | | |
| <i>Etheostoma pottsi</i> | 12 | 12 | 12 | 4 | 3 |
| Totals | | | | | |
| Exotic ? | | | | | |
| <i>Lepomis macrochirus</i> | | | | X | X |
| Total | | | | 1 | 1 |

Key: X Collected, R Rare, = Probably present.

known from good variational data. Considering this situation, the scientific, cultural, aesthetic, and perhaps practical values of the desert fishes, as well as the growing concern of world scientists about environmental degeneration even in the less fragile temperate regions, testified by the abundant literature on the subject, it is upsetting to witness a number of these species vanishing, becoming endangered, or even extinct, due to man's actions.

DOCUMENTARY EVIDENCE OF FISH COMMUNITY COMPOSITION CHANGES

Following the procedure of Miller (1961), Minckley and Deacon (1968), and my former paper on disappearing communities of fishes peripheral to the Chihuahuan Desert (Contreras 1975), a decrease of the native fish fauna can be documented for seven Chihuahuan localities (Map 5).

Río Chihuahua, Chihuahua City, Chihuahua

The fish fauna of the Río Chihuahua is known from the work of Girard (1856, 1859), Woolman (1892, 1894), and Meek (1902). A total of 12 native species was known until 1901; by 1964 only 3 were collected and another was probably present; in 1968 only 3 remained with 1 of them rare (Table 6). *Lepomis macrochirus* probably has been introduced at this locality, since it was known there only after 1964. *Etheostoma australe* and *E. pottsi* are considered endangered. Sources of disruption are channelization, damming of the river, and siltation (possibly agricultural).

Río Conchos at Camargo (= Santa Rosalia), Chihuahua

This fish fauna has been known since 1901 (Meek 1902), when 16 native species were known and probably 2 more were present. In 1964 only eight remained, plus one exotic. Both endangered endemics, the *Etheostoma* spp., no longer lived there (Table 7). Agricultural use has lowered the flow of water, although flash floods still are a menace. The river, formerly more or less clear, is now murky.

Río Conchos at Jiménez, Chihuahua

The fishes of Río Conchos at Jiménez were first collected also in 1901 (Meek 1902), with 15 known and 3 probable species present. In 1964, there were probably 12, confirmed in 1968. Besides the *Etheostoma* endemics, *Catostomus conchos* Meek (1902) has only been seen three times since 1903 (Miller, this volume). No exotics are known here yet (Table 8). Ecological disruption is similar to that found at Camargo.

TABLE 7. Vanishing fish fauna of the Rio Conchos at Camargo (= Santa Rosalia), Mexico, between 1904 and 1964.

| | 1901 | 1964 |
|---------------------------------------|------|------|
| Native species | | |
| <i>Lepisosteus osseus</i> | X | X |
| <i>Astyanax mexicanus</i> | X | X |
| <i>Campostoma ornatum</i> | X | X |
| <i>Rhinichthys cataractae</i> | X | X |
| <i>Pimephales promelas</i> | X | X |
| <i>Notropis chihuahua</i> | X | X |
| <i>Notropis lutrensis</i> ssp. | X | X |
| <i>Notropis braytoni</i> | = | X |
| <i>Pantosteus plebeius</i> | X | X |
| <i>Moxostoma austrinum</i> | X | X |
| <i>Carpionodes carpio elongatus</i> | X | X |
| <i>Pilodyctis olivaris</i> | X | |
| <i>Cyprinodon eximius</i> | X | |
| <i>Gambusia senilis</i> | = | |
| <i>Micropterus salmoides</i> | X | X |
| <i>Lepomis megalotis occidentalis</i> | X | |
| <i>Etheostoma australe</i> | X | |
| <i>Etheostoma pottsi</i> | X | |
| Totals | 18 | 8 |
| Exotic | | X |
| <i>Cyprinus carpio</i> | | 1 |
| Total | | |

Key: X Collected, = Probably present.

TABLE 8. Vanishing fish fauna of the Rio Conchos at Jimenez, Chihuahua, Mexico, between 1901 and 1968.

| | 1901 | 1964 | 1968 |
|---------------------------------------|------|------|------|
| Native species | | | |
| <i>Astyanax mexicanus</i> | X | X | X |
| <i>Campostoma ornatum</i> | X | X | X |
| <i>Gila pulchra</i> | = | = | X |
| <i>Pimephales promelas</i> | X | X | X |
| <i>Codoma ornata</i> | X | | |
| <i>Notropis braytoni</i> | X | | |
| <i>Notropis chihuahua</i> | X | X | X |
| <i>Notropis lutrensis</i> ssp. | X | X | X |
| <i>Dionda episcopa</i> sp. | X | X | X |
| <i>Catostomus conchos</i> | X | | |
| <i>Carpionodes carpio elongatus</i> | X | | |
| <i>Ictalurus punctatus</i> | = | = | X |
| <i>Pilodyctis olivaris</i> | = | = | X |
| <i>Cyprinodon eximius</i> | X | X | X |
| <i>Gambusia senilis</i> | X | X | X |
| <i>Lepomis megalotis occidentalis</i> | X | = | X |
| <i>Etheostoma australe</i> | X | | |
| <i>Etheostoma pottsi</i> | X | | |
| Totals | 18 | 12 | 12 |

Key: X Collected, = Probably present.

Parras Basin, Coahuila

This place of endemism has been treated by Miller (1961, 1964) and Contreras (1969), but the historical changes have not been tabulated yet. In 1880, six species were known there, by 1895 another endemic was described, with one more endemic discovered in 1968. In 1903 two endemics were alive (Miller 1964). In 1953, C. L. Hubbs and party could find only one species of native and one exotic fish. The situation recurred in 1964, but a thorough exploration in 1968 resulted in the discovery of another species of *Gila* and a population of *Astyanax*, and, unfortunately, four exotics. In 1973 one more exotic, the destructive *Gambusia affinis speciosa*, was collected, perhaps as the result of mosquito control measures. The three remaining native fishes are rare and endangered. These changes appear in Table 9.

Potosi, Hediondilla, Nuevo León

This interior basin, composed of a big spring and its distributaries, is inhabited by a recently described endemic genus, *Megupsilon aporus* Miller and Walters (1972), and an undescribed species of *Cyprinodon*. The first collection of the *Cyprinodon* was made in 1948, and in 1961 the new genus was collected, along with the exotic golden carp that seemed not to compete with or harm the natives. The spring was enlarged in the 1950s, probably to the unplanned benefit of both natives. However, early in 1974 black bass were introduced, and subsequently the natives have almost disappeared (Table 10).

Río Santa Catarina, Monterrey, Nuevo León

This river, usually a nearly dry bed with flash floods during the rainy season, flows through the city of Monterrey. Its fishes are known from Girard (1856, 1859) when 10 species were taken or must have been present. In 1903 only eight native species remained (Meek 1904); seven remained in the 1940s and six in 1967-68, when an undetermined number of tropicals was introduced in the stream in a publicity event, although only two were collected a few days later. In 1968, the native *Xiphophorus couchianus* and the exotic *X. v. variatus* were collected in a river bed spring, actively breeding. By 1972 massive hybridization was obvious, and in 1973 only hybrids remained in the spring, and guppies were present in the river (Table 11). Urban development, tropical fish hobbyists, and water depletion for municipal supplies have contributed to the disappearance of the native fishes.

Media Luna, Rioverde, San Luis Potosi

This interesting area of fish endemism, or its neighborhood, was first visited by W. L. Tower in 1903 (Meek 1904). He collected five species and five more probably were present. In 1956, four were rare

TABLE 9. Vanishing fish fauna of the Parras Basin, Coahuila, Mexico, between 1880 and 1973.

| | 1880 | 1895 | 1903 | 1953 | 1964 | 1968 | 1973 |
|-----------------------------------|------|------|------|------|------|------|------|
| Native species | | | | | | | |
| <i>Astyanax mexicanus</i> | X | = | = | = | = | X | S |
| <i>Gila</i> sp. A | = | = | = | = | = | X | S |
| <i>Gila</i> sp. B | X | = | = | X | X | R | S |
| <i>Stypodon signifer</i> | X | = | X | | | | |
| <i>Notropis lutrensis garmani</i> | X | | | | | | |
| <i>Dionda episcopa punctifer</i> | X | | | | | | |
| <i>Cyprinodon latifasciatus</i> | X | = | X | | | | |
| <i>Characodon lateralis</i> | = | X | | | | | |
| Totals | 8 | 6 | 5 | 3 | 3 | 3 | 3 |
| Exotic species | | | | | | | |
| <i>Cyprinus carpio</i> | | | | X | X | X | = |
| <i>Carassius auratus</i> | | | | | | X | = |
| <i>Xiphophorus</i> , hybrids | | | | | | X | X |
| <i>Poecilia reticulata</i> | | | | | | X | X |
| <i>Gambusia speciosa</i> | | | | | | | X |
| Totals | | | | 1 | 1 | 4 | 5 |

Key: X Collected, R Rare, = Probably present, S Seen.

TABLE 10. Endangered fish fauna of the Spring Fotosi, La Hediondilla Basin, Nuevo Leon, Mexico.

| | 1948 | 1961 | 1968 | 1972 | 1974 |
|------------------------------|------|------|------|------|------|
| Native species | | | | | |
| <i>Megupsilon aporus</i> | = | X | X | X | R |
| <i>Cyprinodon</i> sp. | X | X | X | X | R |
| Exotics | | | | | |
| <i>Carassius auratus</i> | | X | X | X | X |
| <i>Micropterus salmoides</i> | | | | | X |

Key: X Collected, R Rare, = Probably present.

(Miller 1956), increasing to 5 rare in 1968. No exotics were known here until 1972, when Robert R. Miller and his group collected the unwelcome *Tilapia aurea* and *Gambusia panuco*. At least seven species are endemic to this big spring or the Upper Rio Verde; only the ubiquitous *Astyanax* and perhaps *Ictalurus mexicanus* and *Cichlasoma labridens* are not yet considered endangered, except that the impact of the exotics is not yet apparent. The recent development to pump water from the main laguna can only harm the native biota. The changes appear in Table 12.

ECOLOGICAL COMMENTS ON THE RARE OR ENDANGERED FISHES OF THE CHIHUAHUAN DESERT

Considering the fishes listed in Tables 6 to 13, and without an attempt to conflict but to complement data given by Miller (this volume), several species have been shown as being affected by environmental changes, ranging from local disappearance to becoming rare, vanishing, endangered, or even extinct. As far as is known, these fishes have wide ecological similarities. The following list includes general statements on fish ecological preferences.

Family LEPISOSTEIDAE

Lepisosteus osseus (Lacépède). Surface feeding, carnivorous fish. Prefers quiet, turbid, warm waters in large rivers. Rare in the Mexican Plateau, common elsewhere in eastern North America.

Family CHARACIDAE

Astyanax mexicanus (Filippi). Ubiquitous omnivore, preferring animal matter. It has wide ecological tolerance and is usually abundant, hence its disappearance from some localities is not understood. It occurs from the Río Bravo and Central Texas southward an undefined distance.

Family CYPRINIDAE

Campostoma ornatum Girard. Herbivorous, bottom feeder, prefers gravel or rocky bottoms, in clear, cool water. Usually common. Endemic around the Sierra Tarahumara and east to the Big Bend area.

C. anomalum pullum. As former species.

Gila pulchra Girard. Probably carnivorous, feeds near bottom or midwater. Prefers clear cool, moving waters and sandy bottoms.

Gila sp. B. As former species. Endemic in western side of Parras basin. Endangered.

Pimephales promelas Jordan. Herbivorous, bottom feeder, on sandy to gravelly streams, with clear, cool waters.

Codoma ornata Girard. Probably omnivorous, otherwise as former species.

Notropis braytoni Jordan and Evermann. Insectivorous, midwater to bottom, on gravelly places, in cool, moving waters.

TABLE 11. Vanishing fish fauna of the Rio Santa Catarina, Monterrey, Nuevo Leon, Mexico, between 1856 and 1973.

| | 1856 | 1859 | 1884 | 1903 | 1942 | 1967 | 1970 | 1972 | 1973 |
|------------------------------------|------|------|------|------|------|------|------|------|------|
| Native species | | | | | | | | | |
| <i>Astyanax mexicanus</i> | = | | = | X | = | X | | | |
| <i>Campostoma anomalum pullum</i> | X | X | = | = | X | | | | |
| <i>Notropis l. lutrensis</i> | X | X | X | X | X | X | | | |
| <i>Dionda episcopa</i> | X | X | X | X | X | X | | | |
| <i>Moxostoma congestum albidum</i> | X | | | | | | | | |
| <i>Poecilia mexicana</i> | = | | = | X | X | X | | | |
| <i>Xiphophorus couchianus</i> | X | X | = | X | = | = | H | H | |
| <i>Gambusia a. speciosa</i> | = | | = | X | = | X | | | |
| <i>Lepomis megalotis</i> | = | | = | X | | | | | |
| <i>Cichlasoma c. cyanoguttatus</i> | = | | = | X | X | X | | | |
| Totals | 10 | | 9 | 8 | 7 | 6 | 1 | 1 | |
| Exotic species | | | | | | | | | |
| <i>Puntius conchonius</i> | | | | | | X | | | |
| <i>Xiphophorus v. variatus</i> | | | | | | X | H | H | H |
| <i>Poecilia reticulata</i> | | | | | | | | X | X |
| Totals | | | | | | 2 | 1 | 2 | 2 |

Key: X Collected, = Probably present, H Hybrids (*X. couchianus* x *X. variatus*).

TABLE 12. Vanishing fish fauna of La Media Luna region, Rioverde, San Luis Potosi, Mexico, between 1903 and 1972.

| | 1903 | 1956 | 1968 | 1972 |
|-----------------------------|------|------|------|------|
| Native species | | | | |
| <i>Ictalurus mexicanus</i> | X | R | S | |
| <i>Astyanax mexicanus</i> | X | X | X | |
| <i>Dionda</i> sp. A | = | = | R | |
| <i>Dionda</i> sp. B | X | R | R | |
| <i>Ataeniobius toweri</i> | X | R | R | |
| <i>Cichlasoma bartoni</i> | X | X | X | |
| <i>Cichlasoma labridens</i> | = | X | X | |
| <i>Cualac tessellatus</i> | = | R | X | |
| <i>Cichlasoma</i> sp. | = | = | X | |
| <i>Cichlasoma</i> sp. | = | = | R | |
| Totals | 10 | 10 | 10 | |
| Exotics | | | | |
| <i>Tilapia aureum</i> (1) | | | | X |
| <i>Gambusia panuco</i> (1) | | | | X |
| Totals | | | | 2 |

Key: X Collected, = Probably present, R Rare, S Seen.

TABLE 13. Fishes of the Chihuahuan Desert impacted upon by environmental changes at: 1 Río Chihuahua, 2 Camargo, 3 Jimenez, from Chihuahua State; 4 Parras Coahuila, and 5 Monterrey, Nuevo Leon.

| Species | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| <i>Lepisosteus osseus</i> | | X | | | |
| <i>Campostoma ornatum</i> | X | X | | | |
| <i>Campostoma anomalum pullum</i> | | | | | X |
| <i>Gila pulchra</i> | X | | | | |
| <i>Gila</i> sp. B | | | | X | |
| <i>Pimephales promelas</i> | | X | | | |
| <i>Stypodon signifer</i> | | | | E | |
| <i>Codoma ornata</i> | X | | X | | |
| <i>Notropis braytoni</i> | | X | X | | |
| <i>Notropis chihuahua</i> | X | | | | |
| <i>Notropis lutrensis</i> ssp. | X | | | | |
| <i>Notropis lutrensis garmani</i> | | | | X | |
| <i>Dionda episcopa punctifer</i> | | | | E | |
| <i>Dionda episcopa</i> spp. | X | | | | X |
| <i>Carpiodes carpio elongatus</i> | | | X | | |
| <i>Catostomus conchos</i> | | | X | | |
| <i>Moxostoma congestum albidum</i> | | | | | X |
| <i>Pilodyctis olivaris</i> | | X | | | |
| <i>Cyprinodon eximius</i> | X | X | | | |
| <i>Cyprinodon latifasciatus</i> | | | | E | |
| <i>Gambusia a. speciosa</i> | | | | | X |
| <i>Gambusia senilis</i> | | X | | | |
| <i>Poecilia mexicana</i> | | | | | X |
| <i>Xiphophorus couchianus</i> | | | | | X |
| <i>Characodon lateralis</i> | | | | E | |
| <i>Etheostoma australe</i> | X | X | X | | |
| <i>Etheostoma pottsi</i> | X | X | X | | |
| <i>Cichlasoma cyanoguttatus cyanoguttatus</i> | | | | | X |
| <i>Lepomis megalotis</i> | | X | | | X |

Key: X Impacted species, E Extinct

N. chihuahua Woolman. As former species.

N. lutrensis ssp. Insectivorous, prefers midwater, on gravel or rubble that may be covered by fine silt layer, and in rather cool pools with good vegetation. Endemic of Río Conchos. Usually common.

N. l. garmani Jordan. As former species. Endemic to the Nazas-Aguanaval complex. Formerly known near or at Parras, but now extinct there.

Dionda episcopa spp. Herbivorous, swims near bottom of shallow streams, in clear, cool, moving waters. Several recognizable endemic subspecies in the Chihuahuan Desert and elsewhere in eastern North America.

Dionda sp., Contreras and Verduzco (unpubl. data). Small predator, prefers thermal springs and outlets. Endemic. La Media Luna-Río Verde complex.

Dionda sp. (Hubbs and Miller, unpubl. data). Herbivorous, swims near bottom, mostly in small streams with clear waters on gravel. Endemic. La Media Luna-Río Verde complex.

Family CATOSTOMIDAE

Carpiodes carpio elongatus Meek. Bottom feeder, prefers large rivers with deep channel.

Catostomus conchos Meek. Possibly extinct. Endemic. Río Conchos.

Moxostoma congestum albidum Girard. Bottom feeder. Middle sized streams, on gravel or rubble; in clear, cool, moving waters.

Family ICTALURIDAE

Pilodyctis olivaris (Rafinesque). Scavenger or carnivorous. Large rivers.

Family CYPRINODONTIDAE

Cyprinodon eximius Girard. Herbivorous, bottom feeder, on sandy to gravelly streams, in clear, shallow waters. Endemic. Río Conchos.

Cyprinodon sp. (Miller unpubl. data). Herbivorous, swims near bottom, usually in deep, open waters in a clear spring. Endemic. La Hediondilla, Nuevo León. Endangered.

Megupsilon aporus Miller and Walters. Insectivorous, swims in dense patches of *Ceratophyllum*. Endemic. La Hediondilla, Nuevo León. Endangered.

Cualac tessellatus Miller. May be herbivorous, swims near bottom. Endemic. La Media Luna. Endangered.

Family GOODEIDAE

Ataeniobius toweri (Meek). Herbivorous. Prefers midwater in shallows, or close to shore. Endemic. La Media Luna. Endangered.

Family PERCIDAE

Etheostoma australe Jordan. Bottom insectivorous, on sandy or gravelly shallow streams, with fast, cool waters. A rare species that may be common locally. Endemic. Río Conchos. Endangered.

E. pottsi (Girard). As former species.

Family CICHLIDAE

Cichlasoma cyanoguttatum (Baird and Girard). Rather omnivorous, preferring detritus. Bottom, on almost any substrate. Rare only in the Río Conchos.

Cichlasoma sp. Bottom, mollusk eater; warm, clear, moving water; on silt. Endemic. La Media Luna region. Endangered.

Family CENTRARCHIDAE

Lepomis megalotis occidentalis (Meek). Predator of small arthropods; bottom, on gravel and rubble; in clear, moving waters.

This partial list shows that most of the fishes of the Chihuahuan Desert that are reducing their distribution primarily prefer the well-oxygenated, clear, moving water, running over sand and gravel, and are bottom forms. Several of them are herbivorous, mainly algae eaters, a kind of food that disappears with turbid waters.

REASONS FOR DECLINE OF FISH COMMUNITIES

1. Agricultural development results in a lowering of the water table, increasing aridity, and hence siltation of the reduced streams; also, the attendant dam building results in higher water temperatures, reducing the oxygen capacity of water.
2. Towns provide untreated sewage, saltier than the already saline desert waters in these highly evaporative areas, and industrial development results in a rise of pollution from untreated residual waters. The rivers, scarce, become heavily loaded with silt and often heavily polluted; their current is scantier and becomes intermittent, with muddy pools; the water temperature rises and its diel cycle fluctuates extremely.
3. Many fish culturists are indiscriminate in planting exotic fishes or do not follow biological and ecological principles. Most of these situations are not favorable to the native fishes nor to the human beings that depend on the same waters.
4. The fishes of the relatively simple desert communities have little or no adaptation to predators or competitors, failing to survive if forced to live with the usually aggressive exotic species that are usually more resistant. Such is the situation of *Megupsilon aporus* and *Cyprinodon* sp. that was once abundant at Hediondilla (Potosí), Nuevo León. These species successfully coexisted with the exotic *Carassius auratus*. However, their lack of fear of other fishes makes them succumb to a newly introduced exotic, the strong predator *Micropterus salmoides*. It is possible that these natives may not long survive.

ORIGIN OF THE ECOLOGICAL DEFICIENCIES IN DEVELOPMENT

If we look for the causes of the lack of integral ecological planning of development in the Chihuahuan Desert, it is obvious that the main one is the insufficient knowledge of its biota, beginning at the taxonomic level and continuing at the ecological, resource, and use levels. Standard developers have no biological data and no idea how to use them efficiently, nor do they have good advisors. Thus, there will be no ecologically sound development. There is an urgent need for biological research and influential ecologists. Moreover, ecologically oriented politicians and planners are needed so that the biota of the Chihuahuan Desert, or any other, may be wisely used for the benefit of mankind.

In concluding, the fish fauna of the Chihuahuan Desert is a living resource worth protection; it represents a set of values: scientific, cultural, aesthetic, and practical. Studying its ways we may learn about its past and present, its dynamics, its possibilities of being useful, how to predict its future, and perhaps

learn to survive in the desert. Lowering the water table increases the cost of its use, contributes to dry springs, wells, and rivers, and destroys natural resources. Pollution makes unusable the already scarce water. This phenomenon endangers fish life and human communities. We need to design a system of development that includes preservation of such fauna. We can no longer permit the destruction of aquatic habitats and life, considering that we share the same basic resource. It can be safely said that species destruction is thoughtless, useless, and fruitless, and is the result of gross ignorance that needs to be cured.

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Summary and Conclusion

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Aquatic environments in the Chihuahuan Desert are limited; consequently, fish populations may be geographically isolated from each other. Gene flow can be precluded whether the spring sources are separated by meters as in Cuatro Ciénegas or by kilometers as, in parts of the Conchos Drainage of Chihuahua. I agree with Miller (this volume) that these populations may be as isolated as are the birds and reptiles studied by Darwin, Lack, and others in the Galapagos. As such they must be retained as "living" examples of evolutionary processes.

Isolation of Chihuahuan Desert fishes is not an either/or situation; rather a complete separation of many species of *Cyprinodon* mentioned by Miller is paralleled by circumstances in *Gambusia*. In both genera, a population may be restricted to one or two springs. For example, *Gambusia amistadensis* naturally occurred only in Goodenough Springs, Val Verde County, Texas; *G. gaigei*, only in the Boquillas area of Big Bend National Park; *G. hurtadoi*, only in a spring near Jiminez, Chihuahua; and *G. alvarezi*, in a spring near San Gregorio, Chihuahua. Each population is separated from each other by kilometers of uninhabited waters (frequently inhibited by the closely related competitor, *G. senilis*). Consequently, it is not possible to use the rule of thumb "sympathy with little or no gene flow" to determine whether they are species or subspecies.

Racial variation in *Notropis lutrensis* (Contreras, this volume) illustrates another level of complexity. The *Notropis mearnsi* population (west of the Continental Divide) is isolated from other members of the *N. lutrensis* complex. *Notropis l. lutrensis* lives in much of the Great Plains and the populations in streams tributary to the Mississippi River may be connected by gene flow along the main river. Essentially, every stage of isolation has been shown by Contreras, but added complexities occur. Breeding colors of males in Rio Grande tributaries (Marivillas Creek, Alamito Creek) are distinct from each other and from those inhabiting the main river when collected or when cultured in the laboratory for two generations. Similarly, the males from the salt-laden midsection of the Pecos can be distinguished from those from upstream or downstream and from those inhabiting tributaries. Whether the multitude or geographic morphs are species, subspecies, or races, each is a unique gene pool that has a value. We must avoid the extinction of those natural resources whose true value only may become obvious after they are extinct.

Preservation of endangered taxa should not be restricted to "zoological garden" rescue operations but rather the organisms should be maintained in their natural ecosystems. That approach will preserve the natural stresses that maintain the natural gene pool. More critically, that approach can also assist in maintaining other endemics that may not yet be known.

Session V
Herpetofauna

Is There a Chihuahuan Desert? A Quantitative Evaluation Through a Herpetofaunal Perspective

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INTRODUCTION

The title appears to be a very simple question with a very obvious answer. The whole symposium itself would seem to be proof of the affirmative response. And yet a brief review of past literature will reveal not only conflicting definitions of the Chihuahuan Desert but challenging rejections of its existence. More serious still are philosophical attacks upon the underlying concept of biotic provinces altogether.

I will now review these considerations in turn. Definitions may be broken down into ecological, spatial, and temporal. The ecological definitions range in scope from total denial (Weaver and Clements 1938) to those which encompassed a spectrum of vegetation from short grass (grama) prairie to nopal woodland (see Shelford 1964).

Spatial definitions again include conservative estimations restricting the desert to southwest Texas (Gelbach 1967) and adjacent Mexico to those which would encompass virtually the entire Mexican Plateau from the Trans-Volcanic ranges north (Goldman and Moore 1946).

Temporal definitions of the desert view it as an ongoing process or phenomenon both ecological and evolutionary in nature. Some analysts have treated the Chihuahuan Desert as a *refugium* of great antiquity in which survive the descendants Madro-Tertiary Geofloras and primitive Young Northern faunas (Savage 1960; Morafka 1974), while others (Wells 1974) view the desert as young as the last altithermal of the Holocene (Recent) Epoch.

Even the labeling terminology designating the region is confused. The Chihuahuan Province of Dice (1943), the Chihuahuan-Zacatecas Province of Goldman and Moore (1946), the Chihuahuan and Austral

Provinces of Smith (1939), the Trans-Pecos Community of Webb (1950) and Correll and Johnston (1970), and the Mapimian Province of Hagmeier and Stults (1964) all correspond to each other in their fundamental characters.

A more fundamental problem is raised by the very act of distinguishing a geographic region as a distinct, biotic province.

Peters (1955) made a forceful attack on the concept of a biological province. Appropriately enough, he chose to use selected herpetofaunal provinces of Mexico to prove his points. These provinces, he charged, made use of a few arbitrarily chosen species distribution in order to artificially delimit a faunal province. In one case, he demonstrated that the herpetofaunal composition varied in a continuous fashion and did not justify the subjectively imposed provincial boundary lines. His arguments suggested such provinces were biologically meaningless.

Hagmeier and Stults (1964) sought to demonstrate that biologically meaningful provinces could be both objectively and quantitatively derived.

What I have attempted to do here is to generate a biologically relevant definition of the Chihuahuan Desert, synthesizing climatic, geological, and botanical criteria. To test this definition quantitatively, I have matched it against the real distribution of the herpetofauna of the Mexican Plateau and the adjacent southwestern United States.

ANALYTICAL PROCEDURES

The specific objectives of the analysis are threefold: (1) to develop a biologically valid definition and map of the Chihuahuan Desert; (2) to test this map against primary faunal areas resolved by quantitative means; and (3) to evaluate the distinctiveness of primary areas in terms of faunal resemblance and endemism.

With some modification, I have employed the procedures of Hagmeier and Stults (1964) to fulfill all three of the objectives just stated. They designed the following format in their quantitative analysis of North American mammal distribution: (1) selection of taxa; (2) definition of a single initial area; (3) determination of the distribution of the selected taxa within the initial area; (4) determination of primary area limits by the positions of maximal IFC (Index of Faunal Change) between squares in a grid across the initial area, using the distributions of the selected fauna; and (5) (dendrogram) analysis of affinities between the faunal assemblages of the primary areas, using the Coefficient of Community as a measure of faunal resemblance. This approach provides a strong quantification and standardization in the construction of primary areas.

I shall now undertake a brief review of each of these steps to explain crucial operational decisions.

The choice of taxa was based on several considerations. First, my previous professional orientation has been strongly herpetological. Second, these are the groups which are closely bound by both physiology and motility to the landscape, closely reflecting both ecological and historical (paleoecological and paleogeographical) influences. The chosen herpetofauna, over 170 species in the involved portion of the Mexican Plateau, is sufficient for quantitative analysis, but it is not so diverse as to overburden a researcher limited to 4 years of active investigation. Finally, amphibians and reptiles from the study region were available in museum collections and accessible in the field in adequate numbers for the construction of functional distribution maps.

The definition of the initial base region of study was a particularly difficult task, one in which lies tremendous potential for arbitrary and subjective distortion. I asked the question, "How is the Chihuahuan Desert to be defined in biologically meaningful terms that may be translated into an operational base map?" Two climatic factors, incident solar radiation and precipitation, combine to determine temperature, light exposure, erosional processes, hydrology, soil structure (in part), and the biota. I have attempted to enhance the value of the defined area by considering a broad range of congruent parameters, purposely omitting consideration of the herpetofauna in map construction in order to avoid circular evaluations. In addition, political boundaries were ignored as biologically meaningless.

Definition of a single initial area constituted the crucial second step. Deserts are ultimately climatic in a causal sense. The specific limits within these parameters are discussed in the result section along with the map (Figs. 1 and 2) based upon them.

The third stage followed the procedure of Hagmeier and Stults (1964) in that general distribution maps of the species of the selected taxa were constructed. However, the maps used here provide more uniform information in that all ranges were constructed by the author himself (Conant 1958; Smith and Taylor 1966; Raun and Gelbach 1972; and Stebbins 1966 were important references) all from the same general sources of information, all were made without regard to artificial political boundaries (in contrast to the United States-Mexican border which limited the study of Hagmeier and Stults). Furthermore, ranges were constructed without consideration of previous and subjectively defined biotic provinces. Hypothetical limits were drawn conservatively, based on least polygons constructed from known localities and/or sharply defined associations with known vegetation, or from the position of specific and established barriers (i.e., mountain ranges).

In addition, the ranges of taxa were considered up to 200 km (120 miles) beyond the limits of the single initial area, thus creating a margin for discriminating error in step four.

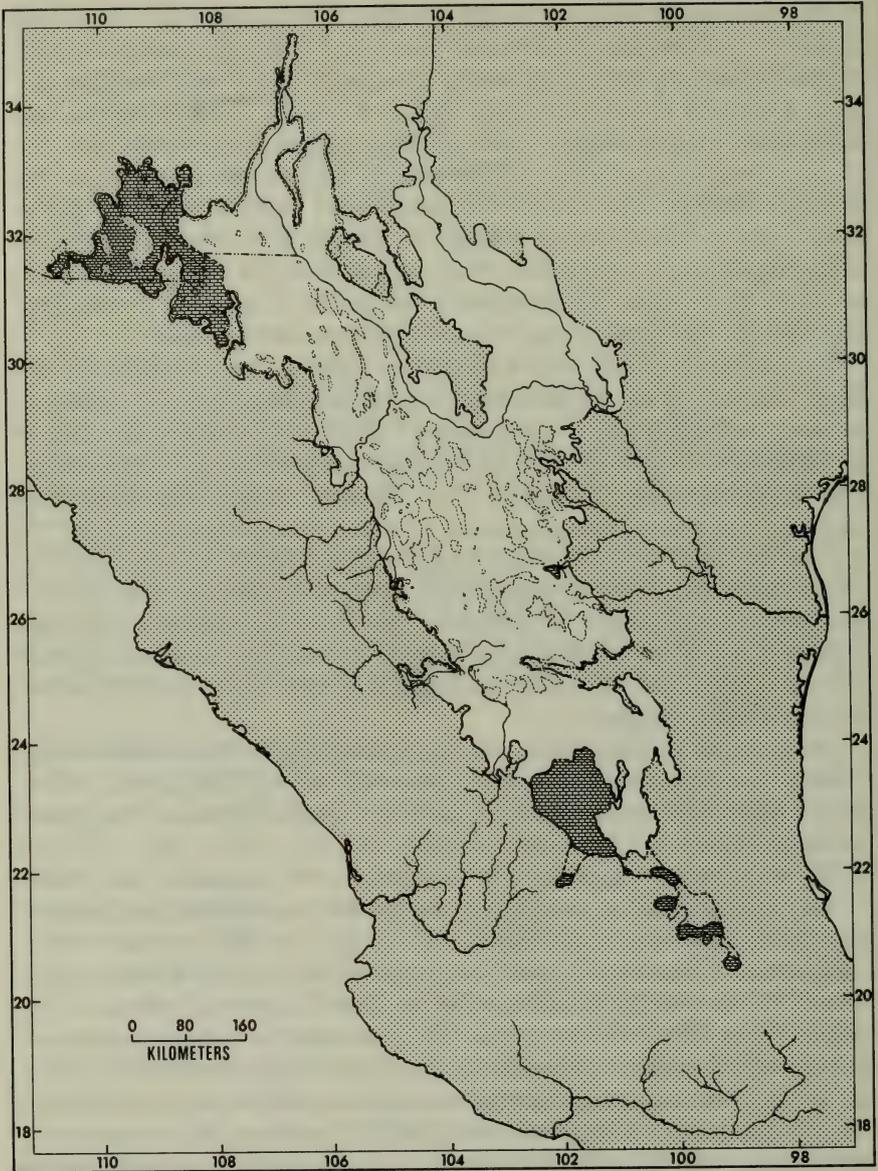


Fig. 1. Base map of the Chihuahuan Desert

Key: White: Chihuahuan Desert
 Gray: nondesert

Bricks: filter barriers and transitional ecotones

This fourth step, the determination of primary areas, seeks further to match the initial area generated in step two against the broad set of species range maps developed in step three. Specifically, the limits of pri-

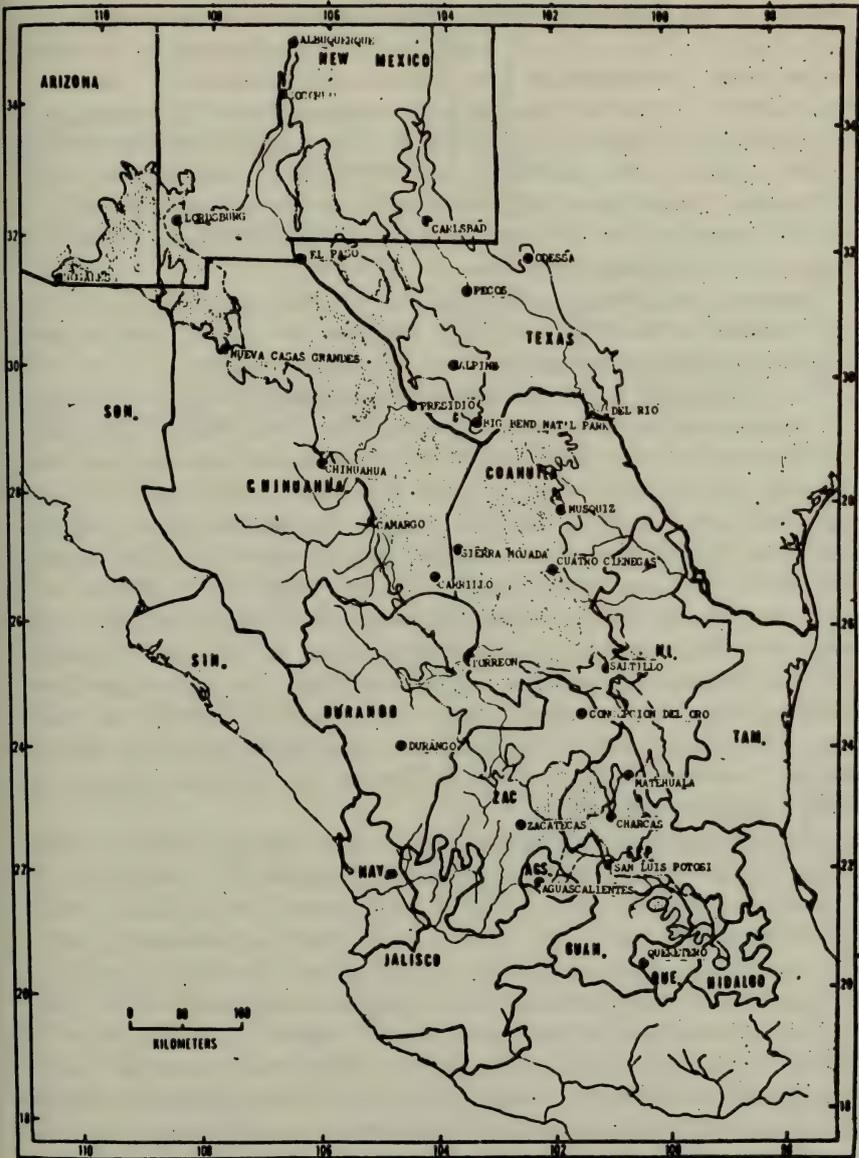


Fig. 2. Base map of Chihuahuan Desert showing political boundaries.

many faunal areas in the general position of the Chihuahuan Desert, namely, on the north Mexican Plateau, are determined here by establishing points of maximal faunal change. These points may be located easily by calculating the Index of Faunal Change (i.e., the per-

centage of the indigenous fauna whose distribution terminated in that unit of space), for a series of equal area squares transecting the entire region under consideration. The squares with maximal IFC values fix the positions of maximal changes in the regional fauna. By joining these maximal points, a primary faunal area may be encribed and thus defined. If the primary area encribed for herpetofauna corresponds to the Chihuahuan Desert base map constructed on other evidence (step 2), it would strongly affirm the general biogeographical relevance of the base map and its underlying definition.

Employing the strategy outlined above, I have constructed the following simplified method for tentatively resolving the primary area or areas within the approximate region of the Chihuahuan Desert.

The Mexican Plateau is skewed across its greatest breadth by latitude, 32° North, and greatest length by longitude, 104° West. Along these lines transecting rows of 80 km (48 miles) (per side) squares have been imposed on the base map covering the inner plateau and adjacent highlands (see Fig. 3). In addition, parallel and perpendicular transects have been drawn East about one-half degree above the 22nd parallel and West along the 32nd parallel. These tangential transects were drawn in order to evaluate the transitional filter barriers depicted on the base map. These transects circumvent the use of grid over the entire Mexican Plateau. Though they are less thorough, two advantages favor their use. First, they are much faster and effectively sample the major axes of the region, and second, they are coincidentally set across the best sampled portions of north Mexican Plateau (i.e., Coshise County, Big Bend, Sierra del Nido, etc.).

After the positioning of transecting squares was determined, the IFC values for those squares were calculated. Using the IFC values from the squares on the grid transect, Fig. 3, I have tested the predictive ability of the initial base map (Figs. 1 and 2). If the base map accurately defines the biologically relevant borders of the desert, the discontinuities in herpetofaunal distributions should be maximal along these borders, intermediate across filter barriers, and minimal within the stable core of the desert. Index faunal change values are a direct measure of the relative discontinuity of the herpetofaunas. Thus these values should correspond directly to borders, transitions, and the core region of the desert depicted on the base map. The Mann-Whitney test (a nonparametric rank-sum test) was employed to evaluate the null hypothesis that the IFC values of squares lying on the base map desert borders would be equal to those that were not. Acceptance of the null hypothesis would not decisively reject the existence of a biologically significant Chihuahuan Desert; acceptance would reject only the specific definition used here, and only in its relation to herpetofaunal distribution patterns. Errors in choice of parameters, their limits, their mapped representation, or errors in faunal range maps could also cause an acceptance of the null hypothesis.

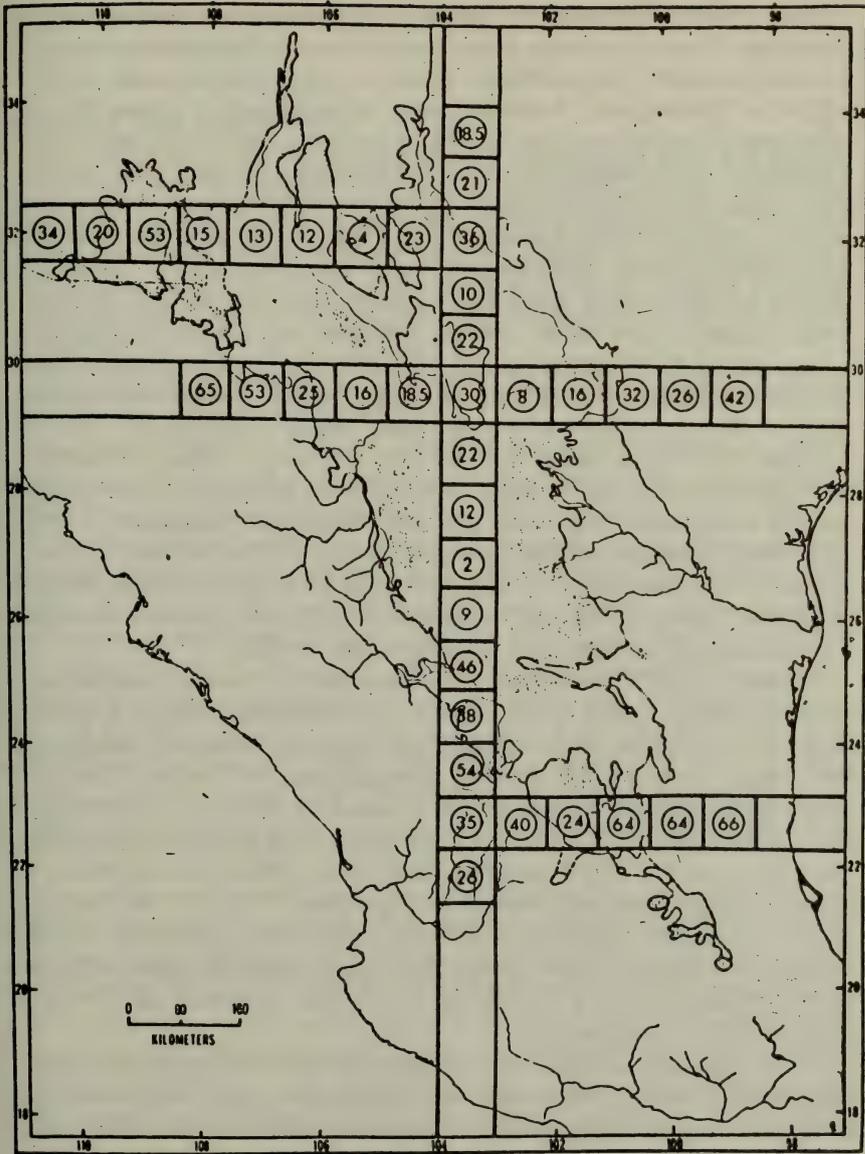


Fig. 3. Indexes of faunal (herpetofaunal) change for the squares of the Mexican Plateau. Key: numbers are percentage values for IFC.

The final analytical step is an evaluation of the faunal resemblance between the primary area and adjacent units. Such an evaluation serves simultaneously to elucidate the internal differentiation and the external affinities of primary areas.

The evaluation of faunal resemblance requires several procedural explanations. First, all primary areas, having been defined on the range of the total terrestrial herpetofauna, were now redefined in terms of their typical or "participant" herpetofaunas. In practice, this means that all relict faunal assemblages occurring in exclusive association with relict vegetation were eliminated from comparison. In the case of the Chihuahuan Desert primary area, all strictly montane and riparian faunas were removed from consideration. Similarly, isolated desert faunas were deleted from comparisons involving more mesic provinces. Second, not all primary areas under comparison were defined quantitatively. Hagmeier and Stults (1964) indicated that the more subjective herpetofaunal provinces of Savage (1960) do correspond quantitatively to their mammalian superprovinces. I have assumed a general applicability of their provinces to the province under examination. This assumption is further supported by the virtually perfect correlation between the Chihuahuan Desert province here defined by herpetofauna and the mammalian Mapimian province defined by Hagmeier (1966). Subjectively constructed Mexican provinces are more difficult to study directly or by comparison. I have generally used the provinces defined by Stuart (1964) as the most compatible with the available evidence from physiography, vegetation, and faunal distribution.

Another major consideration in determining faunal resemblance between primary areas is the choice of coefficients. Simpson (1960) reviewed most of the simpler fractional measures previously employed. For simple presence or absence comparisons, he favored his own Similarity Coefficient (SC) over the classical Coefficient of Community (CC) of Jaccard (1902). The two coefficients tend to mask information. The CC gives the best ecological information where discrepancies in faunal diversity (species density) are important. The SC, in contrast, would only obscure important ecological differences. However, the SC value does effectively demonstrate the relationships of faunas of common derivation, and is therefore a valuable indicator of historical biogeographical relationships.

While Hagmeier and Stults have depended upon CC values for classifying primary areas, I have used both coefficients since both ecological similarity and historical affinity are important characteristics of any faunal assemblage.

As a final measure of faunal differentiation, an evaluation of endemism within the primary area was undertaken. Endemic species are considered individually as a percentage of the whole.

In summary, the analytical procedure evaluates the significance of the Chihuahuan Desert as a herpetofaunal unit by three separate measures: (1) correlation of the initial base map with natural faunal breaks; (2) the evaluation of internal and external affinities by means of faunal

resemblance coefficients; and (3) the degree of faunal differentiation as indicated by endemism.

RESULTS AND DISCUSSION

The resolution of the initial Chihuahuan Desert base map is a crucial prerequisite for all further results and discussion. Since the warm deserts of North America have a highly uniform shared biota, differing strikingly from the colder or mesic regions adjacent to them, I prefer to discriminate warm deserts as those with an average annual incident solar radiation in excess of 500 Langleys and average annual precipitation of less than 300 mm (12 inches).

The Chihuahuan Desert may be defined as the warm desert of North America east of the Continental Divide.

The criteria listed in Table 1 establish an explicit definition of the Chihuahuan Desert and at the same time define the geographical parameters, mutually superimposed, from which the base map (Maps 1 and 2) was constructed. Climate and physiography (including soil and drainage) were primary considerations, but the ranges of indicator plant species were utilized to resolve more detailed boundaries, being viewed as operational indicators of desert climates when direct data was lacking (see Muller 1937; Garcia et al. 1961). Data were drawn from a survey of existing literature (see Introduction) of which the U.S. Vegetational Map of Kuchler (1964), U.S. Climatological Atlas (1968), ecological map of Mexico (Leopold 1950), the work of Marroquin et al. (1964) and West (1964) were most important. In addition, the author personally surveyed the region for a total of 10 months between 1970 and 1974, logging over 25,000 km (15,000 miles) in travel.

The results of the third step, the construction of range maps, are too extensive for presentation here. (The complete dissertation will appear in monograph series *Biogeographia* by spring 1977.) All specific distributions falling within 25 km of the initial area limits were mapped formally. In total, 170 species were mapped. Of these, however, 57 (34%) were present typically in true desert ecosystems. The remainder were montane relicts, ecotonal peripherals, and riparian-aquatic forms. These 57 species constitute the "participant" Chihuahuan Desert herpetofauna analyzed in step five.

The fourth step of the analysis contained two objectives: (1) the generation of primaries; and (2) the correlation of primary area limits to initial area limits set in stage two. The results of each deserve separate discussion.

The crucifex of squares in Fig. 3 does not provide the same resolution of primary areas that would be possible in a complete grid of IFC values. At best, it indicates major stable regions and zones of abrupt

TABLE 1. Defining criteria^a for the Chihuahuan Desert initial area base map.

| Category | Range of Values or Indicator (+/-) |
|--|--|
| I. Climate | |
| a. Average Annual Temperature | : 19(16-22)°C |
| b. Average Annual Precipitation | : 75-300 mm (350 mm on periphery) |
| c. Precipitation/ Temperature Ratio (based on specific annual averages) | : 14.3 (7-21) |
| d. Solar Radiation | : 500 (+) Langleys (annual average) |
| II. Physiography | |
| a. Soil Group | : Sierozem—under 0.5 meters to soil horizon (alluvial soils also common with halomorphic and azonal soils locally important) |
| b. Elevation | : 600-1500 m north of 25th parallel; 1500-1800 m south of 25th parallel |
| c. Hydrographical Divisions | : All east of Continental Divide—except portions of Coshise Filter Barrier in Gila and Yaqui drainage remainder ultimately Rio Grande or closed interior drainage systems southern desert relicts in Rio Panuco drainage |
| d. General Topography | : Basin and range province with fault blocks generally parallel diagonals running north-west, karst landscape, many basins filling with aggregating alluvium |
| III. Vegetation | |
| a. Sclerophyll Scrub (all three indicators in combination <i>only</i>) | : 1. <i>Larrea divaricata</i> (east of Continental Divide) 2. <i>Flourensia cernua</i> 3. <i>Parthenium incanum</i> |
| b. Saxicolous Scrub ("crassicole") | : 1. <i>Agave lechiguilla</i> 2. <i>Parthenium argentatum</i> 3. <i>Euphorbia antisyphylitica</i> 4. <i>Dasyllirion</i> sp. 5. <i>Fouquieria splendens</i> (east of Continental Divide) |
| c. Desert Grassland | : 1. <i>Bouteloua gracilis</i> characteristic but not endemic: 2. <i>Hilaria mutica</i> 3. <i>Tridens puchellus</i> |

^aRoughly in descending order of importance.

faunal changes that could be extrapolated topographically across the Mexican Plateau.

Still the crucifex does depict a stable central region (essentially the Bolson de Mapimi) and peripheral zones of gradual to abrupt change. The IFC values on the crucifex indicate transitional faunal changes on the north and south slopes of the Mexican Plateau, with contrasting abrupt changes along the east and west slopes. The results are not surprising in light of topography, climatic patterns (especially precipitation), and vegetation. All four of these peripheral zones do generally correspond to the borders set for the initial area and could be joined to rationalize a single primary area identical to the Chihuahuan Desert base map of Fig. 1.

However, the same points of maximal IFC values could construct alternative primary areas. This is especially probable since a major internal faunal break is indicated by a square on the Rio Nazas with an IFC value of 46%. Alternative interpretations include the following: (a) the stable Mapimian region is the single primary area with adjacent areas transitional; (b) the Mapimian region is primary area, the desert region north of the Rio Grande and west of the Pecos is a second primary area, the Trans-Pecos; and (c) both Mapimian and Trans-Pecos regions are primary areas with the desert region south of the Rio Nazas drainage basin constituting a third primary area, the Saladan region. (I prefer to use the less specific "region" to the overly committal "province" at this point.) Whether the Chihuahuan Desert should be viewed as one, two, or three primary areas is best resolved by an evaluation of its internal faunal resemblance values, discussed in the results of step five.

The second objective, already explained in the procedural section, does affirm the predictive value of the initial base map in setting the positions of maximal faunal change. Specifically, the Mann-Whitney test rejects the null hypothesis at the $P \geq 0.01$ level of significance. The test does not effectively resolve, however, whether the initial base map inscribes one primary area or several.

After the primary area is established by the IFC test, its relative status as a biogeographical unit was tested against adjacent provinces using Coefficients of Community (CC) and Similarity of Coefficients (SC).

When CC values are used to test the Chihuahuan biotic province, they unequivocally affirm its validity at the province level of 0.65 as determined by Hagmeier and Stults (1964). The Chihuahuan province is compared to its adjacent vertebrate provinces, derived by intuitive and quantitative means (Hagmeier 1966; Stuart 1964) in Table 2. All nine contiguous faunal units proved to be distinct at the province level (see Fig. 4). The Edwards Plateau with a CC value of 0.42 was the only unit with which the Chihuahuan Desert could be combined at even the superprovince level. The Chihuahuan Desert shares smaller common

TABLE 2. Herpetofaunal resemblance between the Chihuahuan Desert and adjacent biotic provinces.

| Province | Coefficient of Community | Coefficient of Similarity |
|-----------------------------|--------------------------|---------------------------|
| Kansan (Great Plains) | 0.32 | 0.55 |
| Balconian (Edwards Plateau) | 0.42 | 0.59 |
| Tamaulipan | 0.22 | 0.37 |
| Sierra Madre Oriental | 0.09 | 0.18 |
| Vera Cruzian | 0.04 | 0.11 |
| Trans-Volcanic | 0.09 | 0.18 |
| Sierra Madre Occidental | 0.07 | 0.13 |
| Sonoran | 0.32 | 0.48 |
| Navahonian | 0.12 | 0.26 |

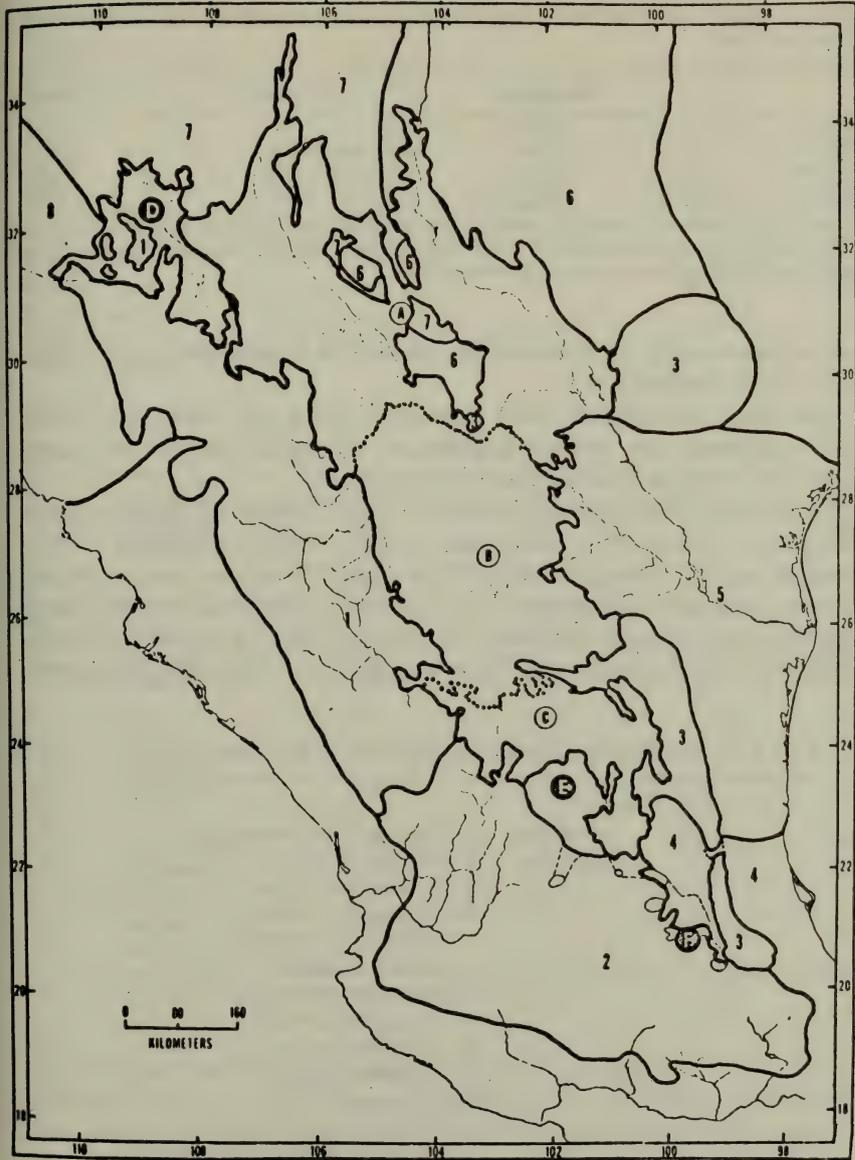


Fig. 4. Biotic provinces and subdivisions of south central North America.

- Key:
- | | |
|---|--------------------------------------|
| Clear Area = Chihuahuan Desert Province | 1 = Sierra Madre Occidental Province |
| A = Trans-Pecos Subprovince | 2 = Trans-Volcanic Province |
| B = Mapimian Subprovince | 3-A = Sierra Madre Province |
| C = Saladan Subprovince | 3-B = Balconian Province |
| D = Cochise Filter Barrier | 4 = Vera Cruzian Province |
| E = Saladan Filter Barrier | 5 = Tamaulipan Province |
| F = Rio Panuco Relict Desert | 6 = Kansan Province |
| | 7 = Navahonian Province |

TABLE 3. Matrix of resemblance coefficients for the compared herpetofaunas of the Chihuahuan Desert.

| | Trans-Pecos | Mapimian | Saladan |
|-------------|-------------|----------|---------|
| Trans-Pecos | (47) | 0.61 | 0.52 |
| Mapimian | 0.75 | (48) | 0.57 |
| Saladan | 0.96 | 0.96 | (29) |

Coefficients of Community appear in upper right triangle; Coefficients of Similarity in lower left; circled figures indicate number of samples (N).

herpetofaunas with the Sonoran Desert and the Kansan Plains provinces, 0.32 in both comparisons.

The same comparisons were conducted using SC values and while they emphasize the relative importance of shared faunas, the same general affinities and distinctions are expressed.

Furthermore, the possible divisions of the Chihuahuan Desert cluster much more tightly than do those western deserts (Morafka 1974), generally at CC levels of 0.60. While these CC values are borderline between provincial and subprovincial levels of differentiation, SC values indicate much stronger affinities. The Saladan fauna is almost completely shared with Mapimian and Trans-Pecos (96%). The more distinctive

TABLE 4. Characteristic or endemic herpetofauna of the Chihuahuan Desert.

| Reptilia: | |
|--------------|--|
| Testudinata: | 1. <i>Gopherus flavomarginatus</i> |
| Lacertilia: | 1. <i>Coleonyx brevis</i> ^a |
| | 2. <i>Coleonyx reticulatus</i> |
| | 3. <i>Cophosaurus texanus</i> |
| | 4. <i>Phrynosoma modestum</i> |
| | 5. <i>Sceloporus cautus</i> ^a |
| | 6. <i>Sceloporus maculosus</i> |
| | 7. <i>Sceloporus merriami</i> |
| | 8. <i>Sceloporus ornatus</i> |
| | 9. <i>Sceloporus poinsettii</i> ^a |
| | 10. <i>Uma exsul</i> |
| | 11. <i>Cnemidophorus inornatus</i> |
| | 12. " <i>Cnemidophorus neomexicanus</i> " ^b |
| | 13. " <i>Cnemidophorus tessellatus</i> " ^b |
| | 14. <i>Gerrhonotus lugoi</i> |
| Serpentes: | 1. <i>Elaphe subocularis</i> |
| | 2. <i>Ficimia cana</i> |
| | 3. <i>Tantilla atriceps</i> |
| | 4. <i>Crotalus scutulatus</i> ^a |

^aNot entirely endemic.

^bParthenogenetic clones.

TABLE 5. Recent distributional affinities of the Chihuahuan Desert scrub association herpetofauna.

| Category | Chihuahuan Province (N:58) | Trans- Pecos Sub- province (N:47) | Mapimian Sub- province (N:48) | Saladan Sub- province (N:29) |
|---|----------------------------------|---|--|---------------------------------------|
| Nearctic Region | | | | |
| A. Ubiquitous | 9% | 11% | 8% | 14% |
| B. American Highland Sub-Region | | | | |
| I. Sierra Madre Super- province | | | | |
| 1. Ubiquitous | 5% | 4% | 4% | 10% |
| 2. Arizonian Province | 2% | 0% | 4% | 0% |
| II. Desert and Plains Super- province | | | | |
| 1. Ubiquitous | 26% | 32% | 31% | 41% |
| 2. Kansan (Great Plains) Province | 8% | 9% | 7% | 7% |
| 3. Chihuahuan Province | 33% | 25% | 31% | 28% |
| (a. Endemics) | 26% | 6% | 12% | 3% |
| 4. Tamaulipan Province | 2% | 2% | 0% | 0% |
| 5. Sonoran Province | 15% | 17% | 17% | 0% |

Trans-Pecos fauna is still nearly devoid of endemics, except for partheno-genetic clonal *Cnemidophorus*. Table 3 makes explicit the clustered relationship between the three divisions. I favor their categorical status as subprovinces.

The Chihuahuan province defined here is also subject to evaluation in terms of faunal endemism within the area it circumscribes. The results are expressed in Tables 4 and 5. One-third of the entire participant herpetofauna has more than half its range contained within the defined Chihuahuan province. In addition, 79% of this third are endemic to the Chihuahuan Desert (isolated relict populations excluded). An ubiquitous desert and plains fauna is second in importance with 26%. A

Sonoran province-centered fauna (i.e., their distributions being more than 50% within the Sonoran Desert by area) is third with 15%. Clearly, the Chihuahuan province is not simply an arid overgrazed extension of the Kansan Plains Province nor just an eastern aspect of the Sonoran Desert. Its largest herpetofaunal unit is Chihuahuan-centered or endemic. This further affirms the biological significance of the base map and the unique nature of the herpetofauna it encribes.

CONCLUSIONS

Four lines of quantitative evidence support the validity of the Chihuahuan faunal province as depicted by the base map. These evidences are as follows:

1. IFC values determined for 80-km (48-mile) squares along the longest axis of the Mexican Plateau indicate that regions of maximal and minimal faunal change occur as predicted by the base map, at the $P \geq 0.01$ level of significance.
2. The primary area affirmed by the IFC values is also distinctive from all contiguous provinces at the 0.60-0.65 level for CC values. This qualifies the Chihuahuan Desert as a faunal province by the quantitative standards established by Hagmeier (1966).
3. The three Chihuahuan Desert subdivisions cluster together at CC values of about 0.60. They are far less differentiated from one another than the Chihuahuan Desert is differentiated from any of the western American deserts. Furthermore, the most distinctive subdivision by CC value, the Saladan Desert, is revealed by SC value to harbor a herpetofauna almost totally shared with the adjacent Mapimian division. It differs only in the depauperate state of its fauna. It is concluded that the Chihuahuan Desert has great internal homogeneity, and that its subdivisions differ from one another only at the subprovince level.
4. The defined Chihuahuan Desert was also analyzed in terms of the general distributions of its herpetofauna. Species with Chihuahuan-centered distributions made the largest single contribution with 33%, of these, four-fifths are endemics.

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Semiaquatic Reptiles and Amphibians of the Chihuahuan Desert and Their Relationships to Drainage Patterns of the Region

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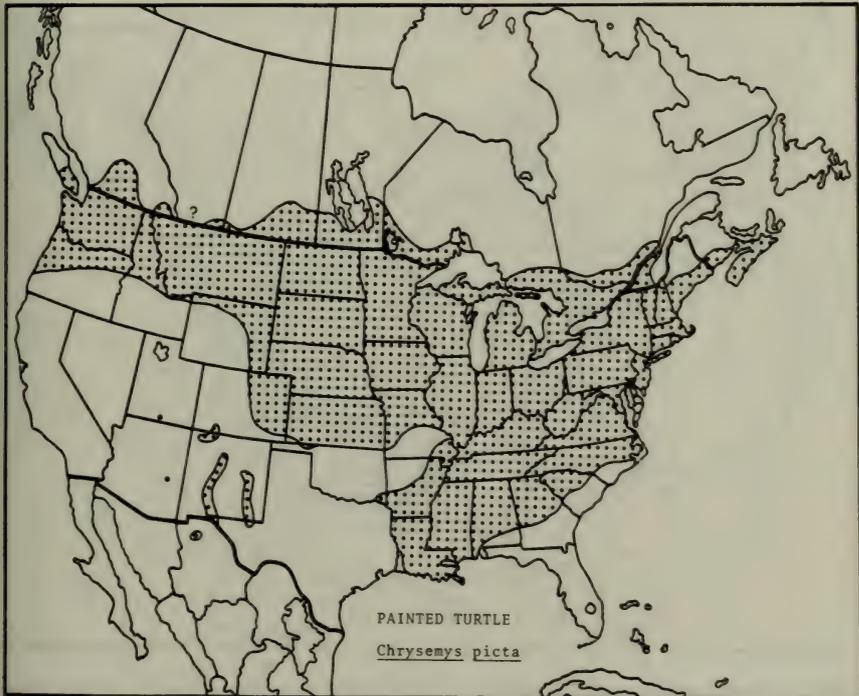
Relict populations of aquatic and semiaquatic organisms are characteristic of many of the desert regions of the world, and they are usually accepted as evidence of climatic changes that resulted in the desiccation of their general environments. Classic examples are the pupfishes of the genus *Cyprinodon*, which survive only in the vicinity of springs in the American southwest and most of which are now endangered because of the usurpation of their water supplies for human activities.

Many deserts are traversed, at least in part, by rivers that have their sources in well-watered highlands and these, almost without exception, have riparian faunas derived from outside the desert borders. For example, the range of the Nile crocodile formerly extended, virtually continuously, along the river of the same name northward from central Africa to its Mediterranean delta (Neill 1971:364), even though the river is directly adjacent to the extremely arid Nubian and Libyan deserts. In Pakistan two softshell turtles, *Trionyx gangeticus* and *Lissemys punctata*, occur in the Indus River and also in the shallow, seasonally fluctuating lakes, marshes, and ditches associated with it (Minton 1966:39, 68, 70). The Indus, in that area, flows between the Thar and Iranian deserts, as mapped by McGinnies, et al. (1968:xxiv-xxv). The water snake (*Natrix tessellata*) in arid Afghanistan is associated with rivers, even some that have interior drainages (Anderson and Leviton 1969:53, Fig. 1). A large number of other examples could be cited.

The Chihuahuan Desert is no exception, and it has its share of relicts as well as species that have followed rivers into otherwise arid terrain. It is not always clear, however, at least in the cases of the amphibians and

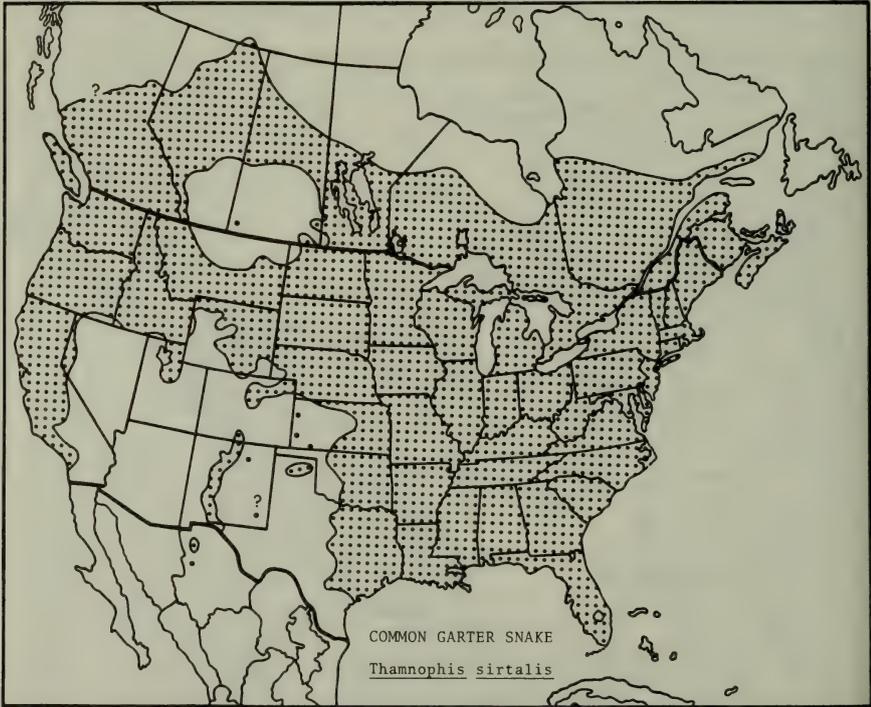
time, with its two principal tributaries, the Pecos River and the Río Conchos, it flowed uninterruptedly to the Gulf of Mexico during all except the driest seasons. Impoundments and diversion of water for human uses, however, have altered the original pattern, and the river is now largely dry downstream from El Paso to its confluence with the Río Conchos. Several lower tributaries of the Rio Grande, the Ríos Sabinas, Salado, and San Juan, have some of their headwaters in the eastern part of the Chihuahuan Desert. Three rivers in northern Chihuahua were formerly part of the Rio Grande system when that stream presumably emptied into the large basin that contains the terminal lakes of the Ríos de Casas Grandes, Santa María, and del Carmen (Brand 1937:15). The upper Rio Grande was eventually captured by the headward-eroding lower Rio Grande-Pecos system, and its waters were diverted to the Gulf of Mexico (King 1935; Kottowski 1958; see summary in Conant 1969:30).

Two other rivers of interior drainage, the Río Nazas and the Río Aguanaval, were part of the Rio Grande system during one or more pluvial periods of the past. Their aquatic and semiaquatic faunas, including



Map 2. General distribution of *Chrysemys picta*. The range is fragmented in the arid Southwest, and the species survives in Mexico only in the Río Santa María.

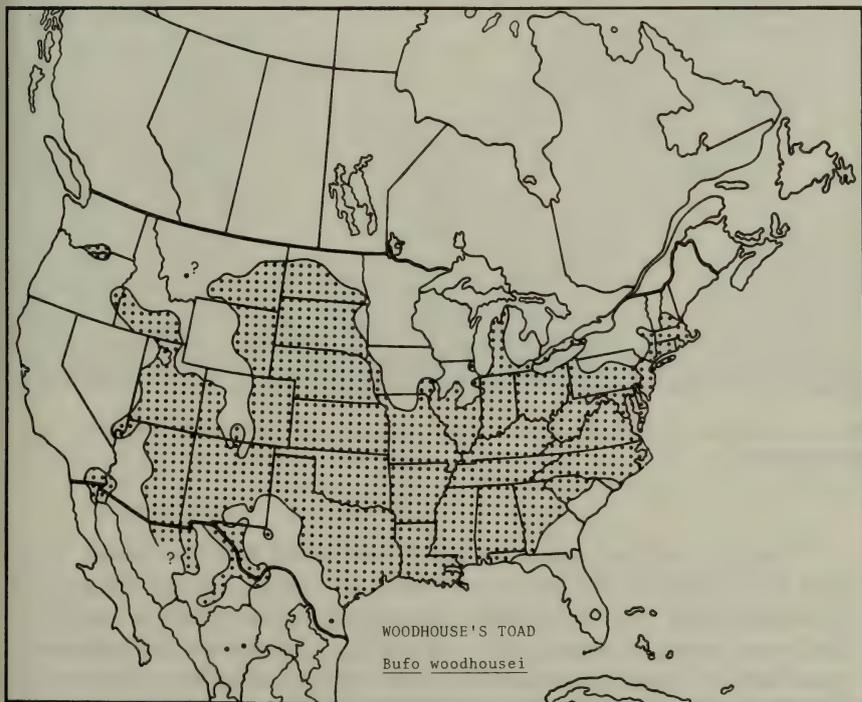
the fishes, are similar to those of the Rio Grande, but the route that they followed across the desert to the master stream is unknown. The Nazas and Aguanaval apparently had a confluence through the gap east of the Sierra de la Peña utilized by the railroad connecting Torreón and Saltillo (Jones 1938:72). The resultant stream, to which I shall refer hereinafter as the Old Río Nazas, may have "flowed north into the Rio Grande near the border line between the states of Chihuahua and Coahuila" as Meek (1904:xxiv) suggested and which Minckley (1969:51) postulated as perhaps the most likely route. Arellano (1951:611 and pers. comm.; see Conant 1963:478) suggested an early eastern exit for the waters of the Nazas-Aguanaval system from the Torreón basin. Another possible route may have been across or near the Cuatro Ciénegas bolsón. Unfortunately, the present status of our knowledge permits little more than speculation. Some of the headwaters of the present Río Mezquital, a stream of Pacific drainage, were once a part of the Old Río Nazas system prior to that river's truncation by vol-



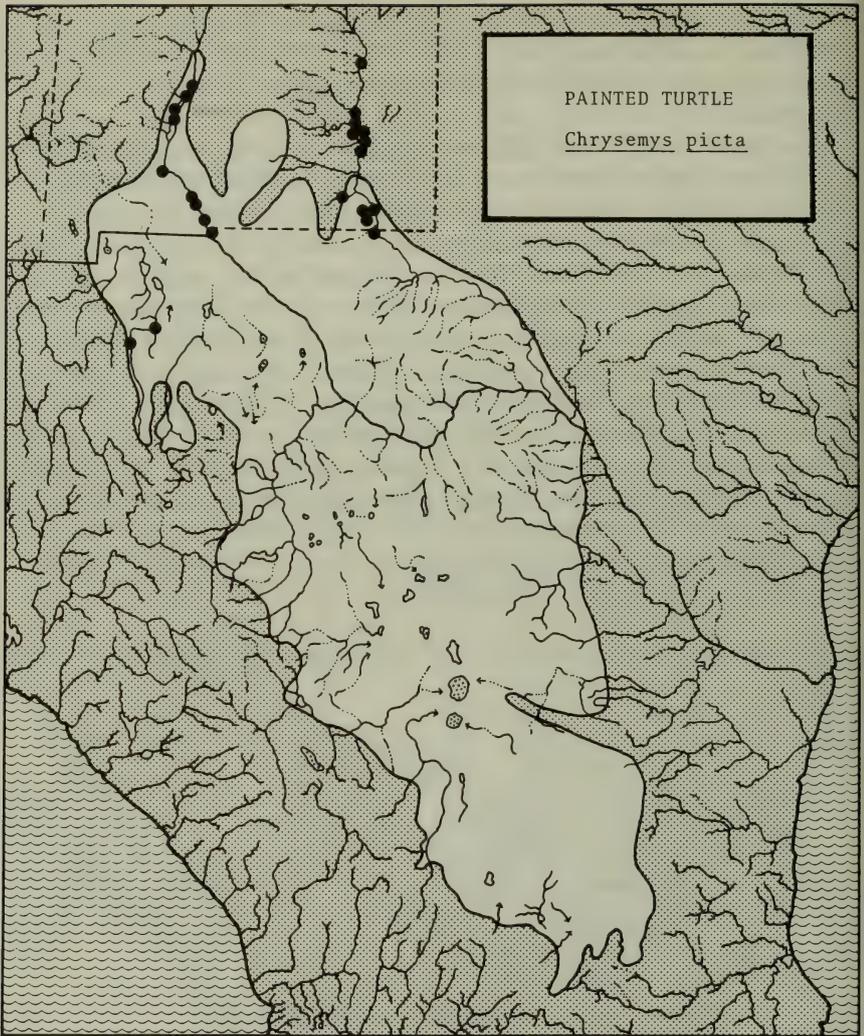
Map 3. General distribution of *Thamnophis sirtalis*. A disjunct population occupies the Rio Grande valley from southern Colorado to the vicinity of El Paso, Texas, and relict populations occur in the Ríos de Casas Grandes and Santa María and in the highlands centered around Yepómera, all in Chihuahua.

canism in the Guadiana Valley. Capture of the Old River headwaters, according to Albritton (1958:1213), may have been initiated at the "canyon incised below the Sierra Registro pediment at the falls of the Mezquital."

The typical river of the Chihuahuan Desert is a narrow, often shallow, stream bordered by a tenuous gallery forest, usually of cottonwoods and willows, but often also associated with Mexican cypress or plane trees. The rivers of northern Chihuahua were described in detail by Brand (1937) and the Río Nazas and the Río Aguanaval, in Durango and Zacatecas, respectively, by Conant (1963). All the Chihuahuan Desert rivers are subjected, virtually every year, to severe flooding during the summer Mexican monsoon and to desiccation during the dry season, which extends from November through much of June. The width and density of the gallery forest is a good indicator of the effects of the perennial low-water period. The flanking rows of trees are virtually uninterrupted along those rivers in which the flow is more or less continuous, albeit often subterranean. They are intermittent or absent for long stretches parallel to those streams that are reduced to isolated, stagnant pools during the dry months.

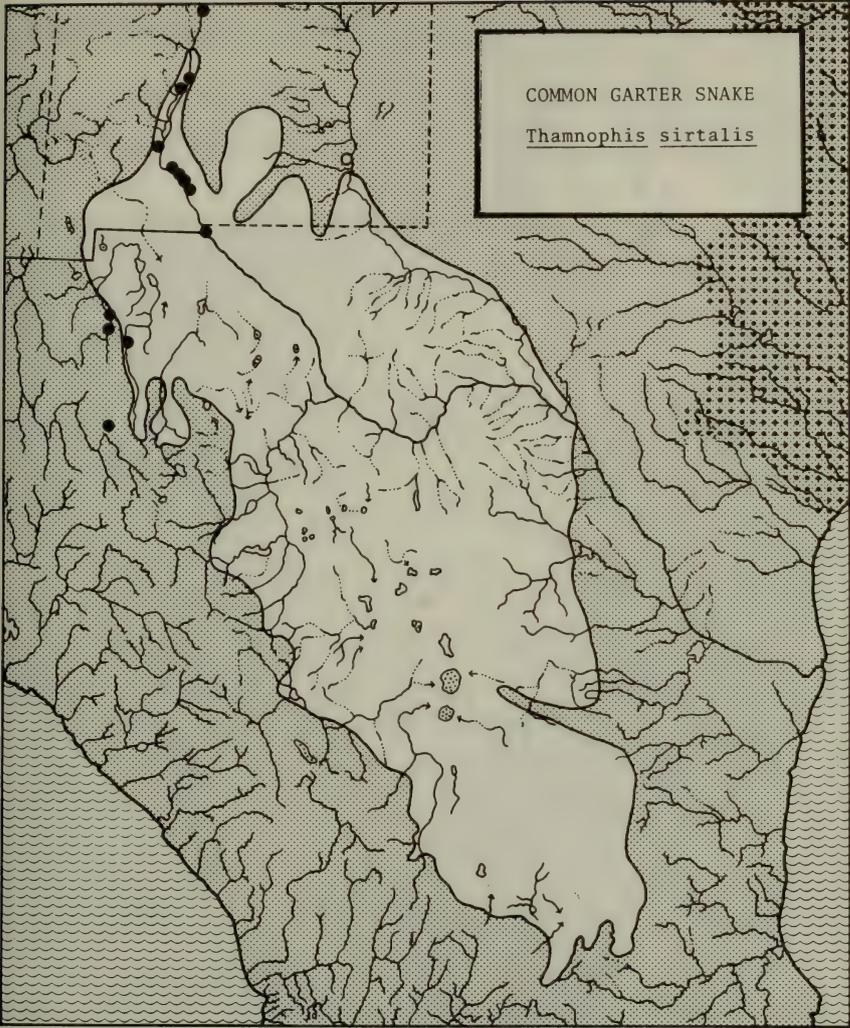


Map 4. General distribution of *Bufo woodhousei*.



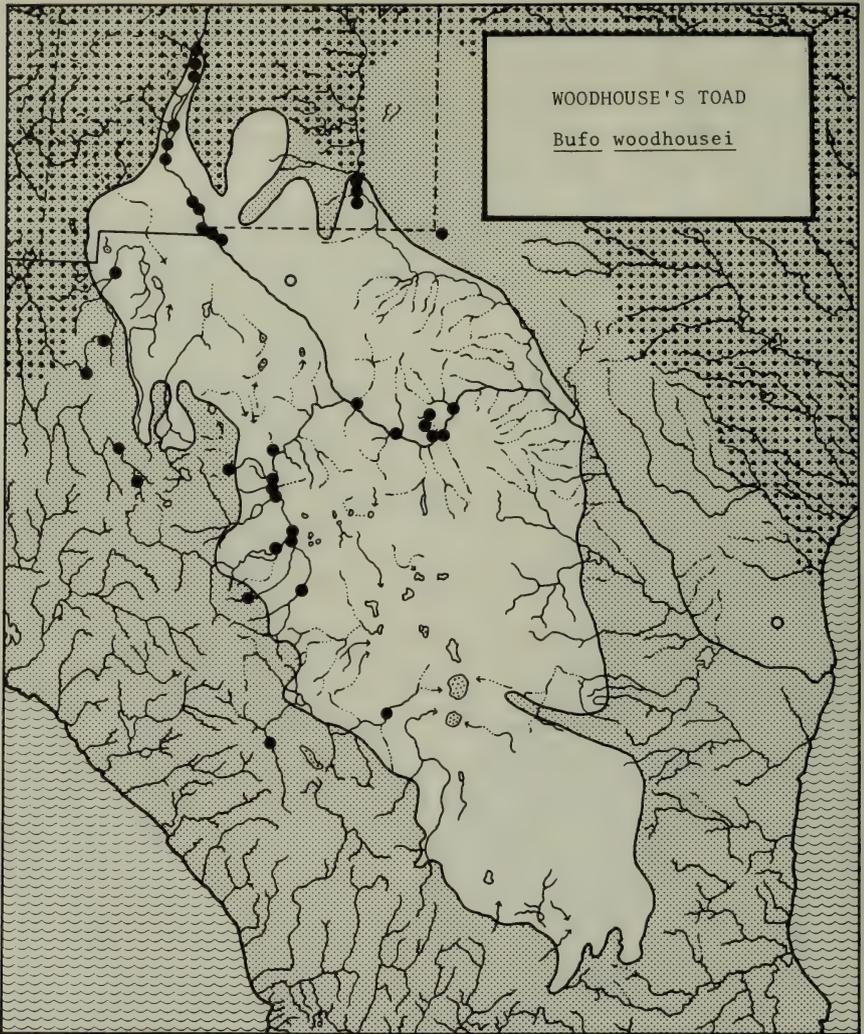
Map 5. Localities for *Chrysemys picta*, a species that presumably entered the Chihuahuan Desert from the north.

All aquatic and semiaquatic animals associated with the desert rivers must be adjusted to the harsh conditions that prevail during the periods of stress—flood and desiccation. During high water, based on personal field observations, snakes often take refuge in trees or partially inundated shrubs. They, as well as the other animals, also may move to the margins of the flooded areas where the current is slight, but, as the waters recede, they may become isolated in temporary pools often at



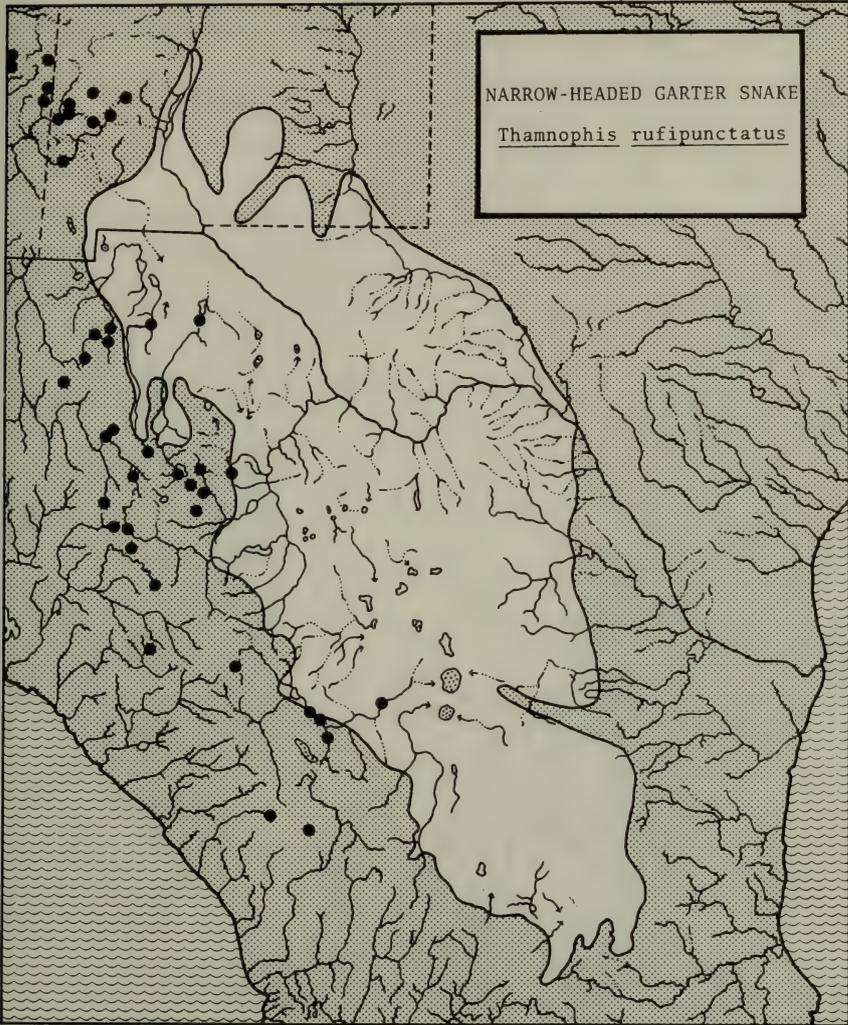
Map 6. Localities for *Thamnophis sirtalis*. The hollow circle in southeastern New Mexico indicates a record that requires confirmation. The stippled pattern in the upper right portion of the map, a device that is also used on many of the other detailed locality maps, represents a nearby portion of the range where the distribution of the species is more or less continuous.

some distance from the retreating streams. Fishes and tadpoles are frequently trapped in such ephemeral habitats where they eventually serve as food for many of the other components of the riparian faunas. The air-breathing reptiles and transformed amphibians can, of course, return to the rivers at will.



Map 7. Localities for *Bufo woodhousei*. Although this species is widespread through Texas, New Mexico, and Arizona, it enters the Chihuahuan Desert only along the rivers.

During the dry season, the various organisms usually retreat to the surviving pools of water. Most such pools are situated where the current engendered by the summer rains has scoured deeply, as against a bank where the direction of flow changes sharply or where rocks, ledges, or logs form impediments. Usually the pools are bordered by trees, often of large size, that have a year-round source of water and among the roots and environs of which small animals find abundant shelter. If the flow ceases altogether at least some of them may estivate.

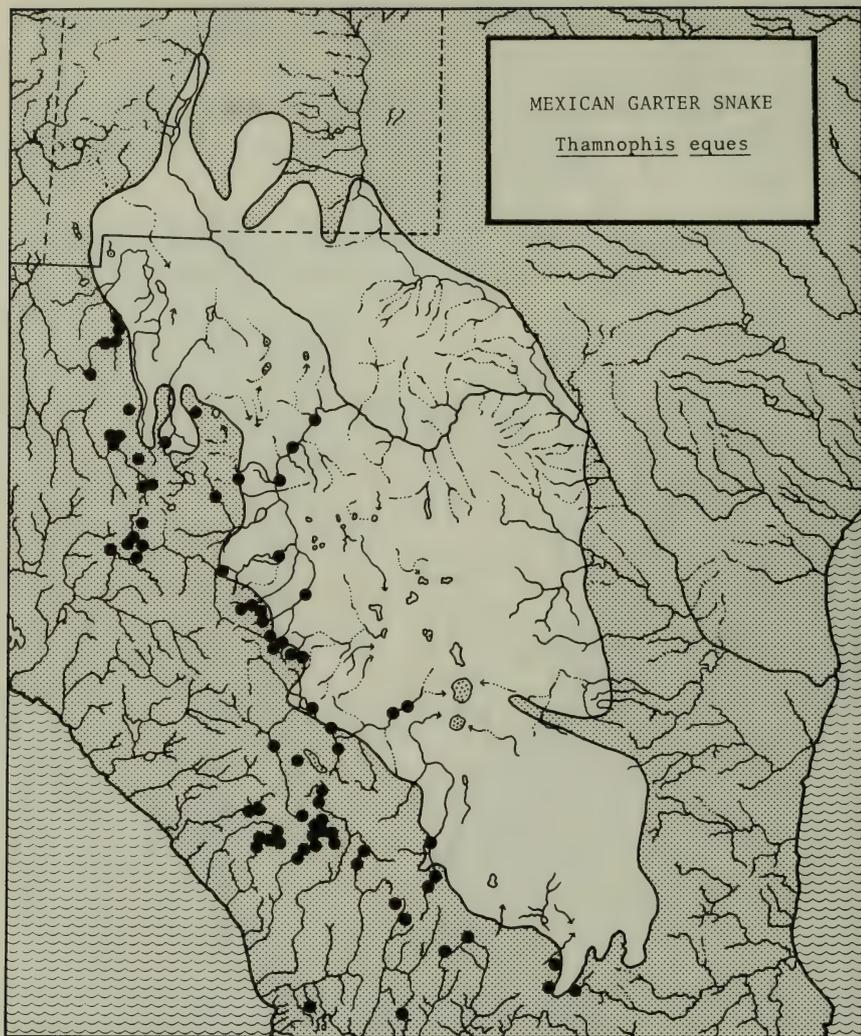


Map 8. Localities for *Thamnophis rufipunctatus*, a species chiefly of the uplands but which also occurs in some of the desert rivers.

The desert rivers, in short, may be described as harsh but fragile environments. Any marked diminution or interruption of stream flow or elimination of the gallery forest as a result of subnormal rainfall or the activities of mankind can have a profound effect on the riparian fauna.

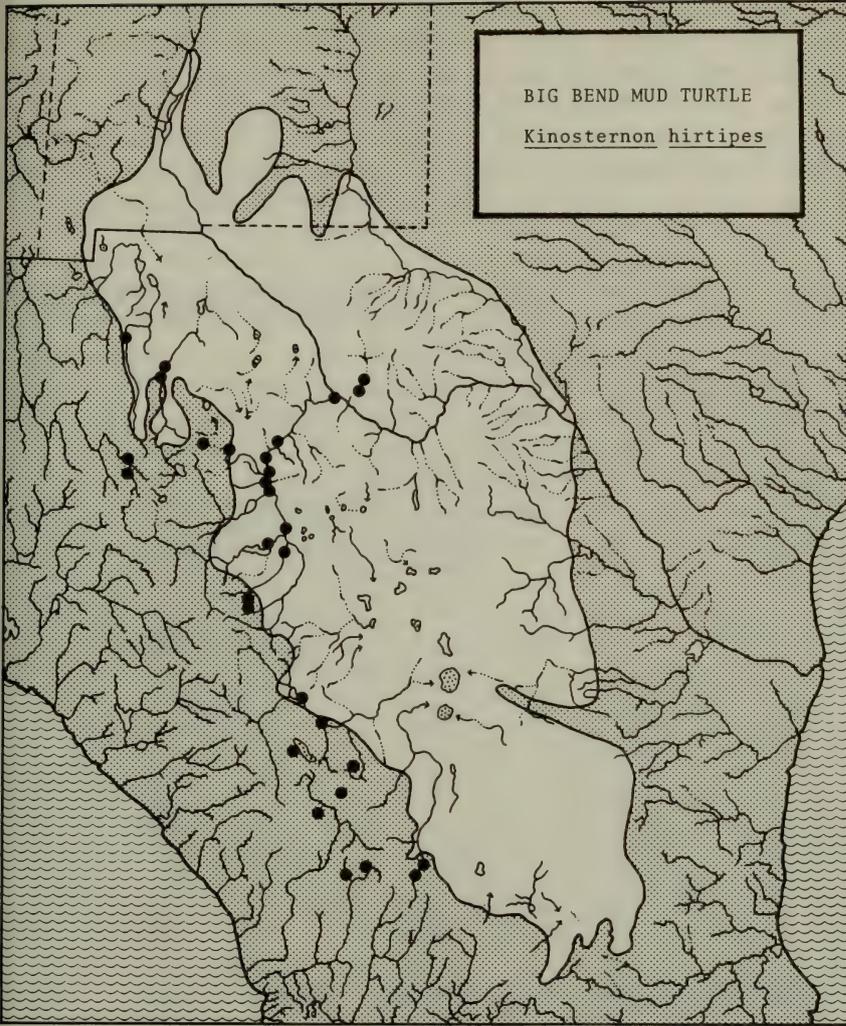
DISTRIBUTIONAL PATTERNS

It is instructive to examine the distributions of the reptiles and amphibians inhabiting the Chihuahuan Desert streams and to speculate on



Map 9. Localities for *Thamnophis eques*. The hollow circle in southwestern New Mexico represents an old record for "Duck Creek."

their avenues of entrance into the region where they survive as relicts or where they are living as components of the well-distributed river faunas. Because this is a continuing study and the fossil record has not been examined in detail, I make no attempt at the moment to estimate when the various species may have reached the desert or when their ranges may have become disjunct. Meanwhile, I accept the statement by Martin (1958:375-376) that: "Until proved otherwise, the more useful working

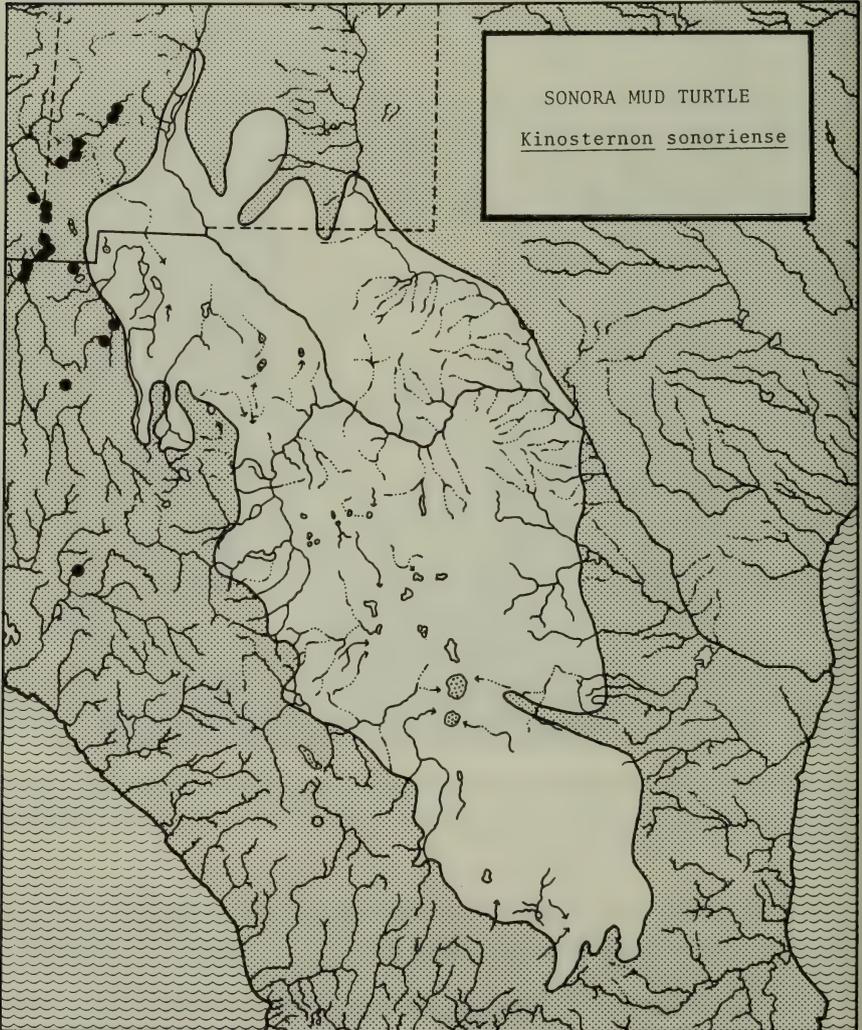


Map 10. Localities for *Kinosternon hirtipes*. This turtle occurs in many of the desert rivers including all three fragmented parts of the Old Río Nazas. As a whole, it ranges from Trans-Pecos Texas at least as far south as the Mexican state of Morelos.

hypothesis is that existing range gaps and relict populations date from the Glacial period.”

Two reptiles and one amphibian presumably entered the region from the north. Both reptiles, the painted turtle (*Chrysemys picta*) (Map 2) and the common garter snake (*Thamnophis sirtalis*) (Map 3), have ranges that extend from the Atlantic seaboard to the Pacific coast. The

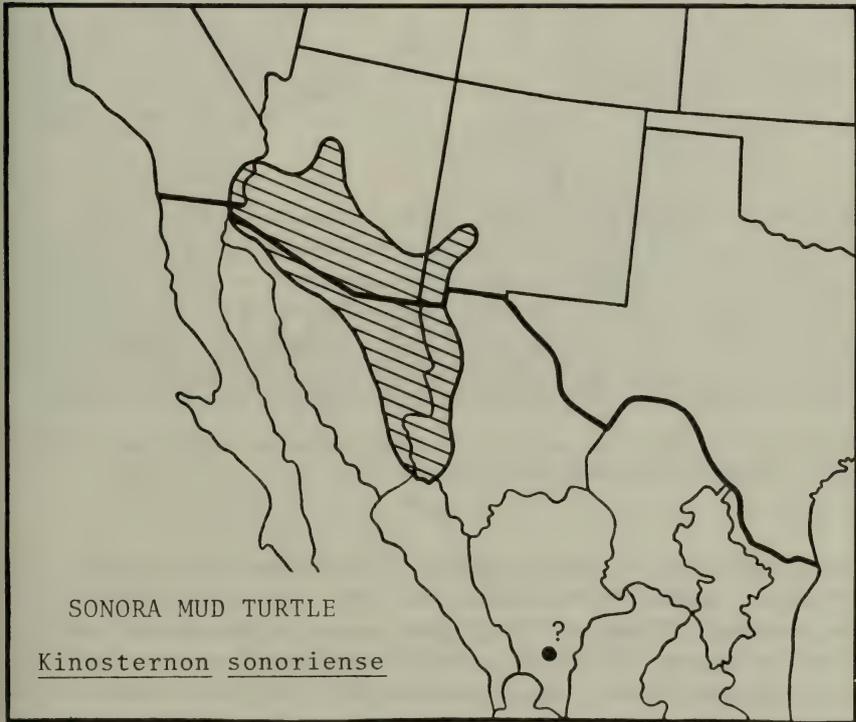
single amphibian, a toad (*Bufo woodhousei*), has a longitudinal distribution (Map 4) that is almost as extensive. All three have fragmented ranges in the southwest, but all are relatively common along the Rio Grande in New Mexico. The occurrence of the two reptiles in the Chihuahuan Desert in Mexico, *Chrysemys picta* in the Río Santa María (Map 5) and *Thamnophis sirtalis* in both the Santa María and Casas Grandes (Map 6), is best explained by the fact that when the upper Rio



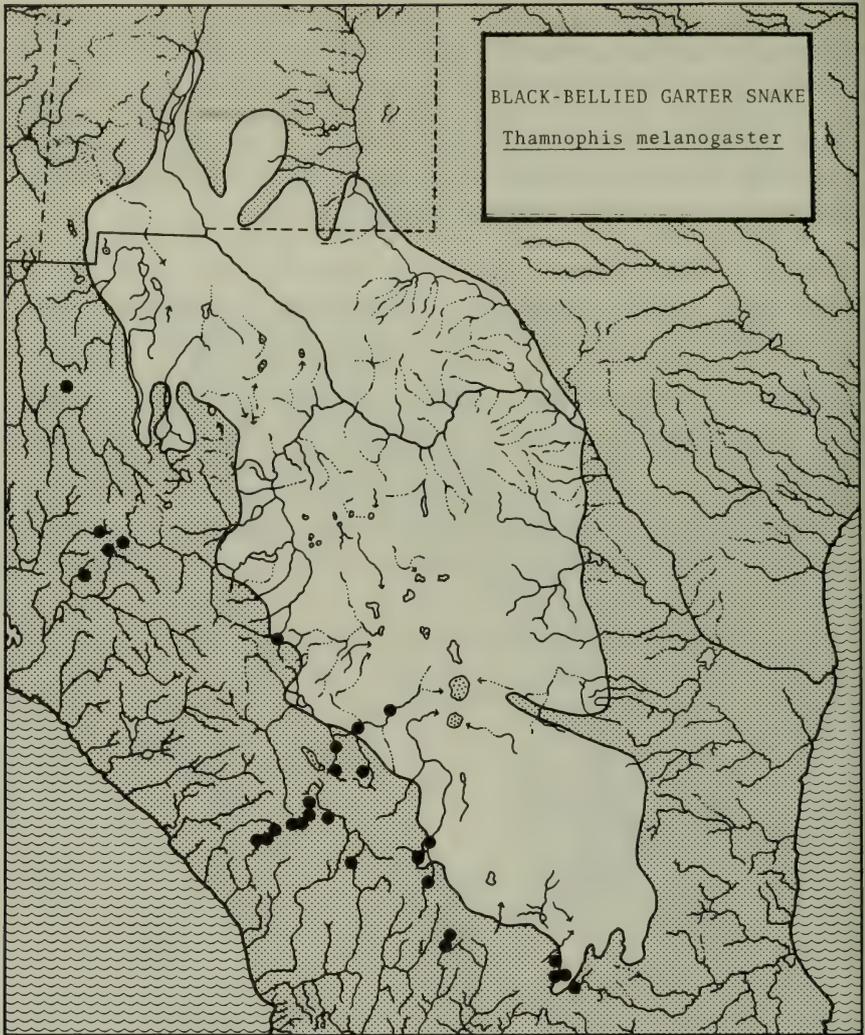
Map 11. Localities for *Kinosternon sonoriense*. The range of this species complements that of *K. hirtipes* northwest of the Chihuahuan Desert.

Grande drained into the great depression of northern Chihuahua and adjacent New Mexico, before its capture by the lower Rio Grande, both species probably were widespread through the region. The now isolated Lagunas de Guzmán, Santa María, and Patos occupied much greater areas and were probably coalescent, at least in part (Brand 1937:15; Axtell this volume). The turtle and the snake have survived in suitable habitats in and near the northward flowing rivers.

Bufo woodhousei is much more widely distributed through the Chihuahuan Desert (Map 7) than either the turtle or the snake. It occurs in many localities along the Rio Grande and in a large part of the drainage system of the Río Conchos. Such a distribution suggests a penetration southward along the streams and utilization of temporary rainpools along and near their banks during the wet season. The populations in the Pecos River and the Río de Casas Grandes presumably have also worked downstream from areas in which this species is widely distributed. *Bufo woodhousei* may be relict in the Río Nazas, but the possibility that it reached that stream by an overland route along the eastern versant of the Sierra Madre Occidental cannot be overlooked. Cur-

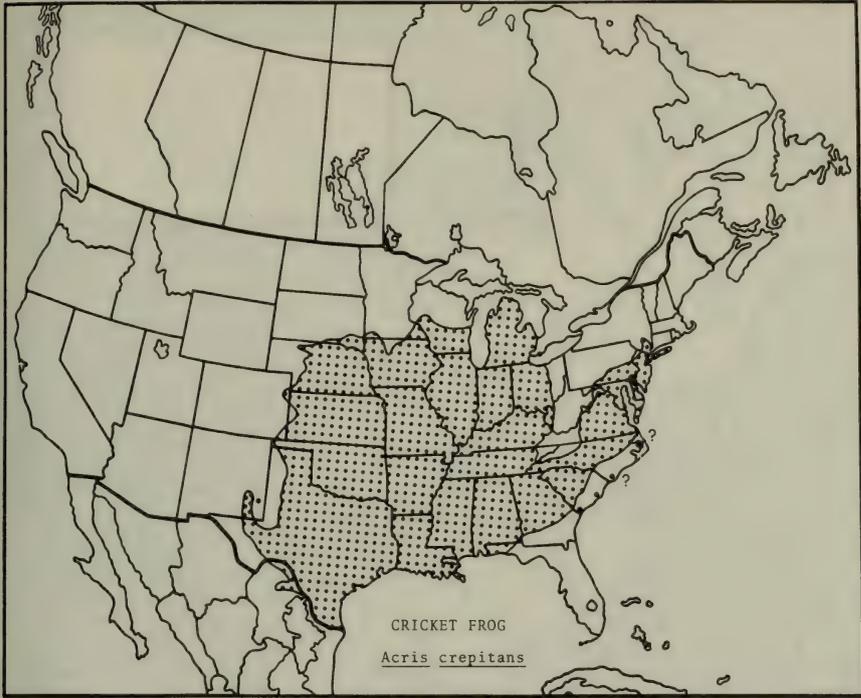


Map 12. General distribution of *Kinosternon sonoriense*.



Map 13. Localities for *Thamnophis melanogaster*, a species that also ranges widely through the volcanic belt across southern Mexico.

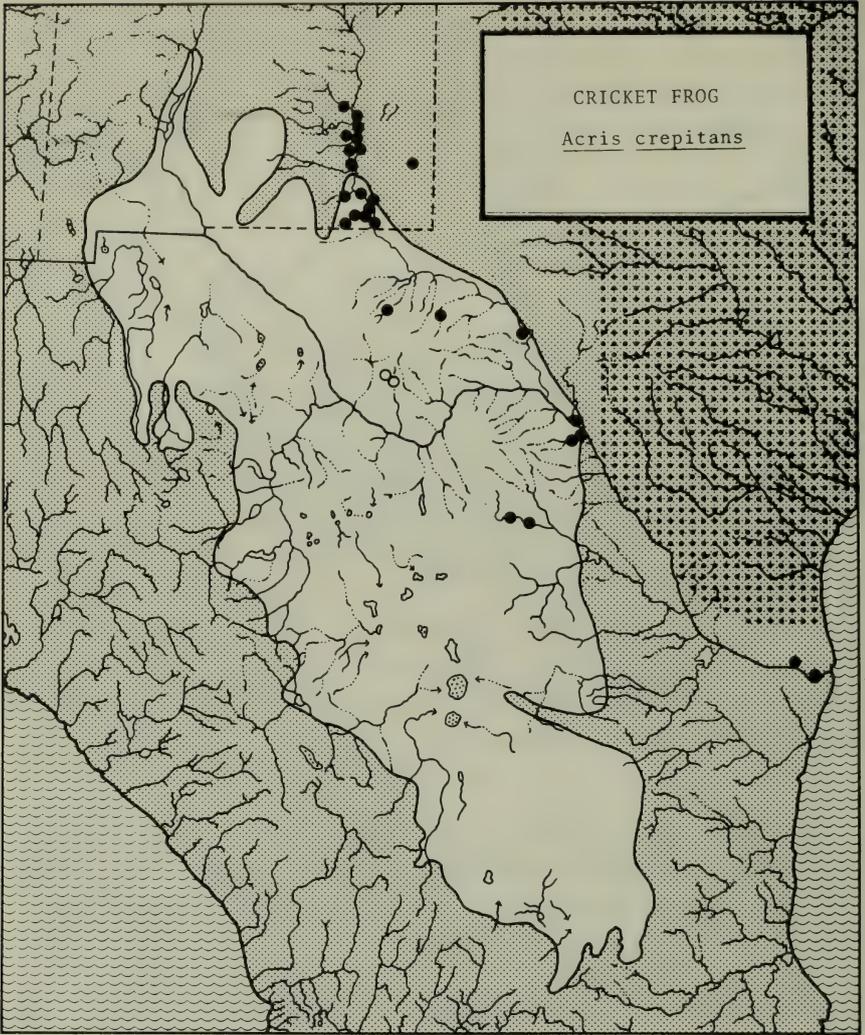
rently, there are no records between Santa Barbara in Chihuahua and Santiago Papasquiario in Durango, which are separated by a distance of approximately 200 km (125 miles), but the area between them is still difficult of access. The presence of *B. woodhousei* may eventually be demonstrated in that region, and possibly also in the direction of Mifiaca, which is the next nearest upland locality northwest of Santa Barbara.



Map 14. General distribution of *Acris crepitans*.

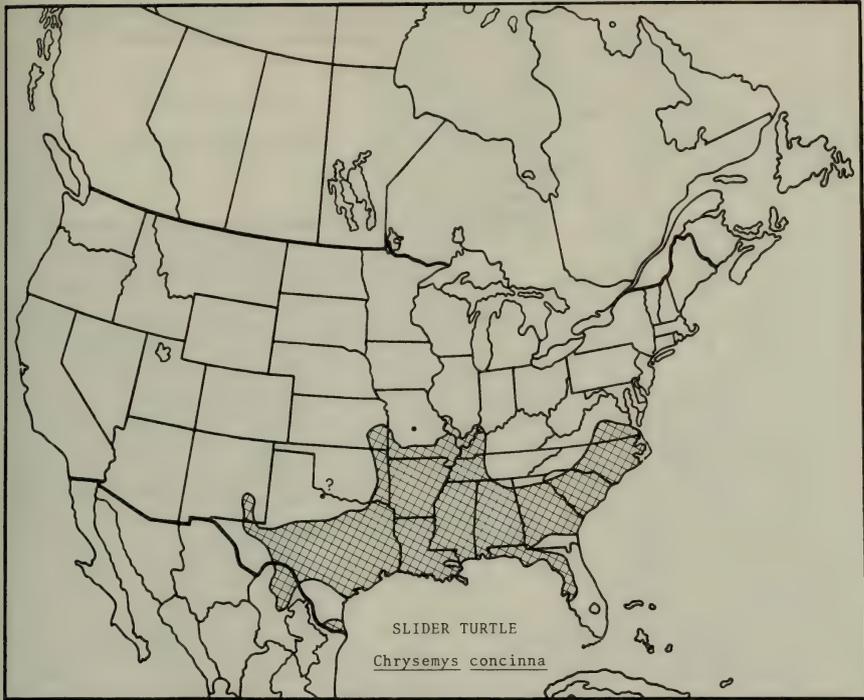
The narrow-headed garter snake or pichicuate (*Thamnophis rufipunctatus*) evidently entered the Chihuahuan Desert from the northwest. Its total range extends from central Arizona to central Durango (Conant 1963; Fig. 8). Most localities for it in Mexico are in the uplands (Map 8), but there is one old record each from the Río Santa María and the Río del Carmen. The latter is based on a specimen collected in the vicinity of Villa Ahumada in 1903. There are recent records for the Río Nazas, including La Goma, which is well out in the desert. The absence of *T. rufipunctatus* from the Río Aguanaval and the Guadiana Valley, adjacent to Ciudad Durango, suggests that it may have entered the Nazas at a relatively recent time.

Three other species, a turtle and two snakes (Maps 9, 10, and 13), occur in all three former components of the Old Río Nazas system—the present Nazas, the Aguanaval, and the headwaters of the Mezquital. Two of these, the Mexican garter snake (*Thamnophis eques*) and the Big Bend mud turtle (*Kinosternon hirtipes*) may have entered the desert from the west. *T. eques* ranges from Arizona to the Valley of Mexico and the Pueblan Desert, and it also has outlying populations in Oaxaca



Map 15. Localities for *Acris crepitans*. The hollow circles in Trans-Pecos Texas, on this and in the same places on other maps, represent localities reported by Strecker (1909). His specimens (of many species) were lost subsequent to their collection (Conant 1969: 30). It is probable that some or all of the species he found are now extinct in the area.

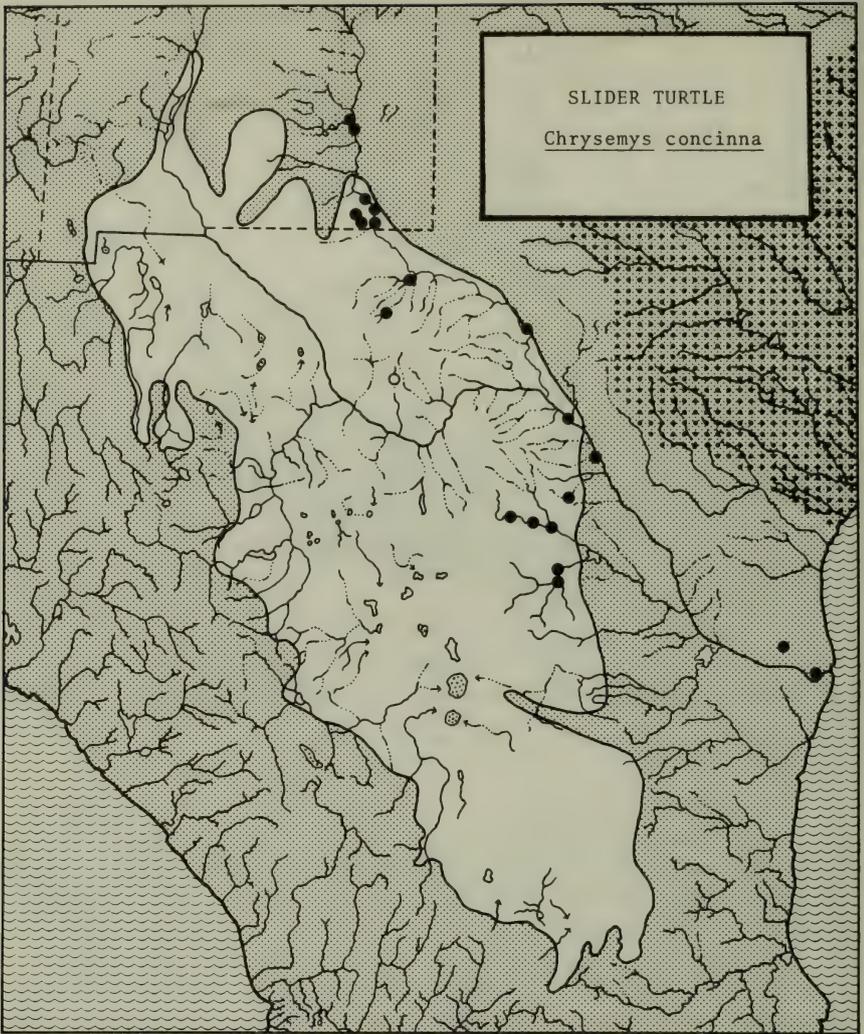
(Conant 1963; Fig. 10). In western Mexico its distribution strongly resembles that of the narrow-headed garter snake. It is abundantly represented in the uplands, but it also occurs in many more localities along the desert streams (Map 9) than does *T. rufipunctatus*. It is widespread through the Río Conchos drainage system, and even descends the main



Map 16. General distribution of *Chrysemys concinna*.

river to the vicinity of Cuchillo Parado, which is close to the Río Bravo. It also occurs in the Río Nazas as far downstream as Ciudad Lerdo in the Laguna District, and in the Río Aguanaval at the Presa Cazadero. It is likely that future field work may demonstrate its presence at numerous other localities in desert streams. Whether its absence from the desert portions of the three rivers of northern Chihuahua is real or an artifact of insufficient collecting may be difficult to ascertain at this late date. Changes in those streams have been pronounced as a result of impoundments. Also, the introduction of the bullfrog probably has had a serious effect on this species as well as all the other members of the riparian faunas. The apparent complete absence of *T. eques* from New Mexico except for an old record for Duck Creek (Cope 1900: 1026) suggests that the range of the species shifts westward in the United States.

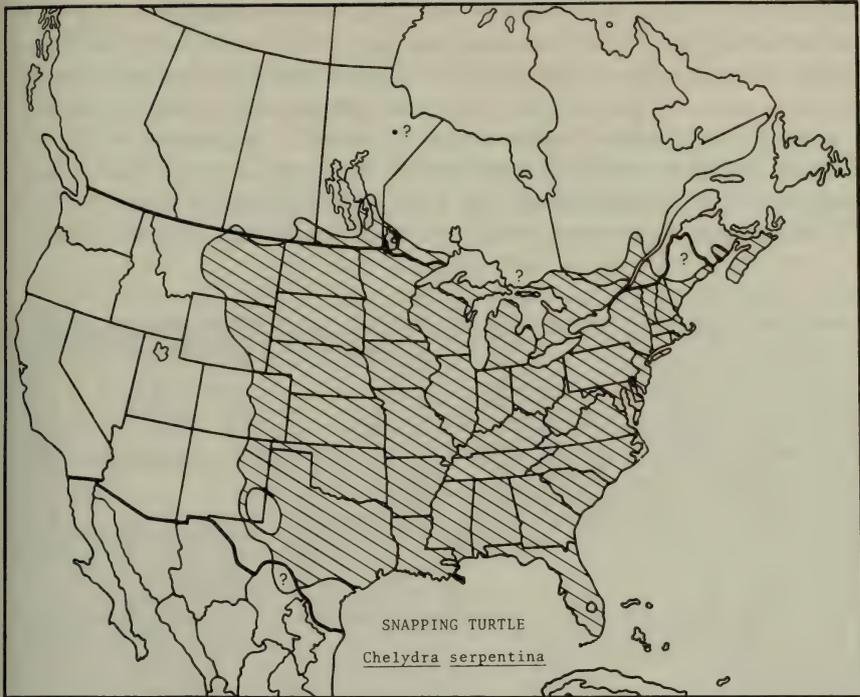
T. eques, although it is closely associated with water, is not so aquatic as the two other garter snakes, *T. rufipunctatus* and *T. melanogaster*, that frequently occur with it. It is capable of overland movement in wet weather, and one can postulate that during pluvial periods its range might have expanded outward from the mountains more rapidly than



Map 17. Localities for *Chrysemys concinna*.

those of its two associates and, conversely, it may have contracted more slowly as the climate deteriorated during extended periods of drought. Its vagility may have been a factor in enabling *T. eques* to reach a number of localities where it now survives as a relict.

Kinosternon hirtipes (Map 10) has a distribution that, in part, parallels that of the Mexican garter snake. It is widespread in the Río Conchos, and it even occurs north of the Rio Grande in the valley of Alamito Creek in western Texas. It is present in the Río Nazas and the



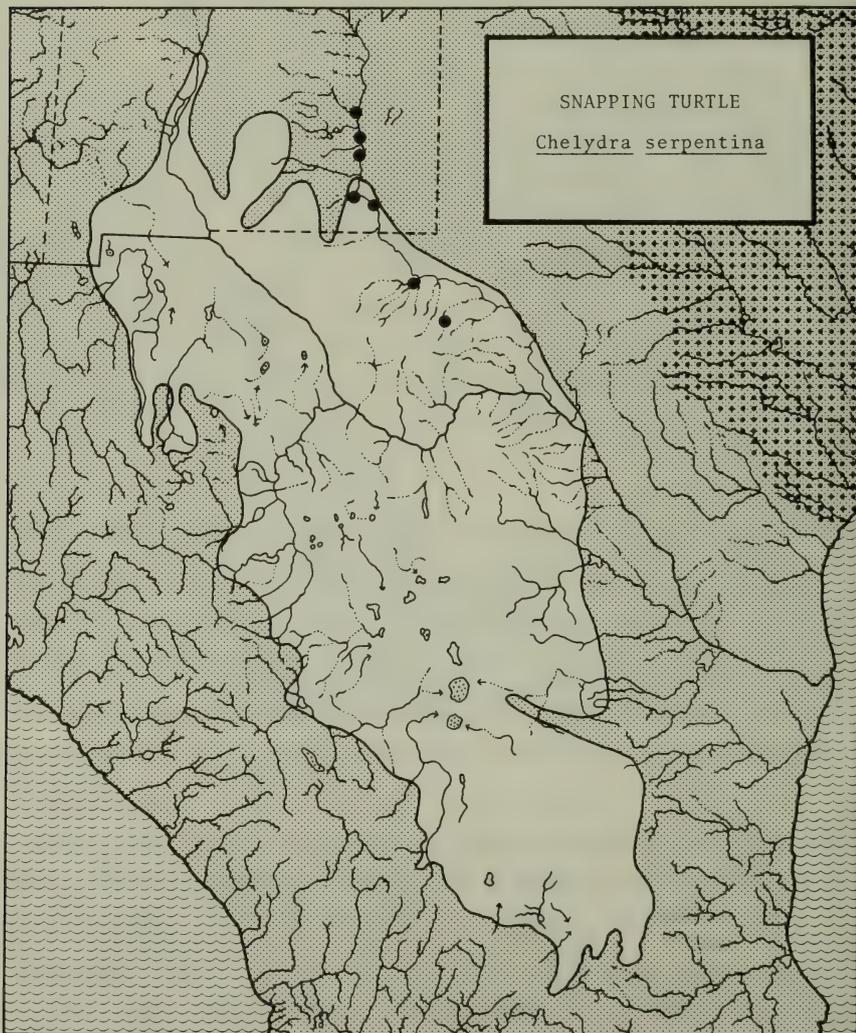
Map 18. General distribution of *Chelydra serpentina*.

Río Aguanaval, and probably enters the desert in the downstream portions of both rivers, although an active trapping campaign would be required to confirm this. During very recent field work, we obtained this species in two of the rivers in northern Chihuahua—at the impoundment behind the Presa las Lajas in Río del Carmen drainage and in roadside pools at Galeana close to the Río Santa María.

The very similar Sonora mud turtle (*Kinosternon sonoriense*) has been erroneously reported from the Chihuahuan Desert. The two species, *K. sonoriense* and *K. hirtipes*, have long been confused, and literature records for them cannot be trusted. Actually, the two species have almost exactly complementary ranges; *K. hirtipes* occurs in many places in the Chihuahuan Desert, but *K. sonoriense* stops just short of it (Map 11). The Sonora mud turtle is a western species (Map 12) that ranges from the lower Colorado River in California to New Mexico and western Chihuahua. There is an isolated record from Durago that requires confirmation. Throughout much of its range *K. sonoriense* occurs in the uplands.

The black-bellied garter snake (*Thamnophis melanogaster*) probably

entered the Chihuahuan Desert from the south (Conant 1963: Fig. 9). It occurs in all three of the now disjunct components of the old Río Nazas (Map 13); pattern characteristics and other evidence indicate that the species was well established in the Old Nazas prior to that river's dismemberment by desiccation and volcanism. It is present within the border of the desert along both the Río Aguanaval and the Río Nazas, and also close to the city of San Luis Potosí. It has achieved the Río Florido in the southernmost part of the Río Conchos system, possibly

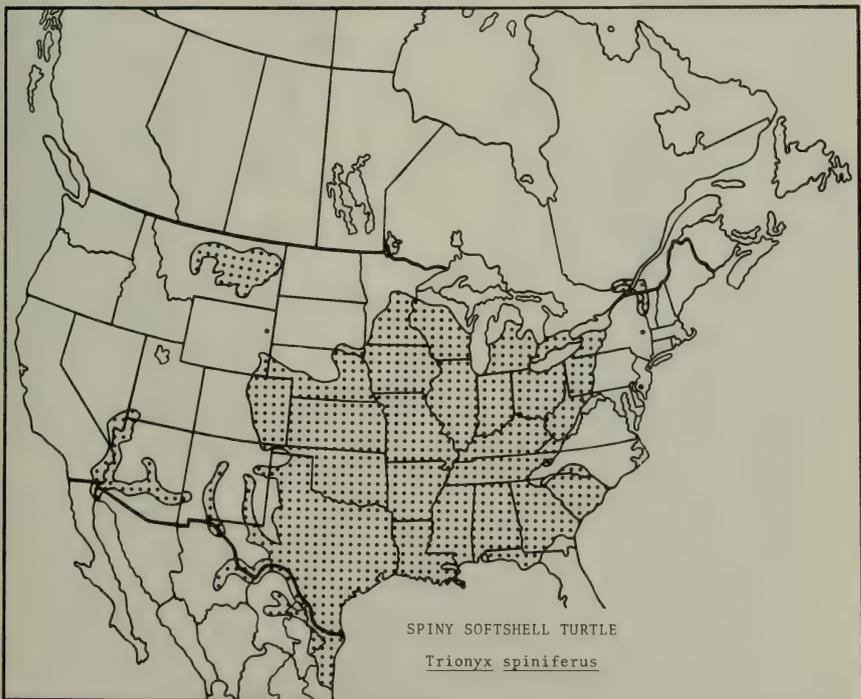


Map 19. Localities for *Chelydra serpentina*.

by an overland route between the Arroyos Tizonazo and del Canutillo as I implied in an earlier paper (Conant 1963:484). This snake is not known presently from any other locality in the Río Florido or elsewhere in the Conchos complex.

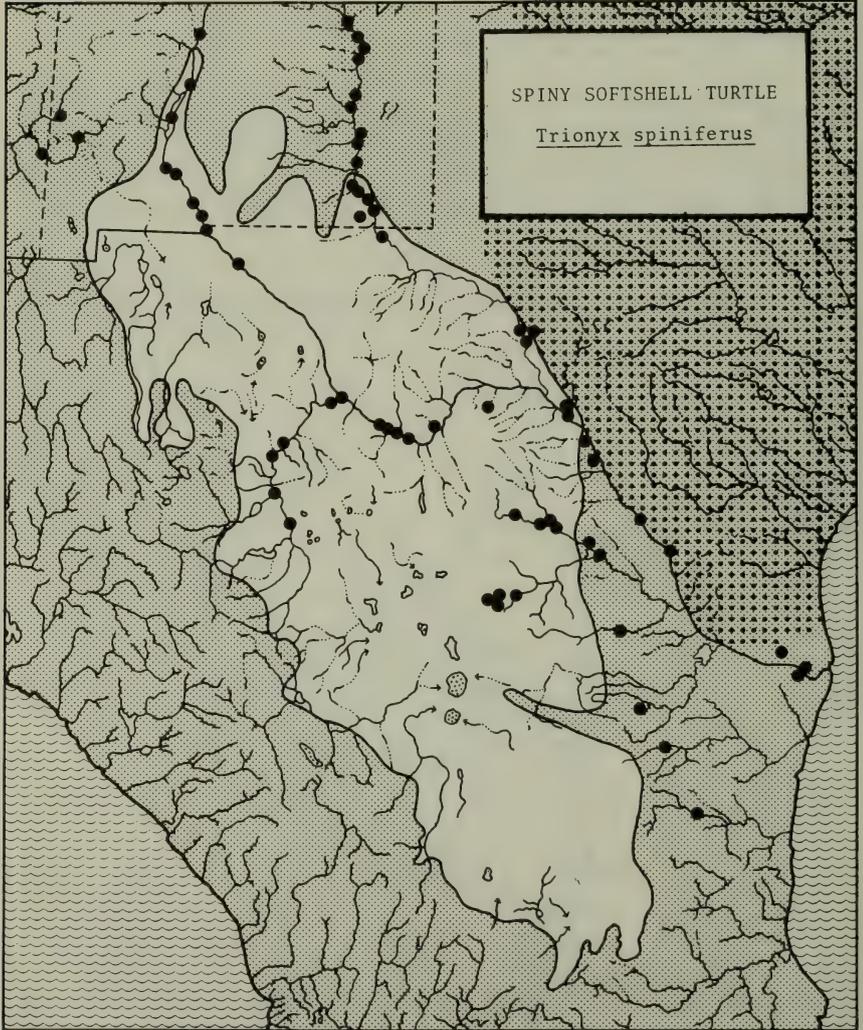
As we have seen, a relatively few species of semiaquatic reptiles and amphibians apparently have entered the Chihuahuan Desert from the north, west, and south. Many more have come from the east as Milstead (1960) pointed out. They achieved their present distributions either by working their way headward along the Rio Grande and its tributaries, or they remain as relicts in favorable habitats within the now partly desiccated dendritic branches of what was a much stronger flowing river system during past pluvial periods.

A frog and two turtles occur in the Pecos or Sabinas-Salado systems or both. The cricket frog (*Acris crepitans*) (Map 14) ranges from Michigan and the mid-Atlantic coast of the United States to Texas and Coahuila. In the latter areas (Map 15) it occurs in the Río Sabinas, along the middle Rio Grande, and in Pecos drainage, and there are a



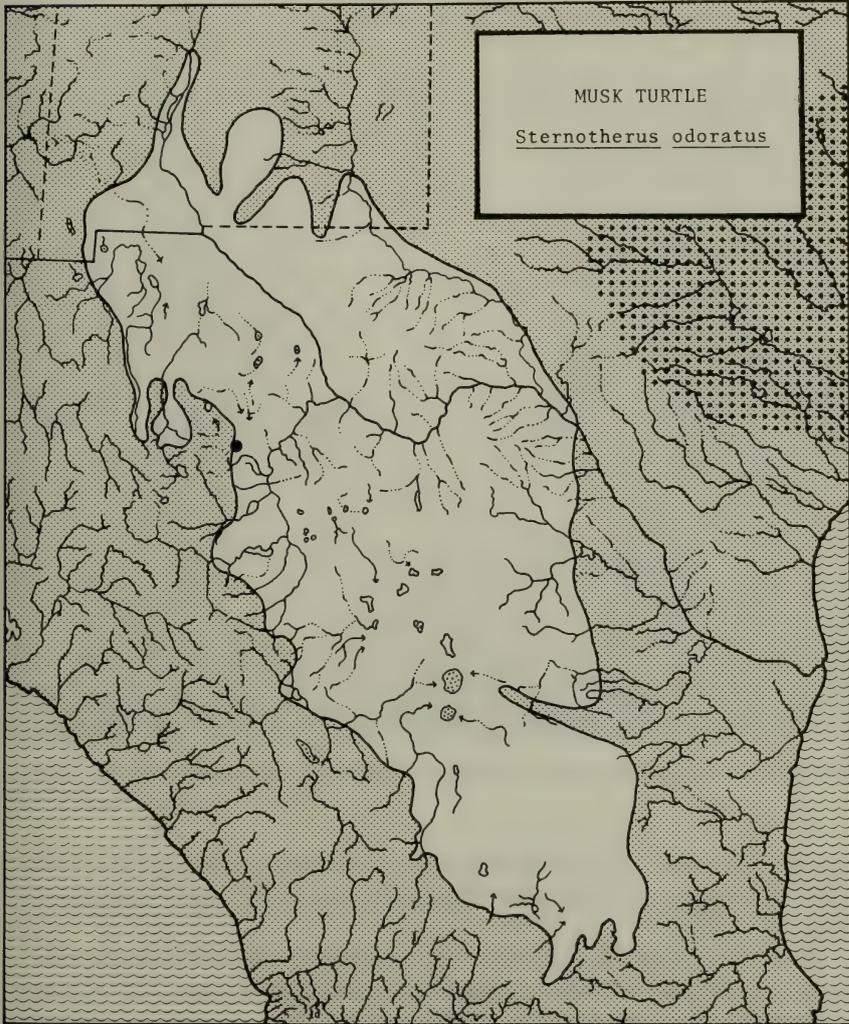
Map 20. General distribution of *Trionyx spiniferus*. This largely fluviatile turtle is restricted exclusively to rivers and their immediate environs in the southwestern portion of its range.

large number of localities for the species in the well-collected lower part of the Pecos Valley in New Mexico. Two old localities from Calamity Creek in the Big Bend region (Strecker 1909:15) cannot be confirmed (see caption for Map 15). The slider (*Chrysemys concinna*) (Map 16), which is more southern in general distribution, has a range in the southwest (Map 17) that closely parallels that of the cricket frog, although it also is known from the Río Salado. The snapping turtle (*Chelydra serpentina*) (Map 18), which ranges widely over the eastern

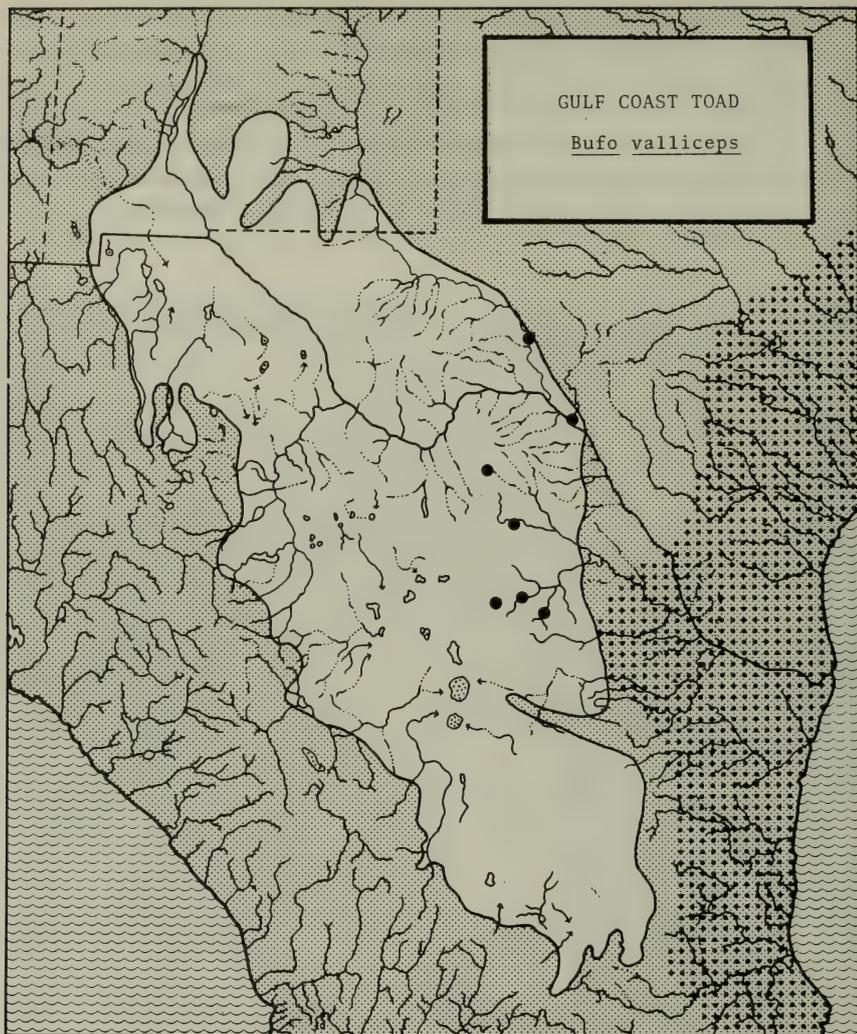


Map 21. Localities for *Trionyx spiniferus*.

United States and from southern Canada to the Gulf of Mexico, also occurs in the Pecos River system (Map 19). The spiny softshell turtle (*Trionyx spiniferus*) (Map 20), a species that is largely associated with the rivers of the central and southern United States, has a fragmented range in the southwest. Its presence in the lower Colorado River basin probably resulted from the introduction of the species into the Gila River system by human action about the beginning of the 20th century



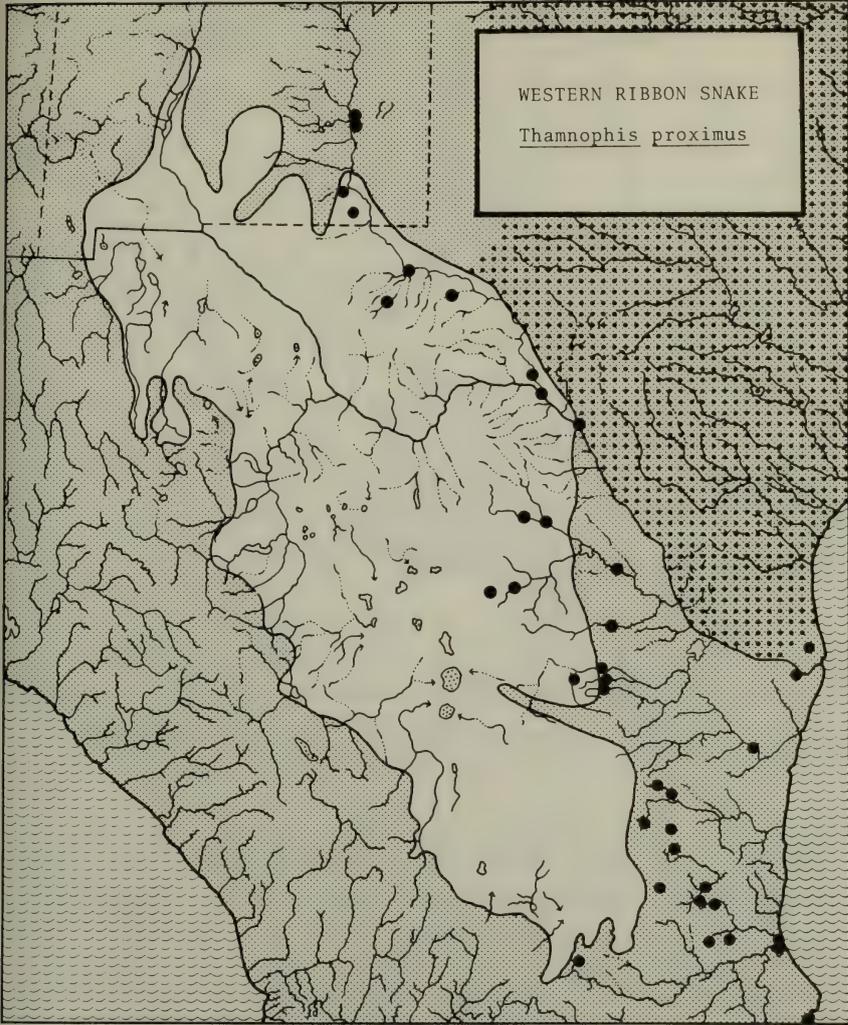
Map 22. Locality near El Sauz, Chihuahua, for *Sternotherus odoratus*. This isolated record, dating from 1903, is based on apparently unimpeachable collecting data.



Map 23. Localities for *Bufo valliceps*, a species that ranges from Louisiana to Costa Rica.

(Miller 1946:46). This turtle (Map 21) is widespread through the Pecos, Grande, Conchos, Sabinas, and Salado systems, and it also occurs in the Cuatro Ciénegas bolsón.

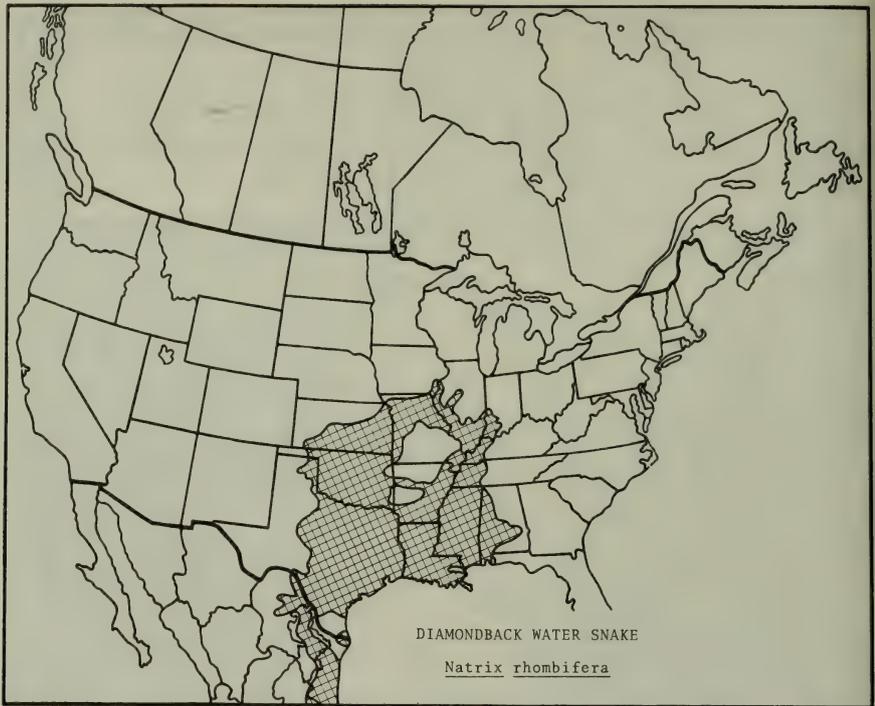
A puzzling isolated record for the musk turtle (*Sternotherus odoratus*) (Map 22) deserves brief comment. A specimen collected at El Sauz, Chihuahua, in 1903 by S. E. Meek, bears cloth tags that presumably were attached to it in the field, so there is little likelihood that data were transposed from another specimen from the main part of the range



Map 24. Localities for *Thamnophis proximus*, the general range of which extends from Wisconsin and Indiana to Costa Rica.

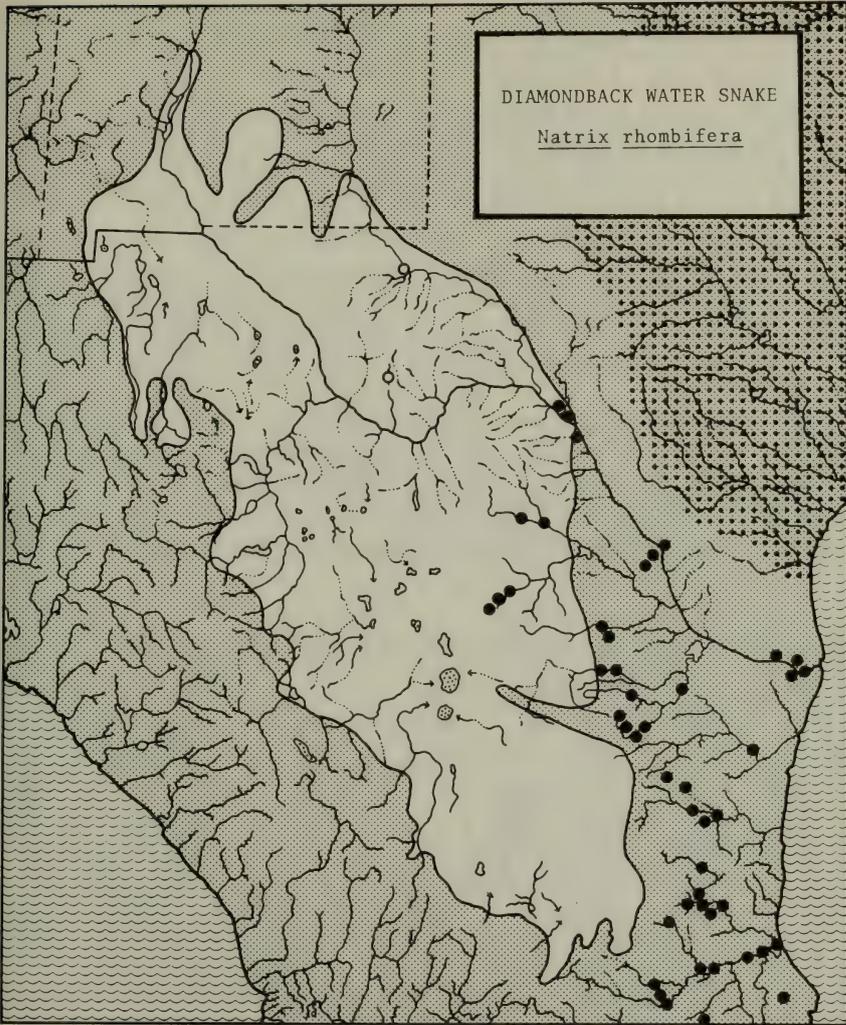
(Moll and Williams 1963). There is no other evidence that this turtle occurs in the Chihuahuan Desert. A dubious record from Presidio County, Texas, that was mentioned by Brown (1950:230), is based on a specimen of *Kinosternon hirtipes* (Conant and Berry, in press).

A toad and two snakes, with ranges extending from the United States southward through Mexico and, in two cases, to Central America, also enter the Chihuahuan Desert, and their distributions in the region ap-



Map 25. General distribution of *Natrix rhombifera* in the United States and northeastern Mexico. This species ranges southward in eastern Mexico to Tabasco.

proximate the ranges of the species just reviewed. The Gulf coast toad (*Bufo valliceps*) (map in Porter 1970) occurs from extreme southern Arkansas and Louisiana to extreme northern Costa Rica. There are localities for it (Map 23) along the Pecos and Devils rivers, in the Sabinas and Salado systems, and at Cuatro Ciénegas. The western ribbon snake (*Thamnophis proximus*) (Rossman 1963: Fig. 2) ranges from Wisconsin and Indiana to the Pecos River system in the United States and (Rossman 1963: Fig. 3) from Coahuila and Nuevo León to Costa Rica. Detailed records for *T. proximus* within the borders of the Chihuahuan Desert (Map 24) include not only the Pecos River system but also the Sabinas-Salado complex and the headwaters of the Río San Juan system. The diamondback water snake (*Natrix rhombifera*) (Map 25) has a somewhat similar range, but it also occurs in rivers of the Gulf Coastal Plain and the eastern versant of the Sierra Madre Oriental as far south as Tabasco (Conant 1969: Map 2). It occurs in the Rio Grande, the Sabinas-Salado system, and within the bolsón of Cuatro Ciénegas, and there are old, unconfirmed records from Calamity Creek and Pecos, Texas (Map 26).

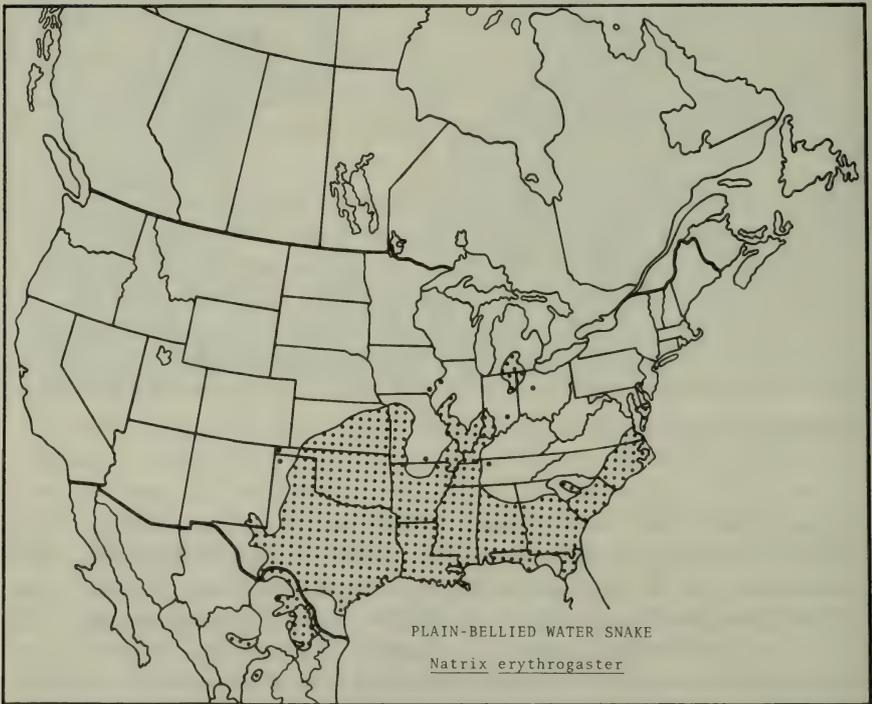


Map 26. Localities for *Natrix rhombifera*.

The plain-bellied water snake (*Natrix erythrogaster*) (Map 27) is noted for the many disjunctions in its range, especially in the midlewestern part of the United States. There are also two disjunct populations in Mexico, one each in the Río Nazas and Río Aguanaval, both of which have differentiated in isolation into distinctive races of *N. erythrogaster*. In many ways the distribution of this water snake in the Chihuahuan Desert (Map 28) parallels that of the diamondback water snake, but there are a number of differences. *N. erythrogaster* has

ascended the Pecos River to New Mexico. It has also ascended the Rio Grande to the Big Bend, and, if an old, unconfirmed record for Calamity Creek is valid, it has passed through Mariscal Canyon as well as Boquillas Canyon. Most significantly, it has crossed the desert from the east, via the Old Río Nazas system, and is relict in two of its old tributaries. Records from the desert proper are lacking from the Aguanaval, but the species in all probability occurs at the Presa Cazadero, upstream from the town of Río Grande, Zacatecas, and probably also is present farther downstream in areas where water is permanent or usually so. Future field work may confirm this. The distribution map of this species invites the speculation that clues to the whereabouts of the course of the Old Río Nazas might be sought to the east or northeast of the mouth of the present river.

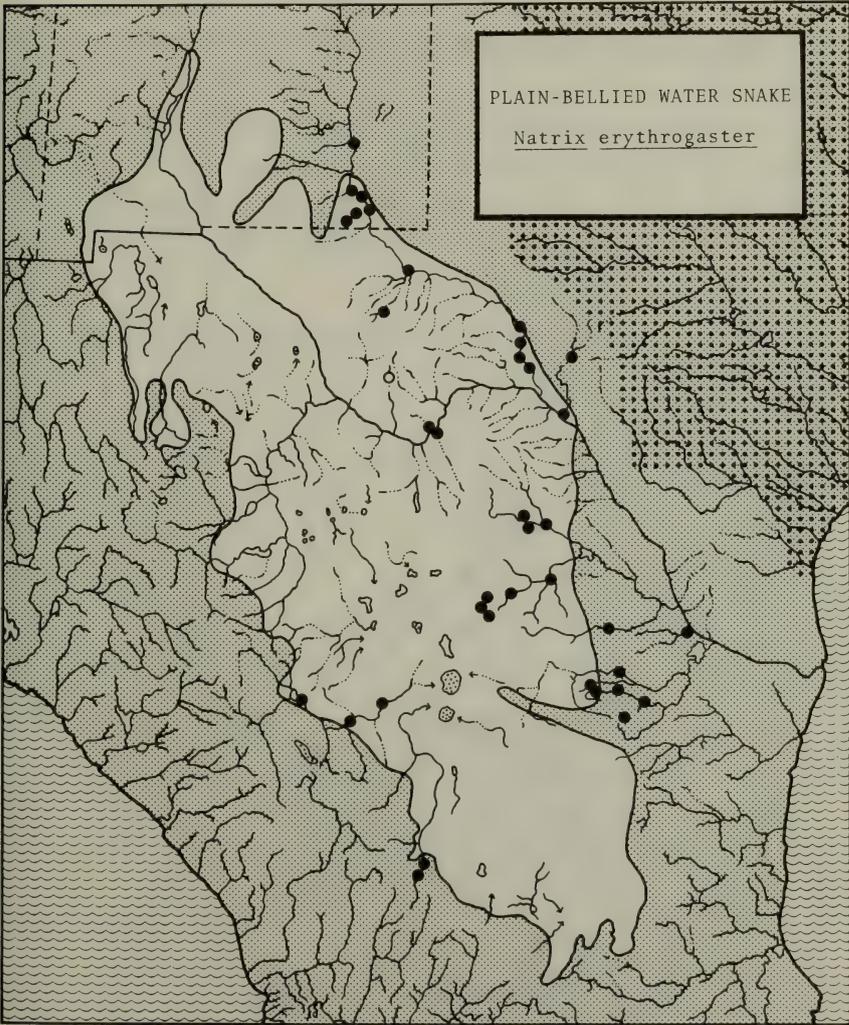
The pond slider (*Chrysemys scripta*) (Map 29), which is widely distributed through the southeastern United States, has numerous disjunct populations in the southwest and in northern Mexico. It occurs in many parts of the Chihuahuan Desert (Map 30), which it probably entered from the east, but it is curiously absent from the Río Aguanaval and the



Map 27. General distribution of *Natrix erythrogaster*.

ivers of northwestern Chihuahua. Like *Natrix erythrogaster*, this turtle has differentiated into a number of isolated races, both in the desert and along both coasts.

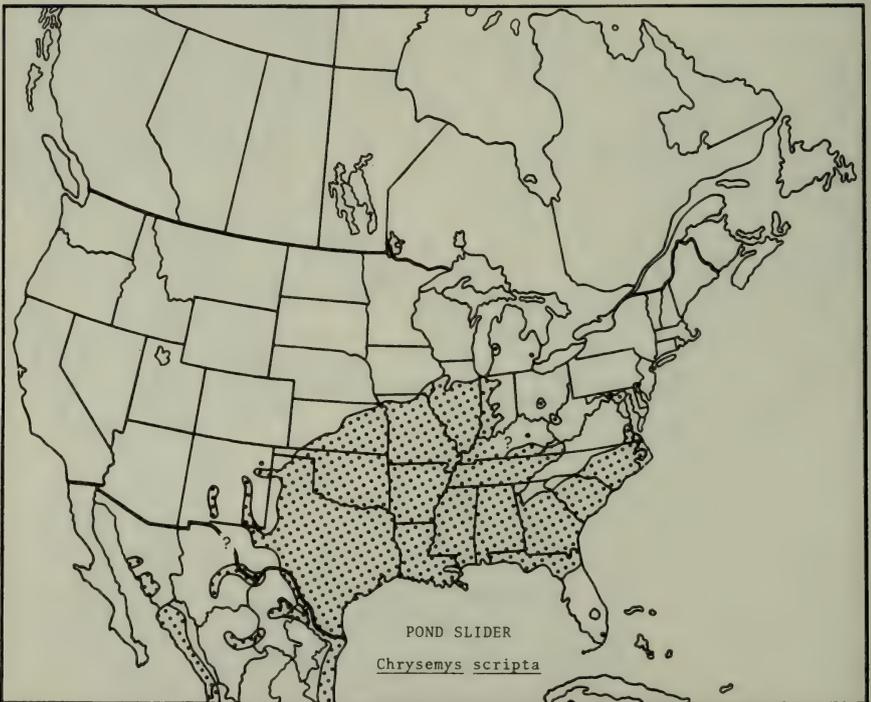
The two species of turtles that are endemic to the Cuatro Ciénegas bolsón must also be included. Both occur in streams of the basin as well as in certain of the formerly isolated ponds or great springs of the area.



Map 28. Localities for *Natrix erythrogaster*. This eastern species has crossed the Chihuahuan Desert by way of the Old Río Nazas, and it survives in the Río Aguanaval and the modern Río Nazas, both of which are streams of interior drainage.

These are the black softshell turtle (*Trionyx ater*) (Map 31) and the aquatic box turtle (*Terrapene coahuila*) (Map 32).

In summary, some 19 species of semiaquatic reptiles and amphibians are associated in one way or another with streams or relict fragments of former streams within the borders of the Chihuahuan Desert. Three species have apparently entered the region from the north, one from the northwest, two from the west, one from the south, nine and probably ten from the east, and two are endemic. Others may eventually be added to the list, among them the great plains skink (*Eumeces obsoletus*) which, although it is not a semiaquatic reptile, may be relict along water courses and in or near "oases" in the Chihuahuan Desert (Conant 1965:7). *Kinosternon flavescens*, *Thamnophis cyrtopsis*, *T. marcianus*, and several species of *Bufo* and *Scaphiopus* have been purposely omitted because they are apt to appear in almost any small body of water, including cattle tanks, temporary pools in borrow pits, seasonally dry arroyos, or wherever else rainwater may accumulate. Seemingly, these

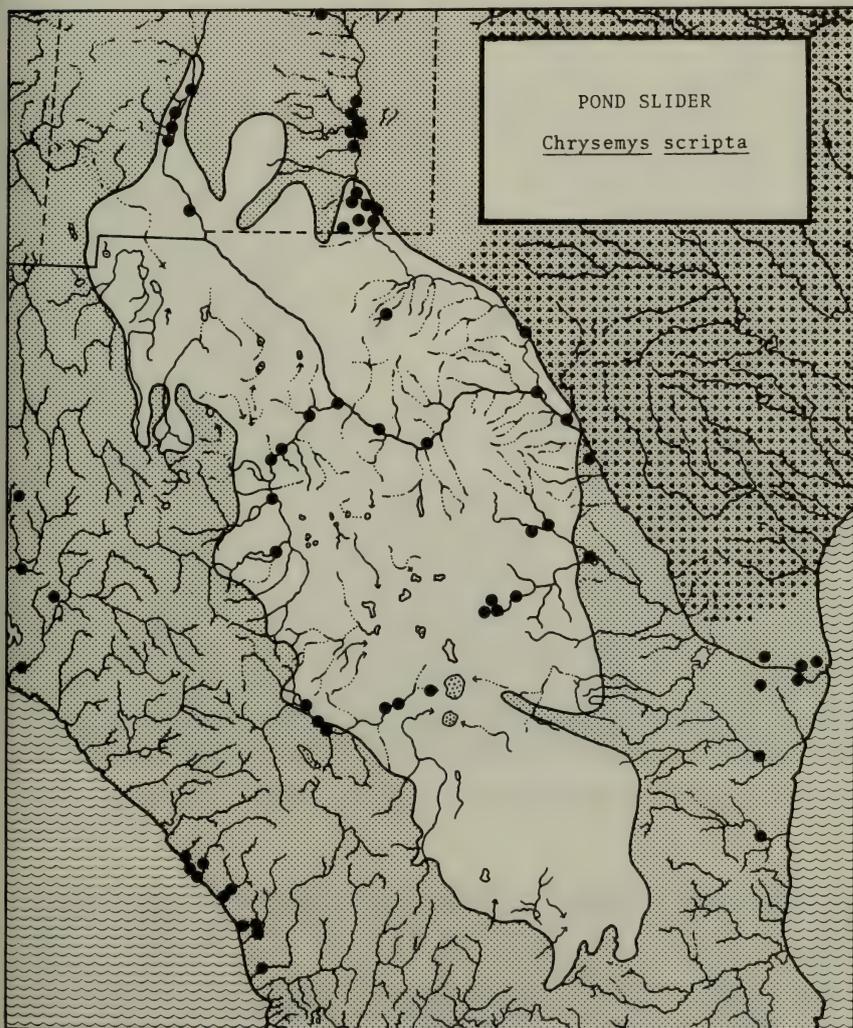


Map 29. General distribution of *Chrysemys scripta* in the United States and northern Mexico. This turtle, of which there are a number of races, extends southward along both coasts of Mexico to Central and South America.

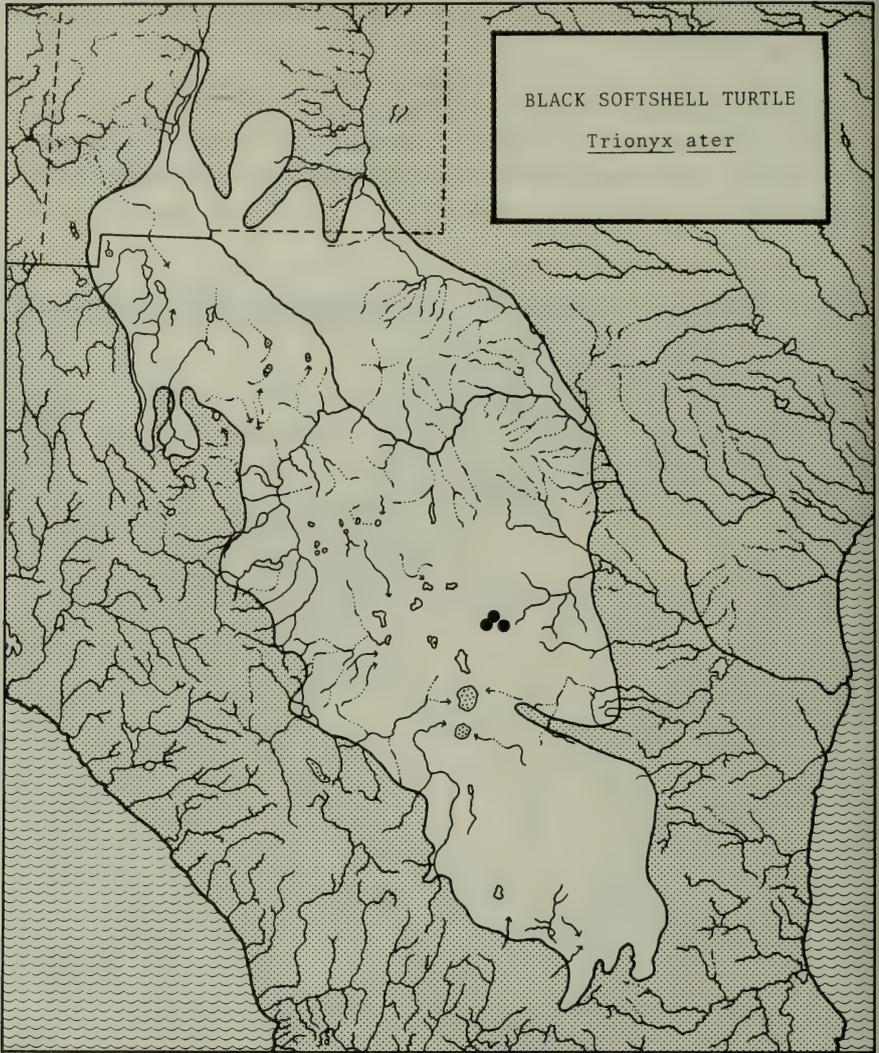
species are independent of the desert streams and can move about freely during wet weather.

CHANGES IN THE RIPARIAN FAUNA

Time is of the essence if we are to obtain even a fairly complete overview of the total ranges of the many species discussed herein. When Brand (1937) published his paper on "The Natural Landscape of

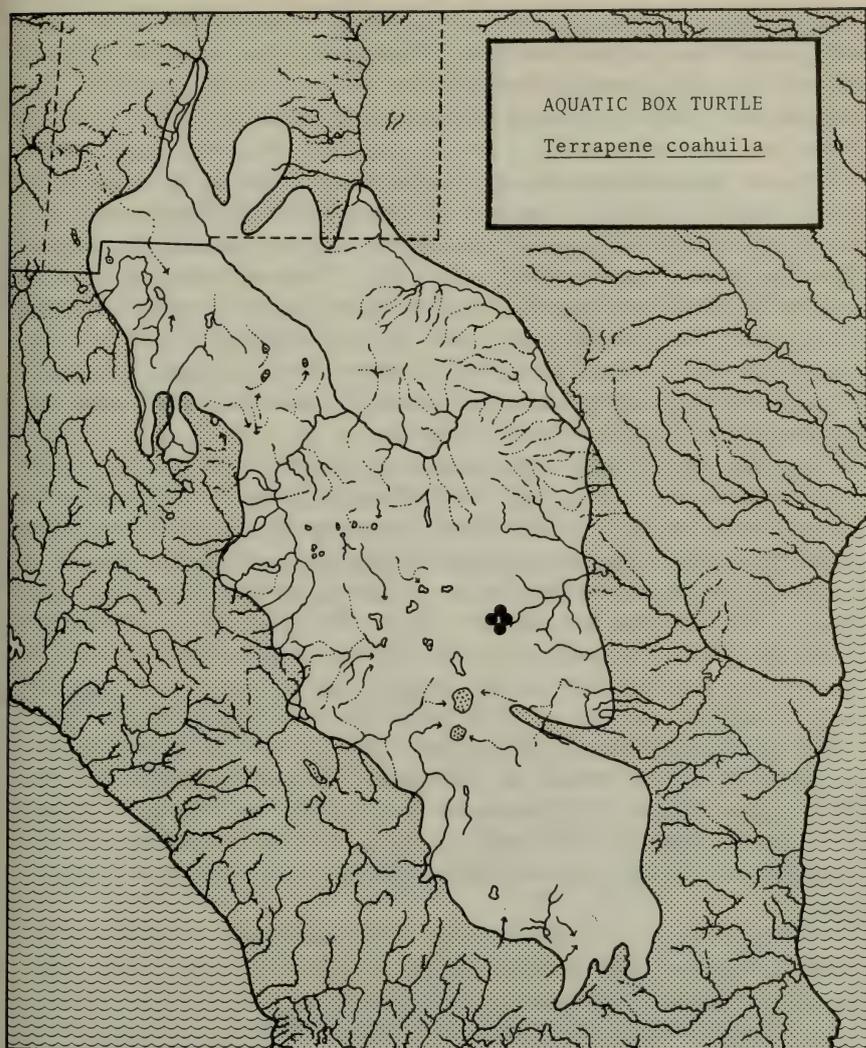


Map 30. Localities for *Chrysemys scripta*. Although it occurs in many of the desert rivers it is apparently absent from the Río Aguanaval and the streams of northwestern Chihuahua.



Map 31. Localities for *Trionyx ater*, an endemic species of the Cuatro Ciénegas bolsón.

Northwestern Chihuahua,” changes in the ecology of the region were already in progress. He commented about the Ríos del Carmen, Santa María, and de Casas Grandes (p. 21) as follows: “No impounding dam exists on any of the main streams, although several diversion dams take water from all three rivers. The increasing use of spring and river water for irrigation on the *haciendas* and *colonias* of the region has contributed markedly to the lessened flow of the rivers in their lower courses.”



Map 32. Localities for *Terrapene coahuila*, a largely aquatic endemic species of the Cuatro Ciénegas bolsón.

There have been marked changes since 1937, and two very recent observations will indicate how serious the impact has been on the local riparian faunas. First, the Río del Carmen has ceased to exist downstream from the Presa las Lajas, which is situated a short distance south of the town of Ricardo Flores Magón (formerly El Carmen). All water leaving the dam is channeled through a sluiceway to be used for irrigation and other human requisites. The gallery forest below the dam

has disappeared, except for fire-blackened stumps and other mute evidence of its former existence. Presumably, no water has flowed through the old channel since the dam was completed in 1964, and, because the river is dammed farther upstream, it is unlikely that the Presa las Lajas will ever fill to the top short of some catastrophic event. We found no evidence of any of the former riparian herpetological fauna during a 2-day visit except the mud turtle (*Kinosternon hirtipes*) which is a member of a genus that readily adapts to almost any body of water in which there is shelter and food. Bass and carp have been stocked in the impoundment. It is almost certain that the other animals which are so dependent on the water of the desert rivers have been extirpated in the Río del Carmen downstream from the dam. And this is the river along which the strongly aquatic *Thamnophis rufipunctatus* was collected virtually at its mouth in 1903.

Secondly, the riparian reptiles and amphibians have been seriously threatened in the lower portion of the Río de Casas Grandes by the introduction of the voracious bullfrog (*Rana catesbeiana*) which is known to eat virtually anything that moves. (Adult toads, which are capable of excreting venomous bufogenins in sizable quantities from their skin glands, may be rejected—Brown 1974.) We camped for two nights along the river at the point where the highway crosses approximately 10 km (6 miles) north of Janos. We prowled the river after dark, and the only animals we saw in our lights were approximately a hundred adult bullfrogs within a stretch of perhaps 100 m (330 ft). There was no evidence of snakes, turtles, or the usually ubiquitous members of the *Rana pipiens* (leopard frog) complex, even though the weather was ideal for general collecting. We took no turtles in our traps although they remained set all night and were checked in the late evening and again at dawn.

The large and notorious bullfrog, when introduced in new habitats where it lacks natural enemies, often makes short work of the native fauna. It is credited with having eliminated the spotted frog (*R. pretiosa*) from western Oregon during the 1930s (Shay 1973:8), and it apparently has contributed to the near extirpation of the Tarahumara frog (*R. tarahumarae*) from southern Arizona, the only area in the United States where this Mexican species occurs (John S. Applegarth pers. comm). Moyle (1973) showed that a combination of alteration of habitats by mankind and the introduction of the bullfrog have caused the disappearance of *R. aurora* and a continuing reduction in range of *R. boylei* in the San Joaquin Valley, California.

The *New York Times* recently published an article entitled "Frogs for the Tables of Mexico" in which it was stated that an effort was being made to fill all irrigation canals and lakes with bullfrogs. The article also quoted an authority as saying that: "Of course, in many regions we'll

have to convince the peasant that the frog is good food." Although our traps failed to catch any turtles, they did yield two large catfishes and an adult bullfrog. These we took to a family living across the stream from our camp. They gratefully accepted the fishes but showed no interest in the frog.

It would be well for authorities on both sides of the border to examine the effects of human activities on the riparian animals and to take steps to preserve at least some of the natural habitats. Mexico could easily lose two reptiles from its Chihuahuan Desert fauna, the painted turtle and the common garter snake. One of these, the turtle (*Chrysemys picta*) occurs nowhere else in the Republic, to the best of our knowledge, except in relict colonies in the Río Santa María. The United States could also lose a turtle and a frog from its fauna. The mud turtle (*Kinosternon hirtipes*) is known from only two localities in western Texas, both of which would be vulnerable to a prolonged drought, and the populations there are already under pressure because ranch hands use the turtles for target practice (Frederick R. Gehlbach pers. comm.). I have already commented on the alarming situation with the Tarahumara frog, although it, of course, does not occur in the Chihuahuan Desert.

COMMENTS ON LOCALITY RECORDS

The individual localities were plotted on the accompanying maps as accurately as possible. In the large majority of cases, I was able to relate towns and ranches to the streams on or near which they are situated, but in numerous instances I could not. Some localities do not appear on any of the large series of maps available to me, possibly because place names have been changed, a common practice in Mexico, or the sites have been abandoned or flooded out of existence by impoundments. By tracing the routes of exploring or collecting expeditions, however, a number of obscure localities have been pinpointed. Other routes remain to be checked in an effort to ascertain approximately where field parties crossed certain of the streams. Several specimens are accompanied solely by such unsatisfactory designations as "Río Santa María."

A major problem faced by anyone attempting to correlate locality data with drainage patterns is the failure of cartographers to show streams accurately or to emasculate them, possibly in the interests of simplicity, by omitting important tributaries. A comparison of almost any two otherwise excellent maps of the Chihuahuan Desert region suggests that the rivers, with the possible exception of the Rio Grande, were drawn freehand and with varying degrees of artistic license.

In a very real sense, this paper is a progress report. Much more field work needs to be done, and I hope that the publication of the accom-

panying maps will result in additional localities being called to my attention.

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Ancient Playas and Their Influence on the Recent Herpetofauna of the Northern Chihuahuan Desert

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INTRODUCTION

The distribution of organisms over the face of the earth is a dynamic not a static phenomenon. Historic knowledge of these patterns has been so short-lived, however, that we often assume that such patterns have a certain permanency without giving much thought to the reasons for this illusion. Changes in local population densities are often so small that they may go unnoticed for years, yet from the limited documentation available such changes occur with considerable frequency. The more obvious changes have generally remained enigmatic.

Except for certain well-studied examples, little is known about the specific factors which affect the spacial distributions of animals. In many situations range-limiting factors are readily apparent, but in others they are not. Many present-day ecologists would have us believe that contemporary factors are paramount in shaping the genetic variability of animal populations, yet the historical component (both spacial and genetic), which must be of considerable importance, is seldom mentioned or even considered. It is to this facet that I wish to direct the efforts of this paper. The ideas and assumptions incorporated herein are admittedly hypothetical, but I think they are reasonably well documented. They offer a defensible explanation for many of the questioned distributional peculiarities evident in the basin and range region of northern Chihuahua, Mexico, and adjacent regions of the United States. Additionally, they offer an explanation which can be subjected to further more critical local evaluation and review. The passage of time will ultimately determine whether any of the explanations has merit.

My attention was first drawn to vertebrate distribution patterns in the Chihuahuan Desert by peculiarities in the ranges of three stream-as-

sociated reptiles. Two turtles (*Chrysemys picta* and *Trionyx spiniferus*) and the garter snake (*Thamnophis sirtalis*) are known from two or three widely separated drainage systems within the northern Chihuahuan Desert (Fig. 1). *C. picta* occurs in the Rio Grande of New Mexico, the Mexican Rio Santa Maria, and the Gila River of Arizona and New Mexico (Fig. 3). Gila River populations apparently were once connected to populations throughout much of the middle and lower Colorado River system. *T. spiniferus* is also known from the middle Rio Grande, the Gila, and the middle and lower Colorado system (Fig. 4). *T. sirtalis*, on the other hand, has been found near or along several sections of the New Mexican Rio Grande and the Rio Casas Grandes in Chihuahua, Mexico (Fig. 5). Despite disjunctions of up to 185 km (111 miles) between known populations, systematists have found no significant character shifts in any of these reptiles; in each case the various populations have been considered disjunct elements of a single racial entity. The three reptiles occur only in or near permanent aquatic habitats and

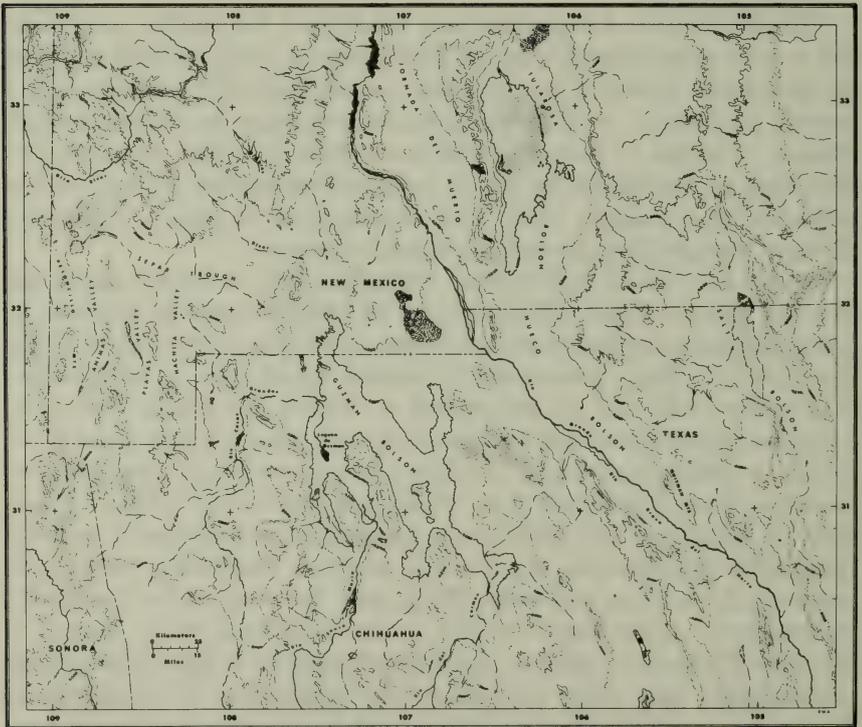


Fig. 1. Base map of northern Chihuahuan Desert showing important physical and topographic features. Dotted contour lines at 1280 (4200 ft), 1524 (5000 ft), and 1829 (6000 ft) m. Adapted from Operational Navigation Charts G-19 and H-23, scale 1:1,000,000.

they would require such situations for either long or short-range dispersion. However, few such habitats presently exist between any of the known disjunct populations, so when and if dispersion took place, it must have happened at a time when environmental conditions were radically different from those prevalent in the area today. Accumulating geologic and geomorphic evidence suggests that such was the case. I present here a general summary of that evidence.

EVIDENCE FROM GEOLOGY AND GEOMORPHOLOGY

Cabeza de Vaca Basin History

Numerous workers (mainly geologists) over the years have contended that the ancestral Rio Grande did not flow along its present course through the El Paso-Juarez gap, but instead flowed directly southward into a huge interior basin located in what is now northern Chihuahua, Mexico (see Lee 1907; Burrows 1910; Bryan 1938; King 1935; Kot-



Fig. 2. Restorative diagram of investigation area, showing ancient lakes at about maximum inundation during early Pleistocene time (stippled) and later Wisconsin pluvial remnants (black). Areas above modified 1524-m contour (5000 ft) shaded with tree symbols. Arrows indicate conjectural dispersal routes mentioned in text and filtering zone of Peloncillo Mountains.

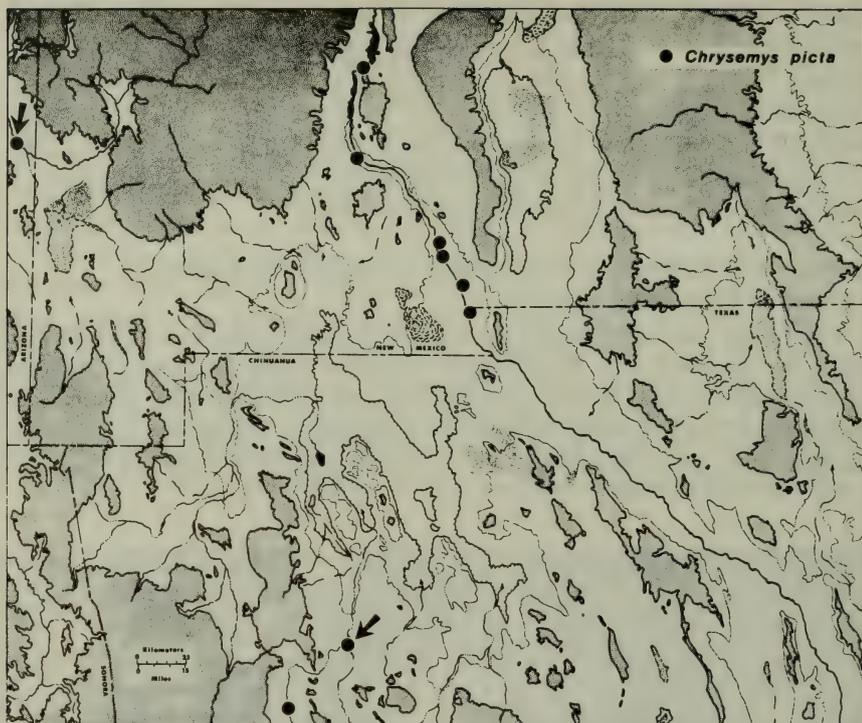


Fig. 3. Records for *Chrysemys picta* showing disjunct populations in Rio Grande, Rio Santa Maria, and Gila River. Gila record imprecise but based on known occurrence. (Smith and Taylor 1950; Ernst 1971; Degenhardt and Christiansen 1974; Conant pers. comm.)

tlowski 1958; Strain 1965, 1966; Reeves 1965; and others). Water and sediments from the Rio Grande and other permanent streams to the south and west accumulated in this basin and formed a huge lake (Fig. 2). The lake probably fluctuated considerably at times because of its position within the arid latitudes, but it is doubtful that it ever completely dried while receiving water from the ancestral Rio Grande. According to Strain (1970), the lake at maximum inundation may have reached water levels in excess of 1311 m (4300 ft). Based on present-day contour lines such a lake would have covered an estimated 23-26,000 km² (9-10,000 miles²). Vast areas of southern New Mexico, western Texas, and northern Chihuahua would have been covered by water (Fig. 2). Evidence that this huge lake existed has been based mainly on two kinds of information, surficial geomorphology and sedimentary profiles. Expansive, virtually unaltered, evaporite basins are still present in the area today along with remnants of ancient wave-cut shore and beach lines which were formed at later, lower lake stages (Reeves [1965,1969]



Fig. 4. Records for *Trionyx spiniferus* showing disjunct populations in Rio Grande and Gila River. (Webb 1962; Degenhardt and Christiansen 1974; Webb pers. comm.)

recognizes several stages of what he has coined pluvial Lake Palomas). Deflation surfaces and extensive accumulations of aeolian sand on the lee sides of these basins reflect later periods of desiccation and water recession. Sands, silts, siltstones, and claystone sediments of undoubted lacustrine origin have been reported from test borings throughout the playa area (Reeves 1969). In one boring in New Mexico, lacustrine sediments reached almost 1829 m (6000 ft) in depth, indicating an extremely long sequence of active sedimentation.

The ancient lake (christened Lake Cabeza de Vaca by Strain [1966]) has been variously considered a late Pliocene to mid-Pleistocene feature, but Strain (1966), using stratigraphic evidence, considered it an early Pleistocene phenomenon. About the mid-Pleistocene (Strain 1969 estimated the probable time as late Kansan), waters from the huge lake breached a rocky barrier to the southeast (probably across the Quitman Mountain trend line, Figs. 1,2) either by overflowing at the lowest point or by southeasterly headwater erosion (King 1935). Such drainage would have rapidly lowered the pool level in the Tularosa and Hueco

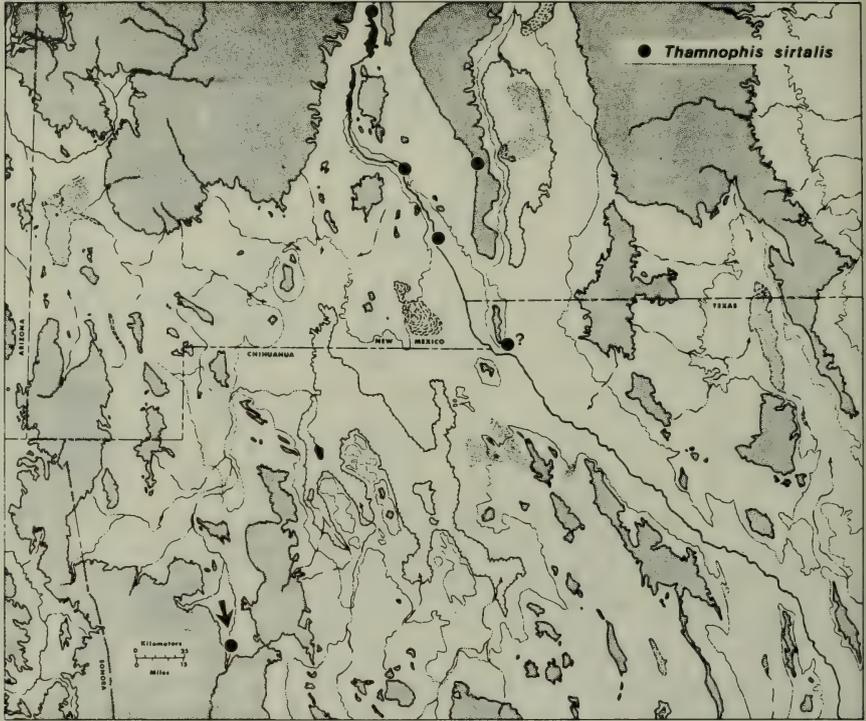


Fig. 5. Records for *Thamnophis sirtalis* showing disjunct populations in Rio Grande and Mexican Rio Casas Grandes (see arrow). Additional populations known farther south in Rio Papigochic (Yaqui drainage). El Paso record indefinite and questioned by some workers. (Van Denburgh 1924; Little and Keller 1937; Smith and Taylor 1945; Fitch and Maslin 1961; Conant pers. comm.)

bolsons, and begun stream channelization along the floor of the lower Hueco Bolson (Fig. 1). The Franklin-Juarez-Presidio Mountain barrier near El Paso most probably would have been breached twice, once during the initial ponding of Cabeza de Vaca, and again after drainage and channelization of the lower Hueco Bolson. The second breaching, which cut through El Paso Canyon, may have occurred as late as upper Illinoian time, or as early as late Kansan (Reeves 1969). Once the Quitman and El Paso Canyon breaches had become established, the increased water supply would have filled rapidly any remaining basins or troughs downstream and this new erosional potential quickly would have eliminated any barriers still remaining to a through-flowing gulf drainage. Gravels of distant western origin (Lissie) do not appear on the Texas gulf coast until about mid-Pleistocene time (King 1935).

Gila Basin History.

Compared to the abundant interest in the ancestral Rio Grande, I

have found relatively little interest in Gila River paleohistory. Morrison (1965) in his geologic survey of two quadrangles along the middle Gila reported ancient lacustrine shore and terrace gravels both north and south of the present Gila valley and southward along the eastern flanks of the Peloncillo Mountains (Fig. 1). Eroded remnants of lacustrine geomorphic features such as bars and shore terraces were found locally throughout the ancient basin area. Morrison found evidence of three distinct lake terraces in this area, the most recent of which could "have been deposited during the higher levels of a lake that had a maximum depth of at least 250 feet." On the map (Fig. 2) I have shown ancient Lake Morrison (name here proposed) inundating both the Animas and Duncan valleys. Morrison (1965) did not state that these two valleys once contained a continuous body of water, but the highest shoreline traces for both lakes is about 1280 to 1311 m (4200 to 4301 ft) so a connection between the two seems probable. Present topography of the Peloncillo range lying immediately west of these basins would seem to preclude such a high lake level, for one pass at 1272 m (4173 ft) would have quickly stabilized the lake level at a lower elevation. Morrison, recognizing this inconsistency, investigated and found no evidence of overflow at this pass. In fact, highest shoreline gravels near the pass were only 1204 m (3950 ft) above sea level. As annectant shorelines only short distances from the pass were consistently at higher elevations, he proposed that the pass area had undergone subsequent local downwarping to bring it to its present elevation. Morrison's geologic map shows extensive and complex faulting in this region.

Animas and Playas Basin History

The Animas and Playas basins have retained their lacustrine character to the present (Fig. 1). Schwennesen (1918) and Gillerman (1958) considered ancient Lake Animas a Pleistocene phenomenon, but they indicated no more specific age. If ancient lakes Morrison and Animas had at one time been confluent, the region inundated would have been approximately 90 km (56 miles) long by 10-15 km (6-9 miles) wide—a sizable body of water (Fig. 2). Schwennesen (1918) detected what he interpreted as beach terraces some 1-5 km (0.6-3 miles) south (near Animas) of the present southern terminus of lacustrine deposits in the Animas depression. Near Animas these terraces reached elevations 58 m (190 ft) higher than the highest shore features of the lower lake basin, so he interpreted this as evidence of late Quaternary uplift in the region south of Animas. Local crustal movement may well have been coincident with a late Pleistocene or early Holocene fissure lava flow west and northwest of Animas, New Mexico (Gillerman 1958). Spiegall (1957) disagreed with Schwennesen's beach terrace interpretation and considered these same features either stream terraces or fault scarps;

therefore, he rejected Schwennesen's uplift hypothesis.

The Playas Valley lies some 25 km (15 miles) southeast of the Animas Valley and is separated from it by the Animas Mountains (Fig. 1). Playas Basin is divided into northern and southern sections by a low, transverse sedimentary ridge (Schwennesen 1918). The northern section is the lowest (floor about 1320 m or 4331 ft) and contains ephemeral Playas Lake. The southern section rises slowly to an elevation of 1372 m (4500 ft) at its southern end. Both sections contain deep lacustrine sediments that were presumably deposited contemporaneously. Schwennesen (1918) believed that the southern section had been tilted northward by recent uplift to the south. Hatchet Gap, a topographic low between the northern Little Hatchet Mountains and the southern Big Hatchet Mountains, forms a natural eastern drainway from Playas Basin. Schwennesen postulated, on the basis of old shoreline remnants, that Playas Basin once contained at least 11 to 12 m (36 to 39 ft) of water, but it probably would not have drained through the gap at these levels. There is ample evidence, however, that water did at one time drain through this gap. Topographic maps (USGS 1:250,000, 1:6,250) show a well-defined, wide, sandy drainageway extending eastward directly from Hatchet Gap across the U.S.-Mexican boundary to the Laguna de Los Moscos in Chihuahua. As the Moscos Basin was once a part of the greater Cabeza de Vaca inundation, later Pleistocene and perhaps Holocene aquatic connections (during mesic periods and at high lake levels) between the Playas and Moscos basins would have been highly probable. The distribution of the semiaquatic turtle (*Kinosternon flavescens*) in New Mexico (Degenhardt and Christiansen 1974) and adjacent Chihuahua appears to substantiate this probability.

Two other lowland areas are important as possible animal dispersal routes, but little is known about them. One is the north-south trending Hachita Valley; the other is the east-west trending Separ Trough (name here proposed) (Figs. 1,2). The Hachita Valley is a continuous sedimentary basin that extends northward from the Big Hatchet Mountains to the Separ Trough. The Continental Divide crosses Hachita Valley just north of Hachita, New Mexico, and a low divide (probably formed from coalescing pediments) separates the drainage at this point. This entire valley is below 1371 m (4500 ft), and its shallow, trough-like nature may be what remains of an ancient channel or waterway. Drainage flowing northward from the Hachita Valley moves into the Separ Trough and thence northwestward to Lordsburg Draw which empties into the Animas Basin. The Separ Trough also extends eastward to the Deming area where an east-west drainage divide about 1359 m (4459 ft) in elevation marks the Continental Divide. Several small, shallow playa-like areas occur in the narrowest part of this trough. At the divide, eastward drainage moves into the Deming Basin (which was once partially covered

by Lake Cabeza de Vaca) while westward drainage eventually finds its way to the Animas Basin.

Possible Connections Between Lake Systems

Assuming that the Gila River once drained into ancient Lake Morrison (see Pleistocene restoration, Fig. 2), we may ask, could this body of water have been connected at some time to ancient Lake Cabeza de Vaca? Two possible lowland connections could have existed: (1) the Separ Trough from the Deming Basin to the Animas Basin; and (2) the Hachita Valley from the Laguna de Los Moscos, via the Separ Trough to the Animas Basin. The lowest corridor now extant (Separ Trough) stands at about 1359 m (4459 ft), and it is extremely doubtful that the waters of ancient Lake Cabeza de Vaca ever reached this elevation. Strain (1970) indicated the present 1310 m (4300 ft) contour as the approximate maximum level reached by Lake Cabeza de Vaca, but there is no evidence to support any higher pool level. Recent local upwarping of the western Cabeza de Vaca region could have altered materially drainage patterns in the area, but geologic evidence for this is inconclusive. Because a completely lacustrine interconnection via the Hachita Valley (at present elevation) also would have been well above maximum estimated pool levels for ancient Lake Cabeza de Vaca, this alternative route also is rejected. With contemporary topography, streamside and intermittent lacustrine habitats might well have existed in both the Separ and Hachita Valley corridors, but these would have been usable only during periods of high runoff, and then probably only by semiaquatic organisms. It appears then that neither of these routes would have been passable to completely aquatic organisms under relief conditions as they exist today.

Although the foregoing lowland dispersal routes have merited primary consideration, an alternative highland route deserves attention. One tributary of the Mimbres River drainage (Pipeline Draw—32°43'25"N-108°20'30"W) southwest of Silver City, New Mexico, connects at the Continental Divide with a tributary (Mangus Creek) of the Gila River (see Fig. 1). This connection, at 1829 m (6001 ft) elevation, probably would not exclude any of the disjunct stream-associated reptiles mentioned earlier. The Mimbres River, now dry along much of its lower course, drains southeastward into the Deming Basin near Deming, New Mexico, and there disappears on the remnant bed of ancient Lake Cabeza de Vaca. The Mimbres route is well worth consideration, especially as regards either *Chrysemys picta* or *Trionyx spiniferus*.

DISCUSSION

The possibility that several contemporaneous Pleistocene and perhaps early Holocene lakes once inundated a huge expanse of the northern

Chihuahuan Desert affords a reasonable explanation for the curious distribution patterns of the three fresh water-associated reptiles mentioned earlier, but if such lakes existed, they would certainly have affected the spacial distribution of terrestrial organisms and fish as well. To many terrestrial animals the original lakes and their later remnants would act as inhospitable barriers to dispersal. Before considering such barriers further, however, let us first examine certain other characteristics of the region which are important to a discussion of dispersal. The western Cabeza de Vaca Basin lies in a tectonically complicated zone where younger igneous geomorphic structures converge with older basin and range structures. The basin and range structures trend generally southeastward and cross the igneous zone in southeastern Arizona, southern New Mexico, and annectant northern Chihuahua. Here a series of intermontane troughs collectively form an east-west trending gap which is not covered by Tertiary igneous material. This is one of the two regions in North America where north-south trending mountain ranges fail to split the continent and its lowland biota into eastern and western halves. This is the only midcontinental region where there has been a substantial interchange of both eastern and western faunas. Among the herpetozoa, at least 4 amphibians and 35 reptiles appear to have used this natural lowland region (here named the Apache Corridor ¹) for either eastward or westward movement across the Continental Divide. Ten of these represent organisms with populations extending from coast to coast. The low Peloncillo range (Fig. 1) is the only north-south trending mountain barrier standing in the way of this corridor, but few herpetozoans appear to have been absolutely limited by it. Lowe (1955) set the eastern limits of the Sonoran Desert along the Peloncillo divide. Many animals have gained access to the corridor via the Gila River Valley, which crosses the Peloncillo trend-line northwest of the mapped area. Except for the corridor itself, igneous highlands extend far to the north and south in essentially unbroken chains. Numerous roughland and montane-adapted herpetozoans (2 amphibians, 13 reptiles) have successfully crossed the corridor and established highland populations (now apparently disjunct) on the opposite side. Other forms presumably have failed to make the crossing and are found only north or south of the corridor. Several workers have noted the screening effects of the varied physiography in the corridor region and have referred to it as a "filter barrier" (Morafka pers. comm.) or "suture zone" (Remington 1968).

¹Auffenberg and Milstead (1965) have commented on this corridor and called it the "Rocky Mountains Corridor." As there are several corridors through the Rocky Mountains (but of less importance), I prefer to use a less generalized name.

The ancient lakes and their remnants lying within and extralimital to the Apache Corridor appear to have played a major role in restricting and isolating animal populations in the northern Chihuahuan Desert. I have prepared lists of those herpetozoans which appear to have been influenced by these lacustrine barriers. Examples are grouped by compass direction according to which sector of their range appears to be affected. This style of presentation has disadvantages—small populations are not well accommodated—but for the most part it is useful.

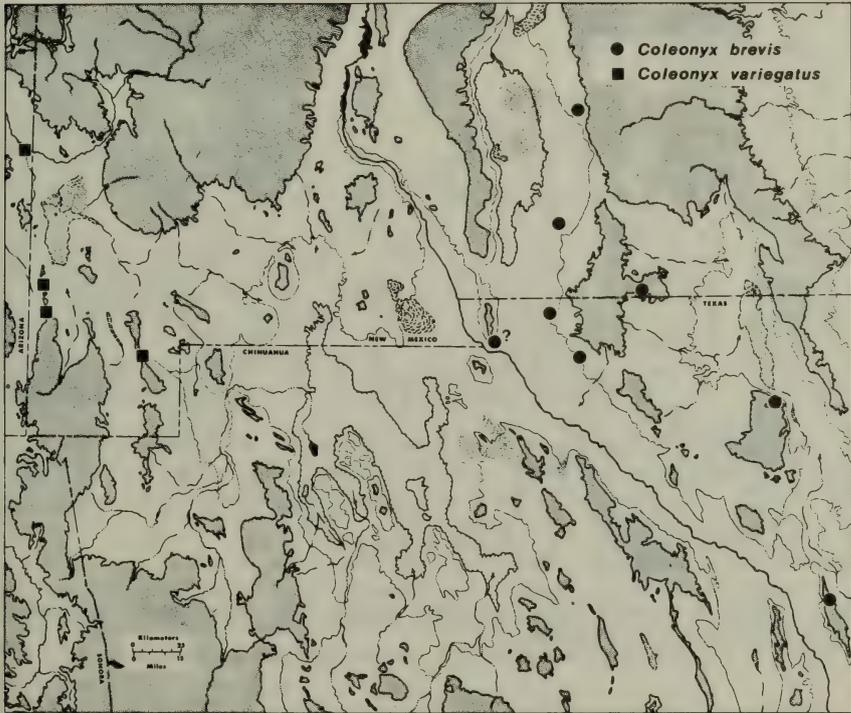


Fig. 6. Records for *Coleonyx brevis* showing limitation on western-range margin and *C. variegatus* with limitation on eastern-range margin. Example of species differentiation in lacustrine area. (Klauber 1945; Jameson and Flury 1949; Lowe 1955; Dixon and Medica 1965; R. D. Worthington pers. comm., questions the old El Paso record for *C. brevis*.)

Herpetozoa that appear to have their western-range margins influenced (Fig. 6): Amphibians. *Ambystoma tigrinum mavortium*, *Bufo speciosus*. Reptiles. *Chrysemys scripta*, *Coleonyx brevis*, *Urosaurus ornatus schmidti*, *Sceloporus poinsetti*, *Cnemidophorus tessellatus*, *C. tigris marmoratus*, *Diadophis punctatus arnyi*, *Sonora semiannulata blanchardi*, *Masticophis flagellum testaceus*, *Rhinocheilus lecontei tessellatus*,

Pituophis melanoleucus sayi, *Elaphe guttata*, *E. subocularis*, *Lampropeltis triangulum*, *L. mexicana*, *Trimorphodon biscutatus vilkinsoni*, *Crotalus lepidus lepidus*.

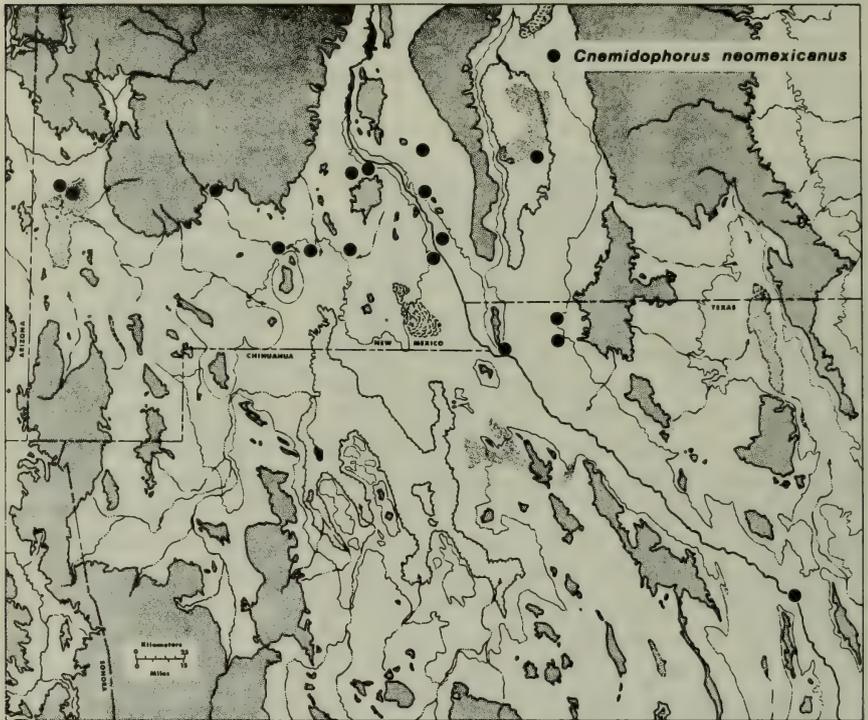


Fig. 7. Records for *Cnemidophorus neomexicanus* showing limitation on southern-range margin. (Pough 1962; Axtell 1966; Wright 1971.)

Herpetozoa that appear to have their southern-range margins influenced (Fig. 7): Amphibians. *Ambystoma tigrinum nebulosum*, *Scaphiopus bombifrons*, *Bufo woodhousei australis*. Reptiles. *Kinosternon flavescens flavescens*, *Trionyx spiniferus*, *Chrysemys picta*, *Holbrookia maculata flavilenta*, *Sceloporus undulatus tristicus*, *Phrynosoma douglasi*, *Eumeces multivirgatus*, *Cnemidophorus neomexicanus*, *C. inornatus*, *Heterodon nasicus nasicus*, *Masticophis taeniatus taeniatus*, *Salvadora grahamiae*, *Arizona elegans philipi*, *Hypsiglena torquata texana*, *Sistrurus catenatus*, *Crotalus viridus*.

Herpetozoa that appear to have their eastern-range margins influenced (Figs. 6,8): Amphibians. *Hyla arenicolor*. Reptiles. *Kinosternon sonoriense*, *Coleonyx variegatus*, *Sceloporus clarki*, *S. scalaris*, *S. jar-*

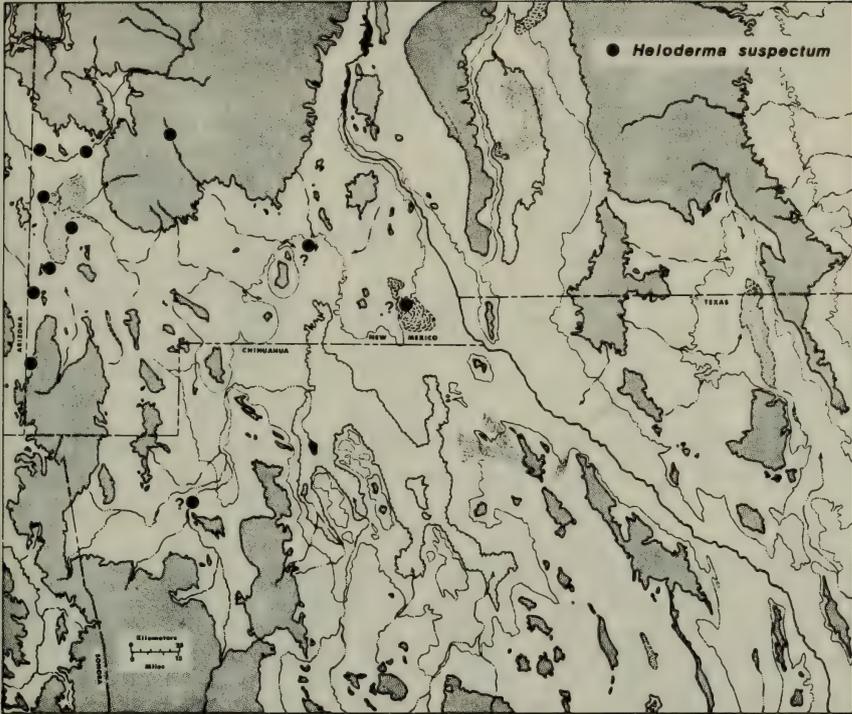


Fig. 8. Records for *Heloderma suspectum* showing limitation on eastern-range margin. Questioned records in New Mexico are doubted by some investigators. Questioned record in Mexico is sight record. (Bogert and del Campo 1956; Dixon and Medica 1965.)

rovi, *Cnemidophorus tigris gracilis*, *Gerrhonotus kingi*, *Heloderma suspectum*, *Rhinocheilus lecontei lecontei*, *Lampropeltis pyromelana*, *Sonora semiannulata semiannulata*, *Trimorphodon biscutatus lambda*, *Micruroides euryxanthus*.

Herpetozoa that appear to have their northern-range margins influenced (Fig. 9): Amphibians. *Gastrophryne olivacea*. Reptiles. *Kinosternon flavescens stejnegeri*, *Holbrookia maculata bunkerii*, *Cnemidophorus septemvittatus*, *Heterodon nasicus kennerlyi*, *Masticophis taeniatus ornatus*, *Arizona elegans expolita*, *Tantilla atriceps*, *Hypsiglena torquata ochrorhyncha*, *Crotalus scutulatus*.

Herpetozoa occurring in the region that show evidence of differentiation (Figs. 6,9) Amphibians. *Ambystoma tigrinum mavortium*, *A. t. nebulosum*. Reptiles. *Kinosternon flavescens flavescens*, *K. f. stejnegeri*, *Coleonyx brevis*, *C. variegatus*, *Holbrookia maculata bunkerii*, *H. m. flavilenta*, *Urosaurus ornatus linearis*, *U. o. schmidti*, *Cnemidophorus tigris marmoratus*, *C. t. gracilis*, *Masticophis flagellum linea-*

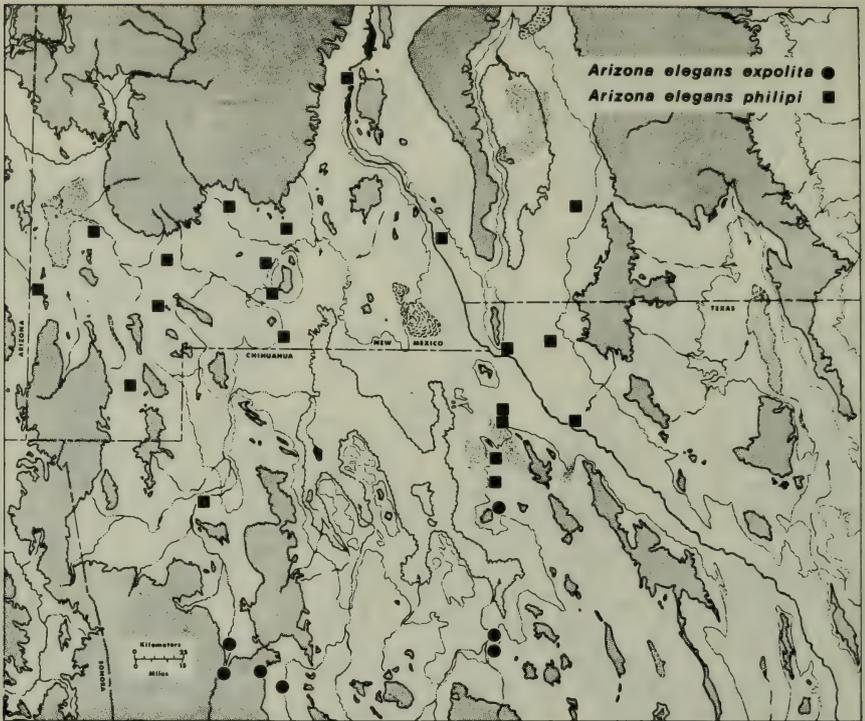


Fig. 9. Records for *Arizona elegans exopolita* showing limitation on northern-range margin and for *A. e. philipi* with limitation on southern-range margin. Example of subspecific differentiation in lacustrine area. (Klauber 1946; Dixon 1959; J. S. Jacob and J. S. Applegarth pers. comm.; R. G. Webb pers. comm.)

tulus, *M. f. testaceus*, *Rhinocheilus lecontei lecontei*, *R. l. tessellatus*, *Arizona elegans exopolita*, *A. e. philipi*, *Pituophis melanoleucus affinis*, *P. m. sayi*, *Sonora semiannulata semiannulata*, *S. s. blanchardi*, *Heterodon nasicus nasicus*, *H. n. kennerlyi*, *Hypsiglena torquata ochrohyncha*, *H. t. texana*, *Trimorphodon biscutatus lambda*, *T. b. vilkinsoni*, *Crotalus lepidus lepidus*, *C. i. klauberi*.

Range Limitation in Herpetozoa and Mammals Compared

To gain some measure of the relative impact of the Cabeza de Vaca lacustrine and postlacustrine environments on two different groups of animals, herpetozoan distribution patterns have been compared with mammalian patterns. Compass-direction limitations have been used as above. Anderson (1972) and Hall and Kelson (1959) have been principal references for the mammals, Stebbins (1966) has been the principal reference for the amphibians and reptiles. Of the 71 herpetozoans

and 64 nonvolent mammals occurring in the Cabeza de Vaca region, we see the following percentage comparisons:

| | Herps (%) | Mammals (%) |
|---|-----------|-------------|
| Indication of range limitation on western boundary | 27 | 20 |
| Indication of range limitation on southern boundary | 28 | 17 |
| Indication of range limitation on eastern boundary | 20 | 23 |
| Indication of range limitation on northern boundary | 14 | 8 |
| No indication of range limitation or insufficient information | 23 | 32 |

In addition to the above, 46% of the herpetozoans and 20% of the mammals show differentiation in the area, either at the specific or sub-specific level.



Fig. 10. Records for *Dipodomys merriami ambiguus* showing limitation on eastern-range margin and for *D. m. olivaceus* with limitation on western-range margin. Example of mammalian subspecific differentiation in lacustrine area. (Lidicker 1960; Anderson 1972.)

Evidence from Fish Distribution.

Published information on fish distribution in the Cabeza de Vaca area is limited, but new information presented in this volume (Miller 1977; Contreras 1977) adds to our knowledge. Miller (1958) indicated that 7 of the 12 primary fish species in the Mexican Rio Yaqui drainage are Rio Grande types. Miller postulated stream capture from either the Mexican Rio Conchos or the Rio Casas Grandes to Pacific drainage tributaries to explain these affinities. Miller listed three fishes (identical or closely allied taxa) common to both the Colorado River system and the Mexican Rio Yaqui, but he did not indicate whether any of these were also found in the Rio Grande or Gila River drainages. Apparently, one fish (*Gila robusta*) does inhabit all the major drainages around ancient lake Cabeza de Vaca. Another fish (*Catostomas* sp.) is common to the Rio Yaqui and Rio Casas Grandes, but has been found in no other drainages. The ichthyological evidence supports the herpetological evidence and indicates that there probably was no through-flowing connection between the ancestral Gila drainage and Lake Cabeza de Vaca. *Gila robusta* probably reached the Gila and Colorado drainages by means other than direct aquatic dispersal. Van Devender and Worthington (this volume) report remains of *Gila* cf. *robusta* in cave deposits in the Little Hatchet Mountains. They postulate that these bones probably had been transported by raptorial birds from a nearby aquatic source (presumably the Laguna de Los Moscos) some 3000 years ago (R. D. Worthington pers. comm.).

CONCLUSIONS

From the evidence accumulated thus far, it seems reasonable to conclude that:

1. There is abundant evidence that until about mid-Pleistocene time (700,000 – 350,000 B.P.) lacustrine environments in the Cabeza de Vaca region provided numerous opportunities for fully aquatic and semi-aquatic animal dispersal between the ancestral Rio Grande, ancient Lake Cabeza de Vaca, and all Mexican streams flowing northward into this huge sedimentary basin.

2. Direct aquatic connection between ancient Lake Cabeza de Vaca or its remnants and the ancestral Gila River, via ancient Lake Morrison, would have been impossible without changes in present-day relief. There is little evidence for such changes. Even without direct aquatic connections, semi-aquatic dispersal routes should have existed between suitable habitat of all these aquatic systems especially during more mesic periods.

3. The original and subsequent lacustrine environments which evolved in the Cabeza de Vaca region had a direct and substantial affect

on the distribution and differentiation of terrestrial vertebrate populations in that area.

4. The medium elevation (1372 m, 4500 ft and below) structural and sedimentary trough extending east-west across the continental backbone in the northern Cabeza de Vaca region forms the most important transcontinental dispersal corridor for amphibians and reptiles in North America. Highlands north and south of this corridor and isolated ranges within the corridor interact with other physical and environmental factors to produce a filter barrier effect on vertebrate populations in the region.

5. The time of initial lake formation (early Pleistocene, Strain 1966) and its eventual drainage and desiccation gives us a time frame within which lake environment-associated dispersal and genetic differentiation may have taken place. Although these dates are now only generally established, we have at least some indication of duration of such processes in the region.

Although late Pleistocene (Sangamon interglacial; Wisconsin glacial) and Holocene events have not been stressed in this report, this time period would have been as important as any other in shaping the populations we see in the region today. During interglacial periods the dried playa flats would have been inhospitable to both terrestrial and aquatic organisms, while during more mesic glacial periods aquatic environments would have once again prevailed. There is indisputable evidence that pluvial Lake Palomas filled at least to the 1225 m (4018 ft) level during Wisconsin time (Reeves 1969), but this still would have left a 32 km (20 mile) hiatus between the Rio Grande and the nearest lake shore. It is conjectural whether semiaquatic reptiles such as *Trionyx* and *Chrysemys* could have crossed this barrier or not.

Although the following are not conclusions, I have made two observations during this investigation which are included here for their general interest.

1. The Rio Grande seems to have served as a focal point for lowland aquatic dispersal in the Cabeza de Vaca region. The three stream-associated reptiles studied have a common occurrence only in this river system. The ancestral Rio Grande, with its interior drainage, may have been an important center of endemism.

2. Records for *Cnemidophorus neomexicanus* in the Jornada del Muerto, but not in the Elephant Butte basin, support contentions by some geologists that the ancestral Rio Grande once coursed through the Jornada. Quaternary basalt flows in the middle Jornada are believed to have diverted the stream westward through the Elephant Butte gap.

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Some Recent Changes in the Herpetofauna of the Northern Chihuahuan Desert

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Papers presented prior to mine have pointed to climatological and geological changes that have occurred within the past 8,000-16,000 years over the area now referred to as the Chihuahuan Desert. These changes have generally tended toward a pattern of increasing aridity. Milstead (1960) adequately discussed the isolation of some mesic-adapted species due to climatic shifts in the Chihuahuan Desert and speculated upon their evolutionary history. "Islands" of mesic habitat in deserts have always intrigued biologists. Such places are natural laboratories for zoogeographical, evolutionary, and speciation studies.

Rivers such as the Pecos in the United States, the Rio Grande, and the Nazas, Conchos, Sabinas, and Florido in Mexico have existed as open corridors for mesic species into the Chihuahuan Desert until very recent times. Each of these rivers in some way eventually "communicates" with biota from areas beyond the Chihuahuan Desert, and in some instances has created habitats that harbor important peripheral and endemic species. But these threads of communication are getting thinner all the time, and in some cases are broken completely, thereby creating newly isolated oases.

Man too is a mesic-adapted species. He has always centered his cultural activities around permanent sources of water. Most of the recent changes in the physiography and fauna of the Chihuahuan Desert can be traced either directly or indirectly to agricultural practices. Some faunal changes can only be speculated upon while those more recent can be documented.

With the advent of the science of agriculture, man learned to irrigate small plots of crops by river overflows. Then he learned to divert water from the streams and move it to more desirable croplands close by via ditches and canals. Up through this period of time, man's effect upon

the habitat was negligible; if anything, it probably favored mesic-adapted species somewhat by creating additional habitats. Spring flow was not affected by these methods, but rivers and streams may have been altered somewhat. Primitive man operated under two basic laws: (1) there was a naturally limited amount of water available; and (2) water flows downhill.

As tools became better and man's engineering skills increased, he became adept at moving water greater distances to more suitable farmland. He could even make cuts through mountains and build dams to force the water to higher elevations. Still, there was the limiting factor of available free-water resources.

This phase began man's ability to have a really significant effect upon landscape alteration and species distribution. This phase is the basis for my use of the term recent in the title of this paper. The word "recent" can mean 10 million years to a geologist or last week to an impatient youngster. As I apply it here, I refer to a time not more than 300-400 years ago, with most of my reference to a time less than 30 years ago.

Irrigation from running streams and rivers brought about problems between men as well as with nature. People living downstream from water sources began to see their water supply diminish as people upstream put more and more land into cultivation. Somewhere about this time the concept of making the desert bloom must have originated and later became the slogan of irrigation land developers throughout arid regions. Conflict over water rights became a common story, and eventually laws of man began to recognize "riparian rights" for surface water.

Laws, however well intentioned, do not always solve problems. We are all familiar with the well-publicized problems involving the Colorado and Salt rivers in Arizona. Perhaps less familiar is the drying up of the Rio Grande below El Paso. The actual flowing portion of the river we call the Rio Grande in Texas is in reality nothing more than an extension of the Rio Conchos from Chihuahua.

Still, this form of irrigation utilized free surface water that was obviously available, and this in turn tended to limit the amount of acreage put into cultivation.

The third phase, the thing we see happening throughout desert regions today, is sometimes the most devastating to natural populations. This is the drilling of deep wells, and pumping of underground water for irrigation purposes. Up to this phase, springs and recharge sources were relatively unaffected. As even underground water must come from some place and eventually go somewhere, concomitant changes have occurred in surface-water distribution. Today, man irrigates vast cultivated areas where free surface water never existed, while once verdant oases with their unique floras and faunas have been obliterated.

No one can argue the fact that man will sacrifice lesser animals and their habitats rather than himself if survival depends upon food and fiber production. However, too many times the trade-out is not only unequal but unnecessary.

What we often witness is simply a transfer of cheaply watered acreage from available surface water to acreage irrigated by expensive pumping methods with a loss of the surface water and its structured habitat. Following is an account of what has occurred in Pecos County, Texas, since 1950.

Pecos County was once well known for its abundance of flowing springs. Comanche Springs at Fort Stockton flowed at a volume of 129 million liters (35 million gallons) per day, with numerous other springs contributing for a total of 251 million liters (66 million gallons) of water daily making up the headwater of Comanche Creek. Leon Springs, Tunis Springs, San Pedro Springs, Cole Springs, and Santa Rosa Springs were other large springs in the area, with a number of lesser springs also present. During the latter part of the 19th century and early 1900s, irrigated farmland was developed below all the springs named. By 1940, networks of canals were delivering water over approximately 3600 ha (9000 acres) of land. Only the Tunis Springs area failed to develop eventually into a large irrigation project.

The result of these irrigation projects was to prevent Comanche and Leon creeks from flowing to the Pecos River, but the primary aquatic habitat around the springs themselves was relatively unaltered. Aquatic and semiaquatic species of reptiles and amphibians such as cricket frogs (*Acris crepitans*), blotched water snakes (*Natrix erythrogaster*), ribbon snakes (*Thamnophis proximus*), snapping turtles (*Chelydra serpentina*) and spiny softshell turtles (*Trionyx spinifer*) were inhabitants of the pools and streams in the city's Rooney Park, including the municipal swimming pool (Fig. 1).

By 1950, a few wells had been drilled to the southwest of Fort Stockton to irrigate some 200 ha (500 acres) of land. These preliminary pump-well irrigation ventures proved so successful that a land boom developed in the area known as the Belding area. Eventually, it was noticeable that as more wells were drilled, the flow of springs began to diminish. Leon Springs were the nearest to the irrigation project, and the first to become unproductive. Efforts to drill out the springs to increase their flow were unsuccessful, and eventually pumps were put into the springs.

Farmers using water from flowing springs became alarmed and tried to apply Riparian Rights Law to the situation to halt the expansion of pump irrigation. However, underground water did not come within the law. By 1954, Comanche Springs ceased flowing during the spring and summer months, but would flow somewhat from December to mid-



Fig. 1. Comanche Springs as it appeared in 1950. The main spring was in the cage seen to left of center. The area pictured was used as a natural swimming pool, and supported a number of species of aquatic and semi-aquatic reptiles and amphibians.

February. All other springs had ceased to flow. The ichthyofauna, turtles, and many amphibians once found throughout the spring system were now extirpated. By 1956, Comanche Springs had ceased to flow at all and has not flowed since (Fig. 2).

United States Department of Agriculture figures show that 2400 ha (6000 acres) of land were irrigated from the Comanche Springs complex in 1950. At least another 1200 ha (3000 acres) were irrigated from Leon, San Pedro and Santa Rosa springs for an approximate total of 3600 ha (9000 acres) irrigated from free-flowing water.

USDA figures from the ASCS office in Fort Stockton show 8000 ha (20,000 acres) presently carried as cultivated land in the Belding area. A recent look at the Belding area indicated that nearly half of that cultivated land is no longer actually being irrigated from pump wells at Belding.

In 1950 the cost per acre foot of water from Comanche Springs Irrigation District was about \$8.00. By mid-1960 the cost per acre foot of water at Belding was estimated to be above \$100.00. What has been the net result of these events in the Fort Stockton area? Nine thousand low-overhead, productive acres were swapped for 10 or 11 thousand very-expensive-to-water acres. The cost of pump irrigation is so costly that



Fig. 2. Comanche Springs today. The springs are dry, and an artificial swimming pool has been built in place of the once large natural pool. All aquatic and most semi-aquatic organisms once plentiful here no longer exist.

only a few crops are suitable for this kind of farming, and the profitable crops change from year to year. Then add to this the cost of constantly drilling wells deeper and deeper in pursuit of a continually retreating water table.

Irrigation from deep wells appears to be a boom or bust enterprise. A drive around pump-irrigated farmland in west Texas reveals many a failure at the endeavor as tumbleweeds, sunflowers, then secondary mesquite appear on land still showing the scars of cultivation.

I think the loss is the most obvious thing to see. A unique peripheral fauna disappeared in only a few years. The aesthetic beauty of springfed streams is gone, and has been replaced by concrete and macadam. Also there is the loss of all those things that only people who once thought such oases were forever can feel. However, I am not sure our modern society would tolerate a municipal swimming pool with frogs, fish, snapping turtles, and water snakes in it.

Two more areas within the northern Chihuahuan Desert may be facing the same fate as Comanche Springs. These are San Soloman and Phantom springs near Balmorhea in Reeves County, Texas, and Cuatro Cienegas in Coahuila, Mexico. An effort to form an underground water district in the Balmorhea area has already been initiated.

Water moving in underground aquifers must at some point be given the same consideration as surface water. When spring flow diminishes concomitantly with nearby well-drilling activity, that point is reached. Admittedly, solutions to complex problems involving underground water cannot be arrived at easily. The issues were never resolved satisfactorily in Pecos County even after years of courtroom battles.

Greater consideration of net gain should be the ultimate criterion of individuals and governmental agencies evaluating new irrigation projects. No new project should be initiated until it can be demonstrated that there will be a significant gain in productive acres without an associated deterioration or loss of hydric and mesic habitats already in existence.

The Pecos River has suffered its own indignities. Hindered in its flow from New Mexico by dams and deprived of fresh-water recharge from now dry tributaries such as Toyah, Leon, and Comanche creeks, this once mighty river is nothing more than a sluggish, heavily saline trickle. Phreatophytes now crowd its banks so thickly that one cannot get to the river bed in most places. The crowning blow has been the drilling of oil wells in the stream bed, with their accompanying webs of oil lines. Leaking wells and oil spills have contaminated much of what is left.

The Pecos River is essentially a dead stream from the New Mexico state line to about Sheffield. Species such as *Natrix erythrogaster* and *Acris crepitans*, once reported along this route, no longer exist except in a single small *refugium* at Balmorhea. Conant (1969) discussed the distribution of *Natrix erythrogaster* in the Pecos River drainage system and mentioned the fact that the species was becoming confined to relictual areas along with *Acris crepitans* and *Thamnophis proximus*.

The Balmorhea area is a typical Chihuahuan Desert oasis. Two large springs, San Soloman and Phantom springs, supply an abundance of free-flowing water. An artificial lake, Lake Balmorhea, stores this and run-off water for irrigation purposes. These springs once represented the headwaters of Toyah Creek which flowed to the Pecos. With the interruption of this flow, mesic and hydric species became isolated in the headwaters. The fauna of the area closely mirrors the fauna that once existed at Comanche Springs. Phantom Springs, San Soloman Springs, Lake Balmorhea, and upper Toyah Creek represent the westernmost stronghold of *Acris crepitans* and *Natrix erythrogaster* in Texas, and perhaps in the Chihuahuan Desert. The status of these species along the Pecos River in New Mexico needs to be clarified.

From below Sheffield to the Rio Grande, the Pecos River begins to pick up fresh water once more. Independence Creek is an important source of fresh water for the Pecos, and harbors a number of relictual reptiles and amphibians (Milstead 1960).

The movement of desert species into once verdant areas is but the

filling in of a pin hole in the total distribution of a species. Superficially, we might say this represents an insignificant range extension, and in considering only faunal distributions, that is true. But these areas present an ideal study plot for serial plant and animal communities.

Again using the Fort Stockton area as an illustration, let me demonstrate what appears to be happening. The genus *Cnemidophorus* (whiptail lizards) is ideal for such studies in the Chihuahuan Desert because there are so many species occupying a diversity of habitats. In the Fort Stockton area, there are three species with varying degrees of adaptation for arid habitats. *Cnemidophorus gularis* is the most mesic-adapted, *C. inornatus* is intermediate in adaptation, and *C. tigris* occupies the most arid habitats.

As youngsters growing up in Fort Stockton, my friends and I referred to these lizards as "pink-tail lizards, blue-tail lizards, and green-tail lizards." Pink-tail and blue-tail lizards were common on vacant lots in town and in the farming district, but one had to go to the mesquite flats toward Grandfalls to find green-tail lizards. Only occasionally did one find a green-tail lizard around the farming district, and never in town.

In 1968, I began a study of *Cnemidophorus* distribution in the Trans Pecos and collected series of specimens around Fort Stockton. One of my study plots was on the abandoned farmland north of Fort Stockton. In 1968, I found *Cnemidophorus gularis* still to be the dominant species, *C. inornatus* was next, but *C. tigris* was showing up at an unexpected frequency. At this time the abandoned farmland was supporting mostly native grasses, snakeweed (*Xanthocephalum*), russian thistle (*Salsola*), and some second-growth mesquite.

By 1971, mesquite had definitely become the dominant plant over many of the abandoned fields. One field that barely showed mesquite growth in 1968 was almost completely covered by it in the spring of 1974. My collection data show that as mesquite growth became established, *Cnemidophorus tigris* replaced *C. gularis* as the dominant whiptail in this field. A field just across the road with little mesquite growth still maintains a predominant *C. gularis* population. My field work in the spring of 1974 indicated that *C. inornatus* had disappeared completely from the area taken over by *C. tigris*. It has also shown that *C. tigris* has utilized heavy mesquite growth along abandoned irrigation canals to move right up to the now dry Comanche Springs. However, I did not find *C. tigris* on vacant lots in town. *Cnemidophorus gularis* and *C. inornatus* still occur there in about the same ratio as before, even though these lots are often covered with dense mesquite and creosote bush.

My findings here are only preliminary, but do seem to suggest a definite trend. I hope to continue monitoring these sites for years to come to secure additional documentation.

Jim Dixon and I have been working on the *Cnemidophorus gularis-septemvittatus-scalaris* hodge-podge of populations in Coahuila, Chihuahua, San Luis Potosí, and Durango. Dixon is concentrating on those populations in Coahuila and San Luis Potosí, while I have been doing most of my investigations in Chihuahua and Durango. We hope to meet at about the Cuatro Ciénegas area of Coahuila and tie our studies together. In discussions with him, he has informed me that he believes *C. gularis* has moved into the Cuatro Ciénegas basin via the irrigation canal that was dug through the mountains between Sacramento and Nadadores, whenever that event took place (within the past 300 years?). Secondary hybridization might now be occurring as the result of the lowland, more mesic-adapted *C. gularis* encountering the highland desert species, *C. septemvittatus*, within the basin. My thanks to Dixon for permission to mention this here. A detailed interpretation of these data will be forthcoming in one of his future publications.

As previously mentioned, *Acris crepitans* and *Natrix erythrogaster* have displayed a parallel distribution pattern throughout the Chihuahuan Desert. They have consequently suffered parallel extirpation as their aquatic habitat has been destroyed or altered.

Strecker (1909) reported *Natrix erythrogaster* from Calamity Creek in Brewster County. Netting and Goin (1946) recorded *Acris crepitans* as also occurring in Calamity Creek. Milstead (1960) searched for both species there and concluded that they probably no longer existed. Conant (1969) supported Milstead's observations and suggested that *Natrix erythrogaster* no longer occurred in the Rio Grande drainage above Boquillas in Big Bend National Park. Ten years of herpetological work in Brewster County on my part has failed to document either species along Calamity Creek. Both of these species have suffered a withdrawal throughout the northern Chihuahuan Desert over the past 40 years. Except for isolates in the Balmorhea area, and possibly in southeastern New Mexico, they now occur only as peripheral species along the eastern edge of the Chihuahuan Desert.

The Mediterranean gecko *Hemidactylus turcicus* has spread rather rapidly inward and westward from its points of introduction at gulf coastal ports. McCoy (1970) summarized documented reports of the westward movement of this little gecko. In his summary, McCoy cited specimens from Cuatro Ciénegas, Coahuila, but did not indicate the date they were collected. This would represent the first records of the species in the Chihuahuan Desert.

On 19 August 1966, I found Mediterranean geckos to be well established at Ciudad Acuña, Coahuila, and collected three specimens (SRSU 842, 843, 844) from the walls of a curio shop. Recently, Wauer and Burdick (1974) found the gecko apparently well established in Boquillas, Coahuila. It is only a matter of time until the species will be

found at suitable localities in the Big Bend National Park, Texas, such as at Rio Grande Village.

I might speculate briefly about some future herpetofaunal changes as a result of agriculture and industrial practices of a different nature than previously discussed. This is the introduction of chemicals through pesticides, fungicides, herbicides, and industrial wastes into the ecosystem. Very little has been done in investigating this aspect in the Chihuahuan Desert. The most thorough investigation of pesticides have been those of Applegate et al. (1971) in the Presidio Basin, Texas. Their findings indicate little effect upon reptilian species by pesticides, but a pronounced effect upon mammals. Saxon (1970), also working in the Presidio Basin, found *Cnemidophorus tesselatus* acquired residues of pesticides by eating contaminated insects, but found no observable effects of the pesticides upon the lizards.

Fortunately, Applegate et al. (1971) found that pesticides break down very rapidly in the Chihuahuan Desert habitat. They attributed this rapid break down to high soil temperature, high ultraviolet radiation, and the alkaline nature of the soil.

Gallagher (1974) investigated the uptake of mercury by lizards (*Cnemidophorus tigris*, *Holbrookia texana*, *Uta stansburiana*) in the Terlingua Mining District of Brewster County, Texas. He used the atomic absorption spectrophotometer method of determining mercury concentrations in various tissues. His purpose was to determine if mercury from cinnabar (a naturally occurring ore of mercury) could get into the ecosystem via food chains. The Terlingua Mining District was a leading mercury producer in the United States from 1905 to 1935, and again briefly from 1964 to 1966. It was speculated that lizards would consume insects that could contain mercury internally as well as in dust adhering to their bodies.

Gallagher found that mercury concentrations varied from site to site and with different tissues. Although gonads often had high levels (14-17 PPM) of mercury, oviducal eggs and juveniles had low levels, thus suggesting that mercury contamination was not passed to offspring.

Whether or not these chemical contaminants will ultimately affect herptile populations is yet to be determined. Both Applegate et al. (1971) and Gallagher's (1974) studies showed concentrations of contaminants in brain tissue. Applegate et al. hypothesized that this could lead to impaired motor ability and/or behavioral changes. Certainly much more needs to be done in appraising the potential effect of such contaminants.

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The Black Gap Whiptail Lizards after Twenty Years

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Some aspects of the population dynamics of whiptail lizards (genus *Cnemidophorus*) were studied at the Black Gap Wildlife Management Area, Brewster County, Texas (just to the east of Big Bend National Park) in the summers of 1951 and 1952 (Milstead 1957a, b, 1958, 1959, 1961). Three species of whiptail were found to inhabit the area in about equal numbers. They avoided competition by ecological separation: *Cnemidophorus tigris* lived on the desert floors in the valleys, *C. inornatus* lived on the sides of the hills, and *C. septemvittatus* (*C. scalaris* of others) (Fig. 1) lived on the tops of the more rugged mountains.

Cnemidophorus tigris, because of its distribution in the relatively level lowland areas, was readily accessible to drift-fence trapping. Trapped specimens were marked and released and efforts were made to recover them by sighting or recapture (Milstead 1959). The resulting data were treated with a Lincoln Index and yielded a figure of 17.85 lizards per acre.

The Black Gap area was revisited in 1962 and a number of significant changes were noted in the whiptail lizard populations (Milstead 1965). *C. inornatus* and *C. septemvittatus* were virtually extinct, while *C. tigris* had spread into all of the habitats previously occupied by itself and by the other two species. Within the area where drift-fence trapping was done in 1952, drift-fence trapping was done again, and it was found that the population had expanded to equal 74.30 lizards per acre.

The most outstanding difference between 1952 and 1962 was the breaking of a severe drought that gripped southwestern Texas from 1949 to 1957. In 1952 the average annual rainfall was 15 cm (6 inches), and in 1953 it was 7.5 cm (3 inches) (Table 1). In 1961 the average annual rainfall was almost 42.5 cm (17 inches) and in 1962 it was a little over 25 cm (10 inches). This difference in rainfall was favored as the best possibility for having caused the differences between the lizard populations of 1952 and those of 1962. It was cautioned, however, that

¹Now deceased.



Fig. 1. *Cnemidophorus septemvittatus* in Big Bend National Park, August 1957.

this might be only an obvious factor and that the actual cause might have been due to more subtle changes.

In the present study, the Black Gap area was visited in 1971 and 1972 and the populations of lizards restudied. Again, there were outstanding changes. *C. tigris*, which was so abundant in 1962, appeared to have become even less abundant than it was in 1952. A Lincoln Index performed in 1972 at the same site used in 1952 and 1962 yielded a figure of 13.64 lizards per acre. Furthermore, *C. tigris* was found to have left the habitats of the other two species and both *C. inornatus* and *C. septemvittatus* were found back in those habitats, although not in the numbers that they were found in 1952.

It is even more difficult to pinpoint the reasons for population changes between 1972 and 1962 than between 1962 and 1952. Rainfall has continued to improve so that the area now receives approximately three times the amount of rainfall that it did in 1952. The average annual rainfall for 1970 was 52.95 cm (21.18 inches) and the average for 1971 was 39.75 cm (15.90 inches) (Table 1). The area has taken on many of the characteristics of a grassland while it has lost many of the characteristics of a desert.

It may be that range-management practices of the Texas Parks and Wildlife Department coupled with the present rainfall (31.28 cm [12.51 inches] per year, 1958-1971) are returning the Black Gap Area to a grassland. Many long-time residents of the area resent its being called a desert and they speak of the turn of the century when times were pluvial and grass was "belly high to a horse." Such places, however, must have been few and far between or memories are not what they should be, because written records of the time do not support the possibility that the area was a grassland circa 1900. The report (Goldman 1951) of the

TABLE 1. Monthly rainfall recorded at Black Gap Wildlife Management Area Headquarters, Brewster County, Texas, 1952-71.

| Month | 1952 | 1953 | 1954 | 1955 | 1956 | 1957 | 1958 | 1959 | 1960 | 1961 |
|--------|------|------|------|------|------|------|-------|-------|-------|-------|
| Jan. | 0.20 | 0.10 | 0.25 | 0.33 | 0.47 | 0.20 | 1.43 | 0.39 | 1.43 | 1.54 |
| Feb. | 0.05 | 0.00 | 0.00 | 0.00 | 0.89 | 2.09 | 0.62 | 0.60 | 0.82 | 0.45 |
| Mar. | 0.12 | 0.98 | 0.00 | 0.00 | 0.00 | 0.22 | 0.66 | 0.00 | 0.42 | 0.25 |
| Apr. | 0.60 | 0.00 | 0.75 | 1.00 | 0.00 | 0.41 | 0.00 | 0.98 | 0.52 | 0.59 |
| May | 2.20 | 0.50 | 0.99 | 0.75 | 0.00 | 0.62 | 1.23 | 4.40 | 1.23 | 3.81 |
| June | 1.00 | 0.41 | 0.00 | 0.75 | 0.72 | 0.52 | 1.18 | 1.30 | 0.00 | 3.95 |
| July | 0.25 | 0.39 | 0.90 | 0.25 | 1.50 | 0.95 | 2.68 | 1.30 | 4.35 | 4.06 |
| Aug. | 0.00 | 0.32 | 1.33 | 0.86 | 0.00 | 0.49 | 0.69 | 2.09 | 1.65 | 0.26 |
| Sept. | 0.17 | 0.00 | 0.00 | 3.60 | 1.37 | 0.81 | 3.73 | 0.26 | 1.50 | 0.21 |
| Oct. | 0.00 | 0.00 | 0.00 | 0.05 | 0.00 | 1.04 | 3.91 | 1.68 | 0.35 | 0.94 |
| Nov. | 0.40 | 0.00 | 0.00 | 0.70 | 0.00 | 0.22 | 0.00 | 0.72 | 0.00 | 0.71 |
| Dec. | 1.14 | 0.21 | 0.00 | 0.00 | 0.00 | 0.20 | 0.39 | 0.36 | 0.08 | 0.00 |
| Annual | 6.13 | 2.91 | 4.22 | 8.29 | 4.95 | 7.77 | 16.52 | 14.08 | 12.35 | 16.77 |

| Month | 1962 | 1963 | 1964 | 1965 | 1966 | 1967 | 1968 | 1969 | 1970 | 1971 |
|--------|-------|-------|------|------|-------|-------|------|------|-------|-------|
| Jan. | 0.05 | 0.41 | 0.47 | T | 0.91 | 0.71 | 0.36 | 0.00 | 0.50 | 0.00 |
| Feb. | 0.14 | 0.73 | 0.00 | 1.06 | 0.26 | 0.00 | 1.05 | 0.00 | 1.16 | 0.00 |
| Mar. | 0.20 | 0.00 | 0.00 | 0.25 | 0.18 | 0.35 | 0.88 | 0.00 | 1.46 | 0.00 |
| Apr. | 0.53 | 1.31 | 0.00 | 0.00 | 0.33 | 0.00 | 0.50 | 0.23 | 0.05 | 0.00 |
| May | 0.00 | 1.87 | 1.70 | 0.25 | 0.30 | 0.64 | 0.64 | 2.43 | 1.85 | 0.75 |
| June | 1.99 | 0.36 | 1.44 | 0.93 | 0.56 | 2.95 | 0.52 | 3.12 | 2.85 | 0.99 |
| July | 1.38 | 4.17 | 1.20 | 1.19 | 0.84 | 0.42 | 0.82 | 0.90 | 1.28 | 2.67 |
| Aug. | 0.00 | 1.31 | 1.58 | 2.59 | 1.84 | 1.74 | 1.00 | 0.00 | 3.32 | 2.89 |
| Sept. | 4.46 | 0.40 | 1.35 | 1.69 | 1.13 | 2.29 | 1.78 | 0.57 | 8.63 | 1.40 |
| Oct. | 0.39 | 0.00 | 0.61 | 0.00 | 4.87 | 1.00 | 0.65 | 1.12 | 0.20 | 6.63 |
| Nov. | 0.05 | 0.75 | 0.00 | 0.60 | 0.00 | 0.00 | 0.00 | 0.02 | 0.00 | 0.00 |
| Dec. | 0.88 | 0.20 | 0.55 | 0.51 | 0.00 | 0.37 | 0.00 | 0.50 | 0.15 | 0.57 |
| Annual | 10.07 | 11.51 | 8.90 | 9.07 | 11.22 | 10.47 | 8.20 | 8.89 | 21.18 | 15.90 |

Nelson and Goldman expedition through Mexico 1892-1906 repeatedly refers to northern Coahuila and northern Chihuahua as arid desert lands. Strecker (1909) in reporting on a 1905 trip to what is now Big Bend National Park referred to the valley floors as "low, hot desert strips." Strecker's list of reptilian and amphibian species does not differ markedly from one that might be made today, although some of the eastern relicts listed by Strecker may have been extirpated by the 1949-57 drought (Milstead 1960).²

²Milstead (1960), writing soon after the close of the drought, extended the Chihuahuan Desert's eastern border as far as the Devil's River. It now seems desirable to withdraw the boundary at least as far as the Pecos River.

The question of whether or not the area is a desert has not been limited to local residents. Various biogeographers have also argued the point (see Lowe 1964 for references). Lowe (1964), however, has concluded: "The idea that none of the Chihuahuan Desert is desert, and that all of it is subclimax grassland, is to be emphatically rejected."

One possible explanation for the lizard population changes from 1962 to 1972 is that the country is now "too good" for whiptail lizards. There is some evidence for this. Not one of the Black Gap whiptails occurs on the Edwards Plateau just east of the Chihuahuan Desert. Furthermore, extensive groundcover has developed at the site where the Lincoln Index was measured. Several species of plants are prominent in this groundcover. The dominant ones are (in decreasing order): *Cryptantha* sp., *Nama hispidum*, *Thelypodium texanum*, and *Oligomeris linifolia*. Whiptails apparently do not do well where there is extensive groundcover. Blair (1960) recorded one species of whiptail in the lizards of Blair Farm near Austin, Texas. After the termination of the drought in 1957, however, as the land recovered, the whiptails completely disappeared (Blair pers. comm.). In particular, *Cnemidophorus tigris* avoids heavily vegetated areas to inhabit desert floors with sparse vegetation. If the many workers on the species are in unanimous agreement on anything, it is that *C. tigris* is a desert species with a preference for open areas (Milstead 1957a,b; Zweifel 1962; McCoy 1965; Pianka 1965, 1970; Degenhardt 1966; Echternacht 1967; Medica 1967; Parker 1972; Burkholder and Walker 1973; Scudday and Dixon 1973; Asplund 1974).

This "too-good" explanation is not entirely suitable, however. It does fit well on the desert floor where the growth of vegetation has been extensive because of rainfall and run-off from the other associations of the area, and it readily explains the reduction of numbers of *C. tigris* on the desert floor. But this explanation must be discounted because it does not explain the disappearance of *C. tigris* in the upland associations, which still have many of the characteristics of a desert, the reinvasion of those areas by the other two species of whiptails, or the reinvasion of the desert floor by *Cnemidophorus inornatus*.

Another possible explanation to explain the decline of numbers of *C. tigris* at Black Gap is an increased number of predators in the area. Rattlesnakes, roadrunners, and evidences of badger activities were greatly increased over what they had been in the previous studies. Rodent populations appeared to be down during the 1971-72 study. Thus, it may have been that the increased predators were concentrating on lizards during this time. Again, however, this would explain the decline in *C. tigris* but would not explain the reinvasion of the area by the other two species of whiptails. Furthermore, Milstead (1957a) and Turner et al. (1969) have discounted predators as having any pronounced effect on changes in whiptail populations.

Sexton (1967) has suggested cyclic behavior as a possible explanation for the decline in *Anolis limifrons* on Barro Colorado Island, Panama Canal Zone. Such an explanation certainly seems to fit the population changes in whiptail lizards at Black Gap over the two decades involved, and it offers a ready explanation for the "crash" of *Cnemidophorus sacki* at the Sierra Vieja (Texas) between 1948 and 1951 (Milstead 1957a) and of *C. tigris* in California 1963-64 (Pianka 1970). Although cyclic behavior is a strong possibility, its acceptance as the explanation for the density changes in whiptails and in *Anolis* must await the accumulation of far more detailed data.

With regard to the Black Gap lizards, Milstead (1965) suggested that *C. tigris* may have an advantage under more mesic conditions, while *C. inornatus* and *C. septemvittatus* have advantages under more xeric conditions. This still may be the best possible explanation (and this does not necessarily contradict the assertion made above that *C. tigris* is a desert lizard). Although there was a steady increase of annual rainfall over the two decades involved in the studies (Table 1), there was an exceptionally high amount of rainfall in 1961 during the 3 months that whiptail lizards are most active in reproduction. In May, June, and July 1961, 29.55 cm (11.82 inches) were recorded at the Black Gap Area Headquarters (less than 4.8 km [3 miles] airline from the whiptail study site). During this same period in 1971, only 10.78 cm (4.31 inches) of rainfall were recorded and in 1970, 13.7 cm (5.48 inches) were recorded. Although rainfall data are complete, there are not enough data on whiptail lizards to reach any definite conclusions. The first year of Black Gap rainfall data was 1952 and in May, June, and July of that year there were only 8.63 cm (3.45 inches) of rainfall. It is particularly bad that there is no rainfall data for 1951 or any population data for 1969, the year following the time that Black Gap had the lowest rainfall in May, June, and July 4.95 cm (1.98 inches).

In support of the suggestion that the excessive amount of rainfall in the summer of 1961 resulted in the *C. tigris* "explosion" in 1962 are the two papers by Pianka and one by Turner et al. Pianka (1965, 1970) has shown conclusively that egg production is up during wet years and down during dry years in *C. tigris* on the Mojave and Sonoran deserts. Turner et al. (1969) have shown population density estimates for whiptails from a number of localities and have emphasized that the *C. tigris* "bloom" at Black Gap in 1962 was associated "with a dramatic ten-year change in the quality of the vegetation." Furthermore, Pianka (1965) has suggested that this species "probably survived the recent pluvials in the Great Basin by moving up the slopes of Hill-sides." This could have happened during Cenozoic pluvials on the Chihuahuan Desert as well and could explain the presence of *C. tigris* in the habitats of the other two species at Black Gap in 1962.

Accompanying the changes of densities in Black Gap whiptail lizards

TABLE 2. Percentage stomach contents by volume of the whiptail lizards of the Black Gap Wildlife Management Area, Brewster County, Texas.

| Item | <i>C. tigris</i> | | | | <i>C. septemvittatus</i> | | <i>C. inornatus</i> |
|----------------------------|------------------|--------|---------|---------|--------------------------|---------|---------------------|
| | Sample | 1962 | 1971-72 | 1951-52 | 1951-52 | 1971-72 | 1951-52 |
| Arachnida | 7.35 | 5.32 | 5.34 | 2.38 | 0.88 | 4.24 | 4.24 |
| Orthoptera | 14.49 | 8.95 | 35.41 | 19.96 | 11.24 | 9.25 | 9.25 |
| Isoptera | 45.89 | 32.42 | 16.02 | 69.65 | 42.68 | 77.66 | 77.66 |
| Coleoptera | 8.11 | 5.97 | 10.99 | 4.90 | 14.10 | 0.97 | 0.97 |
| Lepidoptera | 13.89 | 43.30 | 8.98 | 0.68 | 7.50 | 4.73 | 4.73 |
| Hymenoptera | 1.44 | b | 12.94 | 1.08 | 22.15 | 0.64 | 0.64 |
| Miscellaneous ^a | 8.74 | 4.04 | 10.37 | 1.35 | 1.54 | 2.54 | 2.54 |
| Total | 99.91 | 100.00 | 100.05 | 100.00 | 100.09 | 100.03 | 100.03 |

^aItems less than 5% in all samples.
 bIncluded in Miscellaneous for this sample.



Fig. 2. Termite castle built on a stick, Big Bend National Park, August 1958.

were also changes in their diets (Table 2). In 1951-52, the most prominent items in the stomachs of all three species of whiptails were termites (Fig. 2), with grasshoppers and caterpillars comprising a poor second and a poor third, respectively. In 1962, *C. tigris* was the only whiptail that could be collected in enough numbers for stomach analyses. In that sample termites were the second most important item, with caterpillars being the most important item. In the 1971-72 study, both *C. tigris* and *C. septemvittatus* were available for stomach analyses. With *C. tigris* grasshoppers were now first in importance, termites were still second but they had fallen to a still lower percentage, and caterpillars had fallen below the percentage for 1951-52. With *C. septemvittatus*, termites were still the most important items in the diet although much lower in percentage than they had been in 1951-52. Grasshoppers were lower in percentage and caterpillars, beetles, and ants were up in percentage.

Ignoring the major food items for the moment, the most surprising thing in the 1971-72 stomach analyses was the significant increase in the number of ants (Formicidae) consumed (Table 2). Milstead (1957a) has given considerable discussion to the presumption that whiptails do not eat ants. (Apparently the younger, latter-day whiptails at Black Gap have not read my papers.) Workers in other areas, however, have regularly recorded ants as a part of whiptail diets (see, for example, Pianka

1965, 1970; Echternacht 1967; Medica 1967; Milstead and Tinkle 1969); and Scudday and Dixon (1973) have recorded them in varying concentrations for whiptails from southwestern Texas.

I consider the dietary changes involving caterpillars and grasshoppers to be of little or no significance. It has been suggested (Milstead 1965; Milstead and Tinkle 1969; Scudday and Dixon 1973) that whiptails are opportunistic feeders and will take whatever is most readily available. Lepidopteran larvae tend to reach their peak on the Chihuahuan Desert 2-3 weeks ahead of grasshopper nymphs. Thus, small differences in study times or local aberrations in weather could account for these differences in caterpillars and grasshoppers in whiptail diets.

Termites deserve a more lengthy consideration because of their prominence in discussions of whiptail ecology. Termites have had significant roles in the diets of whiptails studied by Milstead (1957a, 1958, 1965), Laughlin (1958-part), Pianka (1965, 1970-part), Bostic (1966), and Scudday and Dixon (1973). Termites have not been a significant part of the whiptail diets in studies by Pack (1923), Laughlin (1958-part), McCoy (1965), Pianka (1965, 1970-part), Dixon and Medica (1966), Medica (1967-part), and Milstead and Tinkle (1969-part).

Pianka (1965, 1970) noted that his southern populations of *Cnemidophorus tigris* consumed large numbers of termites, while his northern populations did not. This may be simply because the termites eaten by whiptails do not range northward onto the Great Basin Desert extensively, but there is a possibility of more significant biogeographical meaning. All of the studies where termites constituted a significant part of the whiptail diet were done in arid localities more or less ecotonal in nature. Laughlin (1958) worked in San Patricio County, Texas, which is ecotonal between the Tamaulipan (chaparral) and the Texan (grassland) biotic provinces of Blair (1950). Milstead and Tinkle (1969) worked in the Texas Sand Hills which are ecotonal between the Chihuahuan Desert and the Kansan Biotic Province (of Blair 1950). Medica (1967) worked near the extreme northern border of the Chihuahuan Desert in an area also influenced by irrigation. All of the other studies were performed on the Chihuahuan, Sonoran, or Mojave deserts, mostly north of the Rio Grande (i.e., the international border). As Lowe (1964) has noted, 90% of both the Chihuahuan and Sonoran deserts lies south of the border, but most of the work has been done in the 10% that lies to the north. It would be interesting to know if whiptails eat termites in the southern 90%, also, or if it is just a phenomenon of the somewhat ecotonal 10%. (Lowe 1964 considers the Mojave Desert to be a ecotone between the Sonoran and Great Basin deserts.)

The decrease of termites at Black Gap from the most important items in 1952 to the second most important items in 1962 was attributed to increased rainfall followed by increased vegetation and insects. Further-

more, it was suggested (Milstead 1965) that the area could have supported more lizards than it was supporting because there were presumed to have been as many termites in 1962 as in 1952, and those not being eaten constituted an untapped food resource. Several people have accepted these conclusions and applied them to their own work.

Unfortunately, two fallacious assumptions are contained in these conclusions. First, the work was done in the summer months when production is at its zenith. Calculations of the carrying capacity of an area should be based on its lean months and not on its most productive months. Second, it now appears that the population densities of termites are lower in good years than in dry years. In talking with biologists, ranchers, and soil conservation personnel, it seems that there is more deadfall for termite consumption in drought years and, also at those times, range termites are able to attack and kill living stubble after deer or livestock have grazed it close to the ground. Therefore, it must be concluded that termites are the staple food of whiptails during lean months and/or years, but not during better times.

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A Changing Environment: Documentation of Lizards and Plants Over a Decade

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All too often we envision natural populations as changing with evolutionary time but as fixed or constant with historical time. Studies treating changes in plant populations are certainly more in evidence than those treating animals, because plants are easier to see, count, and measure. Furthermore, most animal studies concerned with population changes have been done on game, predatory, or other economically important species. Reptiles being economically unimportant for the most part, as well as difficult to work with under natural conditions, have been relatively neglected. In fact, it has been only within the last decade or two that attempts to estimate reptilian population densities have met with any degree of success. Many of these studies were concerned with lizards and work by Fitch (1958), Carpenter (1959), Milstead (1959, 1961, 1965), Tanner and Jorgensen (1963), Bellis (1964), McCoy (1965), Bostic (1965), Tinkle (1965a,b, 1967), Degenhardt (1966), Turner et al. (1969) and Pianka (1970) serves to illustrate the large variety of methods used for density estimates or population dynamics of one sort or another. In most cases some variation in reported densities is expected due to species differences. In others the species censused were the same but the locality or habitat differed. There are a few instances, however, where differences in density estimates seem to involve primarily methodology, for both species and habitats studied were similar.

Even fewer studies are available that take population changes over long periods of time into account. Milstead's (1965) work is a notable exception to this as he compared population changes over a 10-year period. Milstead has reported another study done after 20 years in a previous paper. The primary purpose of the work reported here was the

reoperation of the six quadrats permanently located and operated in Big Bend National Park during 1956, 1957, and 1958 (Degenhardt 1966). At that time it was hoped that these quadrats would be operated periodically, for their main value lies in evaluating successional trends. In effect, this second operation during the summers of 1968 and 1969 resulted in the further testing of the method as well as the procurement of data for comparison with past and future.

METHODS

The general methods of quadrat operation have been published elsewhere (Degenhardt 1966) and there is no need to reiterate these. The slightly expanded operations in 1968 and 1969 involved personnel, calendar, plant censusing, and photography.

Calendar

The months of June, July, and August were utilized in both summers. In June four persons operated individual quadrats concurrently, utilizing a 2 day on and 1 day off schedule. The quadrats and their operators were: Ted Brown at 1020 m (3400 ft), Ronald Lucchino at 930 m (3100 ft), Paula Degenhardt at 840 m (2800 ft), and myself at 1260 m (4200 ft).

After completion of this first phase, my wife and I were absent during the month of July while Brown and Lucchino operated the 1395 m (4650 ft) and 1575 m (5250 ft) quadrats, respectively. Upon our return in August, the four quadrats operated in June were reoperated by the same persons. The precise dates of operation are included with the tabulated results.

Vegetation

The total of four set photographs for each quadrat for each year was expanded in 1968 and 1969 to eight per quadrat. Besides the four taken from each corner with the camera aimed toward the center, four more were taken from the center aimed at each corner. Only one photograph from each set taken in 1957 and 1968 is reproduced here for comparison purposes (Figs. 2 and 3). Soil-surface photographs taken for the earlier study were not retaken in 1968 and 1969 since there were no detectable changes in the soil surface.

Since the actual operation of the quadrats only takes a short time, the remainder of these days, or the off days, were used for the plant studies. By continual observation and collecting throughout the summer, a fairly complete list of seed plants, including annuals, occurring within the quadrat boundaries was obtained. Voucher specimens for all species on the list are stored at the University of New Mexico.

TABLE 1. Lizard census results on the (4-acre) Tornillo Flat (2800 ft) Quadrat for 1957, 1958, 1960, 1968, 1969. The data from each of the 4 acres within the quadrat was used in computing the means and standard errors; n = 40 except in 1960 where n = 32 and in 1968, set 2, where n = 24.

| | 1957 | | 1958 | | 1960 | | 1968 | | 1969 | |
|--------------------|----------|---------|----------|---------|-----------------|------------------|------------------|------------------|------------------|------------------|
| | 7/14-8/9 | 8/3-25 | 7/24-9/2 | 6/14-30 | Set 1 8/9-21 | Set 2 6/12-26 | Set 1 8/10-21 | Set 2 6/10-21 | Set 1 8/10-21 | Set 2 8/10-21 |
| <i>C. tigris</i> | | | | | | | | | | |
| adults | 34 | 34 | 43 | 68 | 55 | 78 | 102 | | | |
| juveniles | 5 | 8 | 0 | 0 | 2 | 0 | 5 | | | |
| total | 39 | 42 | 43 | 68 | 57 | 78 | 107 | | | |
| mean/acre | 1.0 | 1.1 | 1.3 | 1.7 | 2.4 | 2.0 | 2.7 | | | |
| <i>H. texana</i> | | | | | | | | | | |
| adults | 10 | 11 | 7 | 0 | 0 | 0 | 3 | | | |
| juveniles | 1 | 10 | 0 | 0 | 0 | 0 | 0 | | | |
| total | 11 | 21 | 7 | 0 | 0 | 0 | 3 | | | |
| mean/acre | 0.3 | 0.5 | 0.2 | 0.0 | 0.0 | 0.0 | 0.1 | | | |
| Other ^a | | | | | | | | | | |
| adults | 0 | 0 | 2 | 0 | 0 | 3 | 1 | | | |
| juveniles | 0 | 0 | 2 | 0 | 0 | 0 | 1 | | | |
| total | 0 | 0 | 4 | 0 | 0 | 3 | 2 | | | |
| mean/acre | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.1 | <0.1 | | | |
| All species | | | | | | | | | | |
| adults | 44 | 45 | 52 | 68 | 55 | 81 | 106 | | | |
| juveniles | 6 | 18 | 2 | 0 | 2 | 0 | 6 | | | |
| total | 50 | 63 | 54 | 68 | 57 | 81 | 112 | | | |
| Adults/acre | 1.2±0.2 | 1.1±0.2 | 1.7±0.2 | 1.7±0.2 | 2.3±0.3 | 2.0±0.2 | 2.6±0.3 | | | |
| Totals/acre | 1.2±0.2 | 1.6±0.2 | 1.7±0.2 | 1.7±0.2 | 2.4±0.3 | 2.0±0.2 | 2.8±0.3 | | | |

^aThese are "visitors" from surrounding areas. One was a juvenile *Crotaphytus wislizeni*, but all others were *Uta stansburiana*.

TABLE 2. Lizard census results on the 1-acre Grapevine Hills (3100 ft) Quadrat for 1956, 1957, 1968, and 1969; n = 10 except in 1956 where n = 18 and 1968 where n = 11.

| | 1956 | | 1957 | | 1968 | | 1969 | |
|--------------------|----------|----------|---------|--------|---------|---------|------------------|-------------------|
| | 7/20-8/9 | 7/20-8/9 | 6/6-16 | 6/6-16 | 8/14-29 | 8/14-29 | Set 1 6/12-26 | Set 2 7/25-8/7 |
| <i>C. tigris</i> | | | | | | | | |
| adults | 70 | 42 | 42 | 23 | 51 | 38 | | |
| juveniles | 2 | 0 | 15 | 0 | 0 | 13 | | |
| total | 72 | 42 | 38 | 38 | 51 | 51 | | |
| mean/acre | 4.0 | 4.2 | 3.4 | | 5.1 | 5.1 | | 5.1 |
| <i>C. scalaris</i> | | | | | | | | |
| adults | 11 | 2 | 2 | 2 | 10 | 1 | | |
| juveniles | 0 | 0 | 1 | 1 | 0 | 1 | | |
| total | 11 | 2 | 3 | 3 | 10 | 2 | | |
| mean/acre | 0.6 | 0.2 | 0.3 | | 1.0 | 0.2 | | |
| <i>H. texana</i> | | | | | | | | |
| adults | 61 | 32 | 3 | 3 | 4 | 4 | | |
| juveniles | 0 | 0 | 7 | 7 | 0 | 0 | | |
| total | 61 | 32 | 10 | 10 | 4 | 4 | | |
| mean/acre | 3.4 | 3.2 | 0.9 | | 0.4 | 0.4 | | 0.4 |
| Unidentified | | | | | | | | |
| adults | 14 | 6 | 0 | 0 | 5 | 0 | | |
| juveniles | 0 | 0 | 0 | 0 | 0 | 0 | | |
| total | 14 | 6 | 0 | 0 | 5 | 0 | | |
| mean/acre | 0.8 | 0.6 | 0.0 | | 0.5 | 0.0 | | 0.0 |
| All species | | | | | | | | |
| adults | 155 | 82 | 28 | 28 | 70 | 43 | | |
| juveniles | 2 | 0 | 23 | 23 | 0 | 14 | | |
| total | 157 | 82 | 51 | 51 | 70 | 57 | | |
| Adults/acre | 8.6±0.6 | 8.2±0.8 | 2.5±0.5 | | 7.0±1.0 | 4.3±0.7 | | 4.3±0.7 |
| Totals/acre | 8.7±0.7 | 8.2±0.8 | 4.6±0.7 | | 7.0±1.0 | 5.7±0.7 | | 5.7±0.7 |

TABLE 3. Lizard census results on the 1-acre Burnham Flat (3400 ft) Quadrat for 1957, 1958, 1968, and 1969; n = 10 except in 1968, set 2, where n = 8, 1969, set 1, where n = 9, and 1969, set 2, where n = 11.

| | 1957 | | 1958 | | 1968 | | 1969 | |
|--------------------|-----------|---------|------------------|------------------|------------------|-----------------|------|--|
| | 6/27-7/13 | 8/5-26 | Set 1 6/14-27 | Set 2 8/14-24 | Set 1 6/12-26 | Set 2 8/1-21 | | |
| <i>C. tigris</i> | | | | | | | | |
| adults | 29 | 27 | 38 | 15 | 33 | 11 | | |
| juveniles | 0 | 32 | 0 | 13 | 0 | 12 | | |
| total | 29 | 59 | 38 | 28 | 33 | 23 | | |
| mean/acre | 2.9 | 5.9 | 3.8 | 3.5 | 3.7 | 2.1 | | |
| <i>H. texana</i> | | | | | | | | |
| adults | 8 | 11 | 1 | 4 | 11 | 6 | | |
| juveniles | 0 | 9 | 0 | 0 | 0 | 0 | | |
| total | 8 | 20 | 1 | 4 | 11 | 6 | | |
| mean/acre | 0.8 | 2.0 | 0.1 | 0.5 | 1.2 | 0.5 | | |
| Other ^a | | | | | | | | |
| adults | 3 | 0 | 4 | 3 | 0 | 1 | | |
| juveniles | 0 | 0 | 2 | 0 | 0 | 0 | | |
| total | 3 | 0 | 6 | 3 | 0 | 1 | | |
| mean/acre | 0.3 | 0.0 | 0.6 | 0.4 | 0.0 | 0.1 | | |
| All species | | | | | | | | |
| adults | 40 | 38 | 43 | 22 | 44 | 18 | | |
| juveniles | 0 | 41 | 2 | 13 | 0 | 12 | | |
| total | 40 | 79 | 45 | 35 | 44 | 30 | | |
| Adults/acre | 4.0±0.6 | 3.8±0.6 | 4.3±0.8 | 2.8±0.7 | 4.9±0.4 | 1.6±0.4 | | |
| Totals/acre | 4.0±0.6 | 7.9±0.9 | 4.5±0.8 | 4.4±0.7 | 4.9±0.4 | 2.7±0.4 | | |

^aThese are "visitors" from surrounding areas or unidentified lizards. The visitors were *C. inornatus* or *Uta stansburiana*.

TABLE 4. Lizard census results on the 1-acre Green Gulch (4200 ft) Quadrat for 1957, 1958, 1968, and 1969; n = 10 except in 1958 where n = 9, 1968, set 2, where n = 3, and 1969, both sets, where n = 6.

| | 1957 | | 1958 | | 1968 | | 1969 | |
|--------------------|----------|---------|------------------|-----------------|------------------|------------------|------|----------|
| | 7/24-8/8 | 6/4-7/4 | Set 1 6/14-27 | Set 2 8/9-11 | Set 1 6/12-22 | Set 2 8/10-17 | | |
| <i>C. tigris</i> | | | | | | | | |
| adults | 42 | 33 | 8 | 4 | | | | |
| juveniles | 2 | 0 | 0 | 0 | | | | |
| total | 44 | 33 | 8 | 4 | | | | |
| mean/acre | 4.4 | 3.7 | 0.8 | 1.3 | | | | |
| <i>H. texana</i> | | | | | | | | |
| adults | 73 | 55 | 1 | 0 | | | | |
| juveniles | 7 | 0 | 0 | 0 | | | | |
| total | 80 | 55 | 1 | 0 | | | | NO |
| mean/acre | 8.0 | 6.1 | 0.1 | 0.0 | | | | |
| <i>C. scalaris</i> | | | | | | | | |
| adults | 1 | 1 | 1 | 0 | | | | |
| juveniles | 0 | 0 | 0 | 0 | | | | |
| total | 1 | 1 | 1 | 0 | | | | |
| mean/acre | 0.1 | 0.1 | 0.1 | 0.0 | | | | LIZARDS |
| Unidentified | | | | | | | | |
| adults | 3 | 0 | 0 | 0 | | | | |
| juveniles | 0 | 0 | 0 | 0 | | | | |
| total | 3 | 0 | 0 | 0 | | | | |
| mean/acre | 0.3 | 0.0 | 0.0 | 0.0 | | | | RECORDED |
| All species | | | | | | | | |
| adults | 119 | 89 | 10 | 4 | | | | |
| juveniles | 9 | 0 | 0 | 0 | | | | |
| total | 128 | 89 | 10 | 4 | | | | |
| Adults/acre | 11.9±0.4 | 9.9±0.6 | 1.0±0.5 | 1.3±0.3 | 0.0 | 0.0 | 0.0 | 0.0 |
| Totals/acre | 12.8±0.4 | 9.9±0.6 | 1.0±0.5 | 1.3±0.3 | 0.0 | 0.0 | 0.0 | 0.0 |

TABLE 5. Lizard census results on the 1-acre Green Gulch (4650 ft) Quadrat for 1957, 1958, 1968, and 1969. Lizards disappeared from the quadrat after 2 counts in 1958, after 1 count in 1968, and after the first count in 1969; n = 10 except in 1958 where n = 2, and in 1968 and 1969 where n = 6.

| | 1957 8/12-22 | 1958 6/22-7/1 | 1968 6/29-7/17 | 1969 6/29-7/8 |
|--------------------|-----------------|------------------|-------------------|------------------|
| <i>C. scalaris</i> | | | | |
| adults | 18 | 9 | 4 | 1 |
| juveniles | 3 | 0 | 0 | 0 |
| total | 21 | 9 | 4 | 1 |
| mean/acre | 2.1 | 4.5 | 0.7 | 0.2 |
| <i>H. texana</i> | | | | |
| adults | 14 | 2 | 0 | 0 |
| juveniles | 3 | 0 | 0 | 0 |
| total | 17 | 2 | 0 | 0 |
| mean/acre | 1.7 | 1.0 | 0.0 | 0.0 |
| Unidentified | | | | |
| adults | 2 | 0 | 0 | 0 |
| juveniles | 0 | 0 | 0 | 0 |
| total | 2 | 0 | 0 | 0 |
| mean/acre | 0.2 | 0.0 | 0.0 | 0.0 |
| All species | | | | |
| adults | 34 | 11 | 4 | 1 |
| juveniles | 6 | 0 | 0 | 0 |
| total | 40 | 11 | 4 | 1 |
| Adults/acre | 3.5±0.5 | 5.5±3.5 | 0.7±0.7 | 0.2±0.2 |
| Totals/acre | 4.0±0.6 | 5.5±3.5 | 0.7±0.7 | 0.2±0.2 |

TABLE 6. Lizard census results on the 1-acre Green Gulch (5250 ft) Quadrat for 1957, 1958, 1968, and 1969. Lizards either very rare or absent completely during 1968 and 1969; n = 10 except in 1968 and 1969 where n = 6.

| | 1957 | 1958 | 1968 | 1969 |
|--------------------|----------|---------|----------|----------|
| | 6/20-7/5 | 6/3-7/5 | 7/18-8/2 | 6/29-7/4 |
| <i>C. scalaris</i> | | | | |
| adults | 7 | 10 | | 1 |
| juveniles | 0 | 0 | No | 0 |
| total | 7 | 10 | | 1 |
| mean/acre | 0.7 | 1.0 | | 0.2 |
| Unidentified | | | | |
| adults | 0 | 1 | | 0 |
| juveniles | 0 | 0 | Lizards | 0 |
| total | 0 | 1 | | 0 |
| mean/acre | 0.0 | 0.1 | | 0.0 |
| All species | | | | |
| adults | 7 | 11 | | 1 |
| juveniles | 0 | 0 | Recorded | 0 |
| total | 7 | 11 | | 1 |
| Adults/acre | 0.7±0.3 | 1.1±0.3 | 0.0 | 0.2±0.2 |
| Totals/acre | 0.7±0.3 | 1.1±0.3 | 0.0 | 0.2±0.2 |

TABLE 7. Vegetation counts on the six quadrats for the years 1957, 1958, 1968, and 1969. In 1957 grasses and forbs and overstory were not counted separately. In 1958 no counts were made on the 3100 ft quadrat. Recorded in percent cover. The readings to tenths of a percent are probably not significant.

| Quadrat | Grasses and Forbs | | | | Overstory | | | | Total | | | |
|---------|-------------------|------|------|------|-----------|------|------|------|-------|------|------|------|
| | 1957 | 1958 | 1968 | 1969 | 1957 | 1958 | 1968 | 1969 | 1957 | 1958 | 1968 | 1969 |
| 2800 ft | | 0.1 | 1.1 | 1.7 | | 2 | 4.6 | 6.7 | 4 | 2 | 5.7 | 8.5 |
| 3100 ft | | | 16.2 | 16.1 | | | 25.0 | 26.9 | 17 | | 41.2 | 43.0 |
| 3400 ft | | 19 | 18.6 | 18.7 | | 9 | 19.8 | 21.3 | 32 | 28 | 38.5 | 40.0 |
| 4200 ft | | 22 | 62.2 | 54.0 | | 4 | 10.8 | 20.7 | 23 | 26 | 73.0 | 74.7 |
| 4650 ft | | 23 | 43.3 | 32.7 | | 5 | 25.7 | 15.5 | 21 | 28 | 69.0 | 48.2 |
| 5250 ft | | 30 | 74.8 | 62.7 | | 4 | 16.8 | 24.4 | 36 | 34 | 91.7 | 87.1 |

TABLE 8. Plant species diversity on the six quadrats. Only the seed plants are considered in the species number.

| Years | Quadrats | | | | | |
|---------------------|----------|---------|---------|---------|---------|---------|
| | 2800 ft | 3100 ft | 3400 ft | 4200 ft | 4650 ft | 5250 ft |
| 1957 - 1958 | 20 | 47 | 32 | 42 | 48 | 36 |
| 1968 - 1969 | 53 | 70 | 63 | 107 | 87 | 82 |
| Percentage Increase | 165% | 49% | 97% | 155% | 81% | 128% |

RESULTS

Results are tabulated in Tables 1 through 8. Space limitations prevent the inclusion of a list of plant species and their occurrence on the quadrats but Table 8 figures are from this list.

Summary of Results

1. Lizard numbers have decreased or remained the same on all but the Tornillo Flat (840 m, 2800 ft) quadrat. Significant changes occurred on three.
2. Lizard species composition changed significantly on all.
3. There is definite indication of a population decrease in adult lizards as summer progresses.
4. Lizard density changes were not the same for all species.
5. There has been an increase in plant density on all quadrats.
6. There has been an increase in plant diversity on all quadrats.
7. There has been an overall decrease in the amount of lechuquilla on quadrats.
8. In general, an increase in vegetation above an optimum results in decreased lizard numbers. This optimum varies with the interacting factors of the situation (lizard species, plant form, elevation and exposure, and competition or predation). Increases in vegetation below the optimum result in an increase in lizard numbers.
9. *Holbrookia texana* was seemingly more affected by vegetation fluctuations than *Cnemidophorus tigris*.
10. *C. scalaris* seemingly has a higher optimum and/or maximum vegetation density than *C. tigris* and may replace *C. tigris* under some conditions as the vegetation density increases above the *C. tigris* maximum.

DISCUSSION

Little quantitative work with natural populations of reptiles appears in the literature and what is available reports on work done largely within the last decade. Estimates of population density that appear in the literature vary (Fitch 1958; Carpenter 1959; Milstead 1959, 1961, 1965; Tanner and Jorgensen 1963; Bellis 1964; Tinkle 1965a, b, 1967;

McCoy 1965; Bostic 1965; Degenhardt 1966; Turner et al. 1969). In most cases some variation in reported densities is expected due to species differences. In others the species censused were the same but the locality or habitat differed. The work of Milstead (1965), however, treated the same species as I did (Degenhardt 1966) in areas that were comparable. The estimates differed markedly and the extremely high density estimates by Milstead (73.3 *C. tigris* per acre) seem unrealistic. The highest density recorded by me (4.2 *C. tigris* per acre) for the species, about 40 km (25 miles) away from Milstead's location, was much

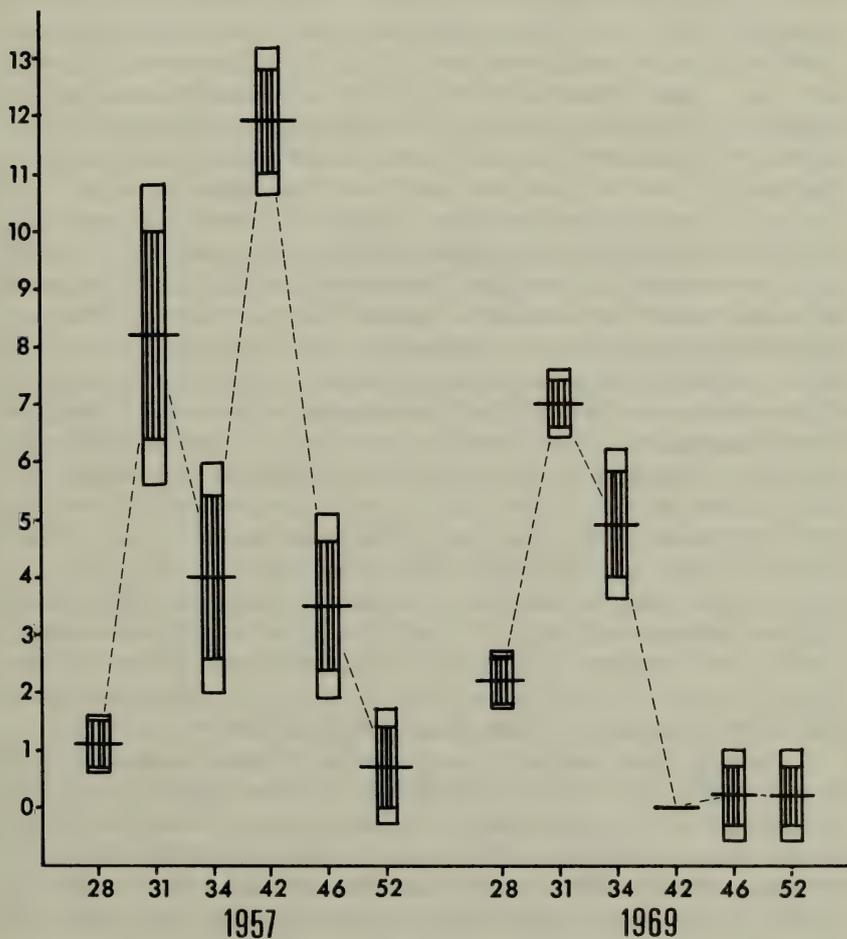


Fig. 1. Visual comparison of lizard numbers in 1957 and 1969. The horizontal lines are the means. The blocks above and below these mean lines are confidence limits computed from Student's T tables. The darkened blocks illustrate the 95% confidence limits and the adjacent nondarkened blocks illustrate the 99% limits.

lower. Of course, my densities were recorded as index numbers rather than true population-density figures. These latter figures are primarily intended for use in comparison and the method devised for obtaining them, as originally contrived, was not expected to give a true population density. It is true, however, that my index numbers are based on a series of samples and the mean of these samples does seem fairly reliable as evidenced by a small variance. I suspect that these index numbers come closer to true population densities than those of Milstead (1965). Recently, Turner et al. (1969) have determined densities for *C. tigris* in southern Nevada. Spring densities from their areas ranged "from around 3 to 8 per acre between 1964 and 1967." Furthermore, McCoy (1965) recorded about 7 per acre in Colorado, and Tanner and Jorgensen (1963) reported a rough estimate of 12. In fact, Turner et al. (1969) state that, "spring densities of *C. tigris* of more than 20/acre would be remarkable. We emphasized that the exceedingly high density of *tigris* reported by Milstead (1965) at Black Gap in 1962 was associated with a dramatic 10-year change in the quality of the vegetation, and is not comparable to the earlier density of 18/acre registered at a time when the area was relatively impoverished. Year-to-year changes in density are to be expected, but we judge that more than 2-fold fluctuations of this nature would be unusual." I believe that the reason for the very high-density figure procured by Milstead (1965) was due to his actually drawing a sample from a larger area than he tried to sample, and most of his captures were actually from areas outside of his sample area. The fourfold increase in numbers lends weight to my proposition. In all, after operating or directing the operation of many quadrats under widely differing conditions, I do believe that my index numbers are as close to a true population density for the species considered as any others published to date and are more accurate than most.

For the purposes of this report, however, whether or not my index numbers are true estimates of lizard density is merely an academic question. We are most interested in changes that have occurred in the lizard population and those changes in the quadrat conditions that may have been responsible for these changes in lizard density.

In general, lizard numbers have decreased or remained the same on all but the Tornillo Flat 840 m (2800 ft) quadrat (Fig. 2). Significant changes occurred on three and include an increase at 840 m (2800 ft) and decreases at 1260 m (4200 ft) and 1395 m (4650 ft). The mean changes at 930 m (3100 ft), 1020 m (3400 ft), and 1575 m (5250 ft) are insignificant when considering total lizards (all species, adults and juveniles).

The species composition of lizards on all quadrats has changed significantly. In general, the composition change was due mostly to particular species decreasing in numbers or disappearing completely from

quadrats previously supporting populations. *Holbrookia texana* is the principal species involved here, and it was recorded in lower numbers on the four quadrats at the lowest elevations and was not seen at all at 1395 m (4650 ft). In 1958, *Holbrookia* often equalled or exceeded *C. tigris* on these quadrats.

As indicated earlier, the vegetation has changed markedly in most parts of the park in the last 10 years. Furthermore, these changes are most pronounced in or near the mountains, and my Green Gulch quadrats are good examples of this vegetation change. Elsewhere (Degenhardt 1966), I have contended that vegetation density seemingly affects lizard numbers. However, I was comparing vegetation densities at different elevations and other factors probably affecting lizard numbers also were present. It was not possible at that time to separate out the various confounded factors involved in lizard densities.

The new data reported here show that the vegetation has changed markedly on the quadrats, and elevation is no longer a prime variable. My earlier indications of lizard densities being affected by vegetation are still present and my original hypothesis is strengthened.

It is true, however, that time is now a variable where it was not present before. It is conceivable and probable that the passing of time has elicited other changes affecting lizard numbers. Predation may now be a more important factor than it was in 1957 and 1958, for at least one important lizard predator, the roadrunner, has undergone an unmeasured, but obvious, increase over the last decade. Lizards may not be preferred morsels in the very varied diet of the roadrunner, for studies show a preference for insects over lizards. However, these same studies will also show an extremely high lizard predation rate during the time when roadrunner pairs are rearing young. Since recent workers in Big Bend believe that a number of broods may be reared during the same year, appreciable numbers of lizards may be utilized during broodrearing alone. Besides, if insects are prime roadrunner food items, this competition with lizards for food may be another factor affecting lizard numbers.

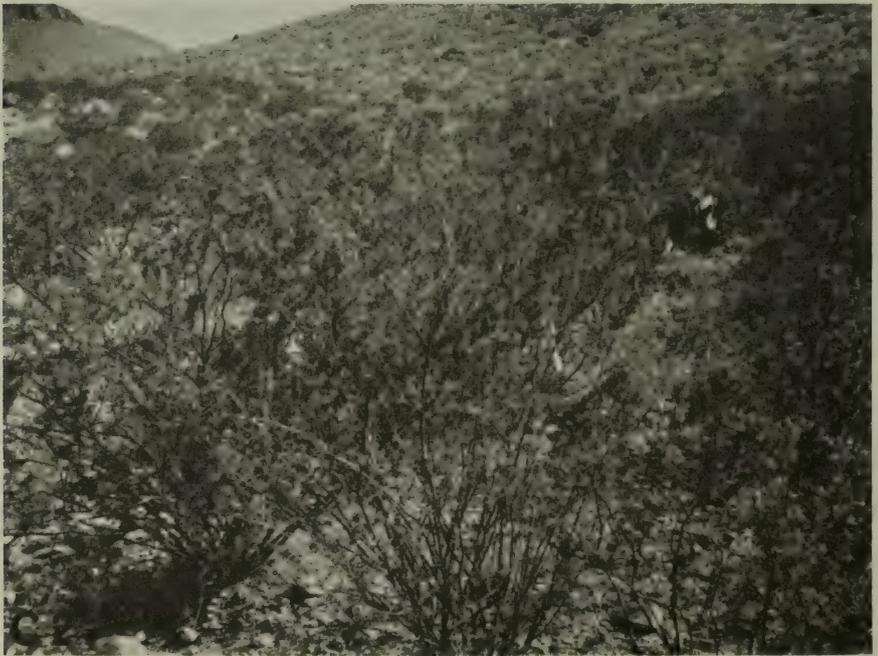
Still another vegetation-lizard-roadrunner interaction is very possible. The increase in vegetation has certainly resulted in an increase in insects. This fact of insect increase with vegetation might logically result in a lizard increase were it not for the roadrunner. Since insects are a prime food item, lizards may be considered a buffer species in the roadrunner diet. The increase in insects then would result in an increase in roadrunners which, in turn, would utilize lizards during times of heavy need (brood-rearing) or decrease in the insect population.

A literal and shallow interpretation of the 1957 data might lead us to believe that, since at 1260 m (4200 ft) lizard densities were greatest (Fig. 3), this would be near the point of optimum vegetation density.





Fig. 2. Photographs taken from the lower right corner of the quadrats with camera aimed at the center. A1: 2800 ft., 23 August 1957. A2: 24 August 1968. B1: 3100 ft., 28 August 1958. B2: 24 August 1968. C1: 3400 ft., 25 August 1957. C2: 24 August 1968. →



The vegetation density was 36% on the quadrat supporting the fewest lizards (1575 m [5250 ft]) (Table 5); 23% should be near the optimum vegetation density for lizards. The 1969 data do not contradict this interpretation because all quadrats do show a vegetation increase and all of these increases, except at 840 m (2800 ft), are above this supposed optimum of 23% (Table 7). Furthermore, the vegetation increase at 840 m (2800 ft) should have resulted in an increase in lizard numbers, which it did (Fig. 2). All other quadrats should have shown a decrease in lizard numbers, which they did not; however, two did show a significant (at 95% confidence level) change in lizard numbers.

Like justice, statistics are also often blind, and I should certainly not care to interpret the above data too literally since there are too many confounding factors involved. I do believe, though, that the indication is clear that vegetation density does indeed affect numbers of lizards, at least, with those with which we were working. I believe that for a given location, if all contributing factors could be removed or accounted for, it would be possible to define the vegetation minimum, optimum, and maximum for a lizard species. It is apparent that we must consider the fact that species of *Cnemidophorus* are long-lived, and lags due to this and other factors would be expected. The direct reading of the standing crop of vegetation and lizards for a single year would not be sufficient for analysis.

It is interesting to explore the supposition that the preservation policies of the park, concerning grazing in particular, may be resulting in the decrease of certain of the native species. Lizard numbers were certainly higher when the park was in a more impoverished condition. It is doubtful though that areas such as Tornillo Flat will ever support the amount of vegetation found at higher elevations, so the result should be one of redistribution of species rather than extermination of them. Tornillo Flat is indeed showing an increase in lizards with an increase in vegetation. Green Gulch may continue along the trend of decreasing diurnal ground lizards but there is already some indication of other species (*Sceloporus*) appearing where they were previously not seen, and a possibility of more montane forms (*Eumeces*, *Gerrhonotus*) migrating down. Studies involving the substitution of one lizard species for another as the environment changes would prove most productive.

Actually, this recent work has already given us data concerning species substitution on the quadrats. *Holbrookia texama* has shown a definite decrease in numbers compared to the species of *Cnemidophorus* and seems to be more responsive to vegetation change than the latter. This is not unexpected as it does seem that visibility is an important item in *Holbrookia* behavior. The increase in plants, and resulting reduction in visibility, might explain the decrease of these lizards. This dependence on visibility is seen in other behavioral characteristics of the spe-

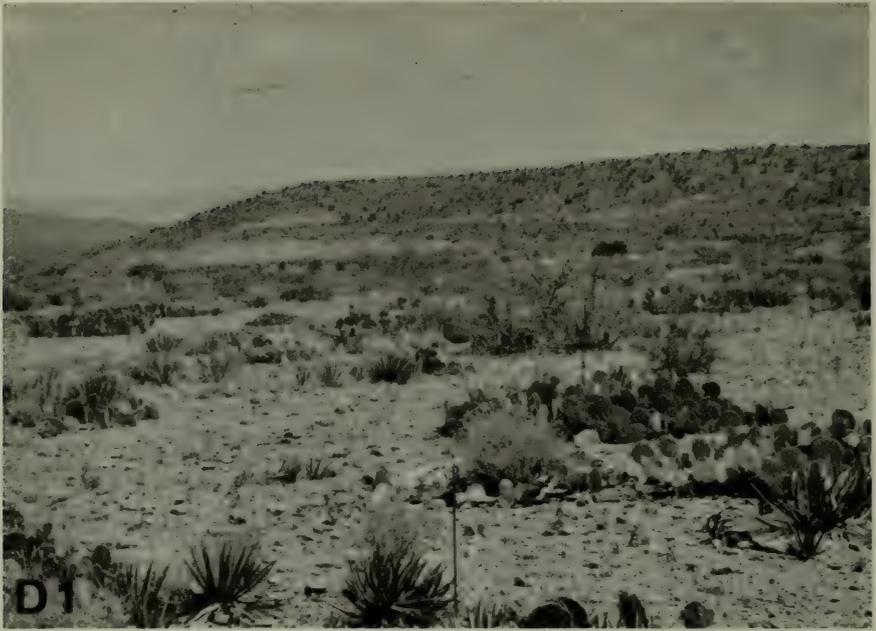
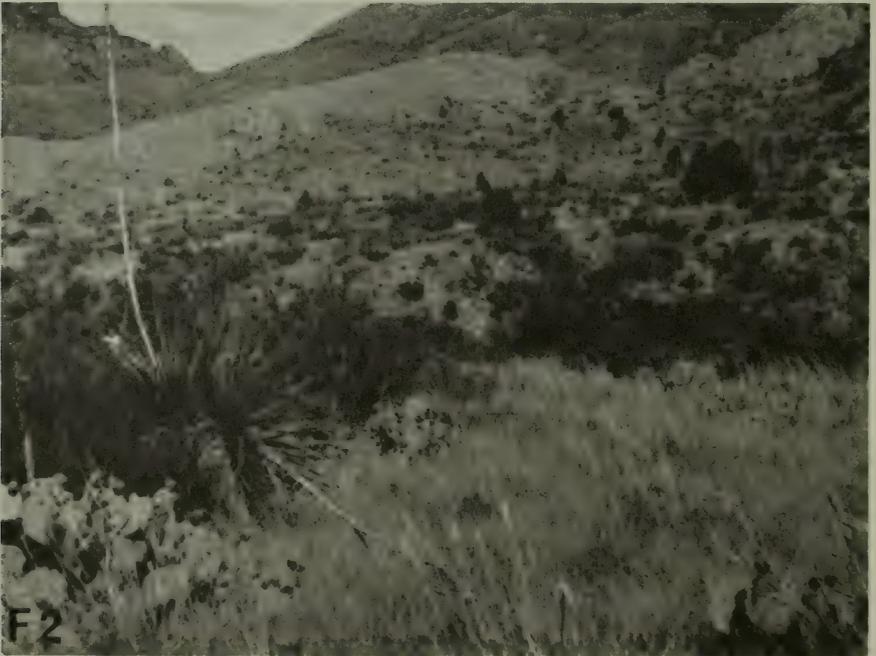


Fig. 3. Photographs taken from the lower right corner of the quadrats with camera aimed at the center. D1: 4200 ft, 26 August 1957. D2: 21 August 1968. E1: 4650 ft, 29 August 1957. E2: 22 August 1968. F1: 5250 ft, 29 August 1957. F2: 22 August 1968. →





cies: the tendency to climb onto high perches; and the habit of running from an intruder for some distance, then stopping and watching this intruder for threatening actions.

Another substitution that is indicated but not as obvious as the decrease in *Holbrookia* is the replacement of *C. tigris* by *C. scalaris*. This was expected due to an indication of this same phenomenon in 1958 (Degenhardt 1966) when wet and cool conditions seemed to cause the temporary disappearance of *C. tigris* on the 1260 m (4200 ft) quadrat. During this time *C. scalaris*, a species normally occupying the arroyo at the eastern border of the quadrat, was found foraging on the quadrat. Even though apparently not active, some form of competition is evident between *C. tigris* and *C. scalaris*, *C. tigris* being the stronger competitor in choice habitats. I predict that where conditions are suitable for the activity of both species *C. tigris* will be found occupying the habitat.

There are recorded changes in the quadrat vegetation other than the density increase I have been discussing. Those changes such as the increase in species diversity, coupled with changes in density of individual plant species, are probably all related. Even though it is doubtful that the lizards recognize plant species and are therefore not affected by these changes per se, nevertheless, these changes may be indicators of conditions that do affect the lizard population. Besides, many of these changes, such as the noted decrease of lechuguilla, are of interest in any consideration of the general ecology of the park.

As is often the case with most studies utilizing natural populations, more questions are posed or left unanswered than those answered. This is certainly true here and I have indicated a number of instances where more research should prove challenging and productive. I shall outline a few more areas where I believe research is needed.

More quadrats are sorely needed, especially at elevations below 1260 m (4200 ft). An attempt should be made to locate areas where there are conditions comparable to those found on the quadrats when first operated. I believe that this could be done by running transects at elevations just below 1200 m (4000 ft).

Quadrats would be useful where lizard species are different. *C. inornatus* was rare on the original quadrats but is almost a codominant with *C. tigris* at some locations. It is seemingly a codominant with *C. scalaris* in another vicinity. A population of *Phrynosoma cornutum* appears to be present at another location, and *Uta stansburiana* is sometimes locally abundant but rare on our existing quadrats.

Certain areas seemingly support a single species of diurnal ground lizard. A quadrat here would rule out interaction with other species. Other areas where multiple species are present should also be searched out for quadrat locations. Here, the comparison potential in determining this site is important.

Since vegetation does seemingly affect lizard numbers, more stress should be put on its analysis when lizard populations are studied. Inclusion of a finer and more comprehensive vegetation survey is recommended. Densities of each plant species should be determined for deeper insight. I have been grouping grasses and forbs as one plant form, but these may actually have a different effect on lizards since grasses may be largely perennial and forbs are largely annual. The resulting difference in seasonal aspect is probably of some importance to the lizard population. I have likewise been grouping all shrub-form plants for the reason that they offer more shade and less obstruction to movement. Besides the difference in aspect in some cases (e.g., *Xanthocephalum sarothrae*), shrubs do differ in form and may have a differential effect on lizards. It may also be realistic to do some plant analyses in the area bordering the quadrat because many individuals recorded on the quadrat do have a portion of their range lying outside or are affected in some way by the surrounding vegetation. I believe that this circumstance accounts for the very high densities recorded for *Cnemidophorus sexlineatus* (Fitch 1958; Carpenter 1959; Bellis 1964).

I have mentioned density estimates by others that are available in the literature. These estimates vary and those reporting them have used different methods for their procurement. A comparison of these methods within a single area, using lizards from the same population, would be extremely valuable in evaluating the validity of the reported densities. This type of comparison would require the use of a group effort in a number of consecutive years. The lag in population size, due to some species living as long as 6 years or more, must be taken into consideration for any understanding of population dynamics and the effects of the environment on population size. To date, few investigators have studied their populations in sufficient detail. Such studies as Turner et al. (1969) and Tinkle (1967) are notable exceptions and more studies of this nature are worthwhile. The workers named, although they did compare their results with the results of others, did not compare the methods used in obtaining these results. I am reluctant to consider the results comparable when the methods used were so very different.

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Session VI
Avifauna



The Avifauna of the Southern Part of the Chihuahuan Desert

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The southern half of the Chihuahuan Desert — south of latitude 27° — includes major parts of Coahuila, Durango, Zacatecas, and San Luis Potosí. But publication of work on the birds of the area has been meager, save for routine mention in standard reference works such as the Mexican Check List (Friedman et al. 1950; Miller et al. 1957). Desert birds of southern Coahuila were reported on by Burleigh and Lowery (1942) and Amadon and Phillips (1947); of eastern Durango, by Amadon and Phillips (1947), Webster and Orr (1952), Davis and Fowler (1959), and Fleming and Baker (1963). Webster (1964 a, b; 1968) made a winter bird-population study and a breeding-bird census in eastern Zacatecas and reported on some specimens collected there.

My own field work in the designated area totaled 28 days, plus 24 days of casual observations when driving along various highways, and spread over the years 1950 to 1968. As a definition and map of the desert, I have used, with satisfaction, the map presented by Leopold (1950, with modernization in 1959). For the grasslands, Leopold's maps and the descriptions and map by Gentry (1946) have been relied upon.

Table 1 summarizes the results of the two breeding-bird censuses in the southern desert. The census by Davis and Fowler (1959) was of 20 ha (50 acres) of desert shrub southwest of Lerdo, Durango; mine (1964b) was of 12 ha (30 acres) of desert shrub south of Concepción del Oro, Zacatecas. All densities are in males per 40 ha (100 acres). The fourth column lists the means of the two areas censused by Dixon (1959) and the one by Raitt and Maze (1968) in the shrub desert of Texas and southern New Mexico. A “+” indicates a density less than 0.5 per 40 ha (100 acres); “V” indicates that the species was a visitor, breeding nearby. Additional species censused in Texas or New Mexico, but not present in the deserts of Durango or Zacatecas (or even seen or heard there) in the rainy season, were Elf Owl (*Micrathene whitneyi*) and White-throated Swift (*Aeronautes saxatalis*). Presumably, geographic factors restrict them to the northern part of the

TABLE 1. Breeding bird censuses on the Chihuahuan Desert. Densities in males per 40 ha (100 acres). Explanation in text.

| Species | Webster, Zacatecas | Davis, Durango | Dixon, Texas and Raitt, New Mexico |
|---|-----------------------|-------------------|---------------------------------------|
| Turkey Vulture, <i>Cathartes aura</i> | + | + | V or 0 |
| Red-tailed Hawk, <i>Buteo jamaicensis</i> | + | | V or 0 |
| Swainson Hawk, <i>Buteo swainsonii</i> | | + | V or 0 |
| Scaled Quail, <i>Calipepla squamata</i> | 3 | 1 | + |
| Mourning Dove, <i>Zenaida macroura</i> | + | 1 | 2.5 |
| White-winged Dove, <i>Melopelia asiatica</i> | | + | V |
| California Roadrunner, <i>Geococcyx californianus</i> | | + | + |
| Great Horned Owl, <i>Bubo virginianus</i> | | + | V or 0 |
| Lesser Nighthawk, <i>Chordeiles acutipennis</i> | | + | 2 |
| Common Nighthawk, <i>Chordeiles minor</i> | + | | |
| Poor-will, <i>Phalaenoptilus nuttallii</i> | 6 | 1 | + |
| Black-chinned Hummingbird, ^a <i>Archilochus alexandri</i> | | + | V |
| Lucifer Hummingbird, <i>Calothorax lucifer</i> | 2 | | |
| Ladder-backed Woodpecker, <i>Dendrocopos scalaris</i> | 2 | + | + |
| Red-shafted Flicker, <i>Colaptes auratus</i> | 3 | 1 | |
| Cassin Kingbird, <i>Tyrannus vociferous</i> | 2 | | |
| Ash-throated Flycatcher, <i>Myiarchus cinerascens</i> | 3 | 1 | 0.5 |
| Common Raven, <i>Corvus corax</i> | V | + | V or 0 |
| Verdin, <i>Auriparus flaviceps</i> | 2 | | 1.5 |
| Bewick Wren, <i>Thryomanes bewickii</i> | 10 | | V |
| Cactus Wren, <i>Campylorhynchus brunneicapillus</i> | 20 | 3 | 1 |
| Mockingbird, <i>Mimus polyglottos</i> | V | + | 1 |
| Curve-billed Thrasher, <i>Toxostoma curvirostra</i> | 3 | 2 | V |

TABLE 1. (Continued)

| Species | Webster Zacatecas | Davis, Durango | Dixon, Texas and Raitt, New Mexico |
|--|----------------------|-------------------|---------------------------------------|
| Crissal Thrasher, <i>Toxostoma dorsale</i> | 4 | | + |
| Black-tailed Gnatcatcher, <i>Polioptila melanura</i> | 16 | 2 | 2 |
| Loggerhead Shrike, <i>Lanius ludovicianus</i> | 2 | 1 | + |
| Scott Oriole, <i>Icterus parisorum</i> | 3 | + | 0.5 |
| Brown-headed Cowbird, <i>Molothrus ater</i> | 1 | + | + |
| Pyrrhuloxia, <i>Pyrrhuloxia sinuata</i> | | 1 | 2 |
| Blue Grosbeak, <i>Guiraca caerulea</i> | | + | |
| House Finch, <i>Carpodacus mexicanus</i> | 6 | + | 2 |
| Brown Towhee, <i>Pipilo fuscus</i> | 4 | 3 | V |
| Black-throated Sparrow, <i>Amphispiza bilineata</i> | 23 | 4 | 6.5 |
| Total Density | 115 | 22 | 21 |
| Species Number | 23 | 25 | 11 |
| Species Diversity | 3.65 | 3.39 | 2.05 |

^aI regard the inclusion of the Black-chinned Hummingbird as a breeding species by Davis and Fowler as a mistake. The dates were July; I think the bird was a transient with a temporary feeding territory.

Chihuahuan Desert. A few other species such as the Gambel Quail (*Lophortyx gambelii*) probably fit in this category.

Missed in the southern censuses were several other species which I have seen regularly in the rainy season in the area. I believe that they belong in the breeding avifauna of shrub desert or desert flat.

Harris Hawk, *Parabuteo unicinctus*

Golden-fronted Woodpecker, *Centurus aurifrons*

Sparrow Hawk, *Falco sparverius*

Horned Lark, *Eremophila alpestris*

Inca Dove, *Scardafella inca*

White-necked Raven, *Corvus cryptoleucus*

Barn Owl, *Tyto alba*.

Additional species, which I have seen often, I take to be only migrants, or only inhabitants of irrigated land or riparian habitat. Five species, however, I have seen once each in what appeared to be breeding populations in shrub desert: Phainopepla (*Phainopepla nitens*), Wagler Oriole (*Icterus*

wagleri), Hooded Oriole (*Icterus cucullatus*), Cardinal (*Richmondia cardinalis*), and Varied Bunting (*Passerina versicolor*). Probably further work will show that these species belong in the list of southern desert shrub avifauna.

Dixon (1959) and Raitt and Maze (1968) devoted considerable effort to choosing which species to include in their lists of desert shrub birds. My list (Table 1 with above additions) is very similar to theirs, except for a few geographical differences as discussed above.

The list provided recently by Hubbard (1974:162-4) of, "what I consider to be essential avifaunal elements of the arid lands of North America," is different. Of course, it was provided in an evolutionary rather than ecological context, but its ecological implication is misleading. I find it faulty on three counts: (1) Grassland and desert forms are lumped. (2) Because only endemic *species* are listed and discussed, several of the most successful, and presumably best adapted, desert birds are omitted — these include Mourning Dove, Red-shafted Flicker, Bewick Wren, and House Finch; the last three of these have endemic desert races. (3) No less than 11 characteristic desert species, typical of desert shrub in the Sonoran or Chihuahuan deserts, or both, are omitted — Elf Owl, Poor-will, Lucifer Hummingbird, Golden-fronted Woodpecker, Gila Woodpecker (*Centurus uropygialis*), Cassin Kingbird, Ash-throated Flycatcher, Curve-billed Thrasher, Phainopepla, Scott Oriole, and Varied Bunting. All of these are almost endemic to the desert, extending into either the grassland or the arid tropical.

Clearly, number of species in the avifauna increases with decreasing latitude in the Chihuahuan Desert. This doubling southward in species number, with a 50% increase in species diversity, may be exaggerated by the scanty data. For instance, the mean of 2.05 for species diversities in the United States represents a range from 0.79 to 3.33, though species number for those three censuses ranged from only 7 to 14 (mean of 11). It may be that bird-species diversities and densities in the census plots are determined as much by plant heterogeneity, as suggested by Raitt and Maze (1968), as by latitude. Judging from photographs and my acquaintance with the two southern plots, the order of vegetational diversity is about the same as the order of avian species diversities and densities, viz.:

| | Species diversity | Density males/100 acres |
|------------------------------------|----------------------|----------------------------|
| Most heterogenous—Webster— | 3.64 | 115 |
| Dixon, Black Gap— | 3.33 | 40 |
| Davis and Fowler— | 3.39 | 22 |
| Dixon, Burnham Flat— | 0.79 | 11 |
| Least heterogenous—Raitt and Maze— | 2.03 | 13 |

Species diversities (\bar{H}_2) were calculated using the Shannon-Wiener formula ($H_2 = -\sum P_i \log_2 P_i$ where P_i = density of males of species i /total density of males). The distance involved from north to south, from Alpine, Texas, to Concepción del Oro, Zacatecas, is 640 km (400 miles) or 5° of latitude.

Following the example of earlier workers, I compared the avifauna of shrub desert in the southern Chihuahuan Desert with that found elsewhere: (a) with the northern fringe of the Chihuahuan Desert in New Mexico and Texas as censused and analyzed by Dixon (1959) and Raitt and Maze (1968), see above; (b) with the southeastern California desert as censused by Hutchinson (1941 and 1942) and Robert (1967) and described in faunal detail by Miller (1951); (c) with the Arizona desert as censused by Hensley (1954), Tainter (1965), and Radke and Jones (1969, 1970, 1971) and described by Phillips, Marshall, and Munson (1964). In brief, it appears that the California desert avifauna is an impoverished selection of the Sonoran Desert avifauna in Arizona, as Dixon pointed out. Similarly, the western Texas-southwestern New Mexico desert avifauna is an abridged version of the Chihuahuan Desert avifauna as found farther south. More detailed analysis of comparison (Arizona versus Zacatecas-Durango) may be summarized:

| Item | Southern Chihuahuan Desert | Arizona Sonoran Desert |
|---|----------------------------|------------------------|
| Average density of breeding bird censuses, males/100 acres. | 69 | 84 |
| Mean species number/breeding bird census. | 25 | 14 |
| Total species number, all breeding bird censuses. | 32 | 37 |
| Bird species diversity, mean (and range) from all breeding censuses. | 3.51 (3.39–3.64) | 3.79 (3.01–4.61) |
| Number of species on censuses in this area absent from the other. (Supplemental faunal information used for the other.) | 2 | 7 |
| Total species number, all information on breeding avifauna. | 39 (5 more?) | 53 |
| Number of species that breed in this area but not in the other; all information on avifauna. | 4 | 11 |

Evidently the Sonoran desert is richer in breeding bird species than the Chihuahuan, but not by nearly so wide a margin as earlier workers supposed.

Several ornithologists have suggested, at least jokingly as they hurried on to the tropics, that the desert extends far west of the boundary as mapped by Leopold and earlier ecologists. This is not a serious exaggeration, because most of the 39 species listed above are just as common west of the desert, in cactus-acacia grassland or cactus-acacia scrub where the rainfall is much greater. (Compare my 1957 paper on the birds of the Mexican grasslands.) For instance, Charles Harper and I in 1968 censused 12 ha (30 acres) of cactus-acacia grassland near Villa Madero, Durango, 96 km (60 miles) southwest of the desert (delimited as 30 cm [12 inches] or less of rainfall). The annual rainfall in this grass-dominated, shrub-dotted area is 50 cm (20 inches). But 17 of the 22 censused breeding-bird species are on the list of 39 southern desert birds above; these represented 56% of the density of the census. More broadly, 38 of the 39 southern desert birds (only the *Pyrrhuloxia* is an exception) are common, or at least regular, in the grasslands to the west. Evidently, the adaptations of the bird species to the desert are primarily to *Opuntia* and *Acacia*, rather than to aridity or to type of ground cover (or lack thereof). The species of *Opuntia* and *Acacia* in the desert and the grassland are different, by the way.

Conversely, in my list of 61 regular breeding-bird species on the grasslands (Webster 1957, with a few subsequent additions), the 38 breed on the desert to the east. (Remember that the Durango-Zacatecas grasslands include pure short-grass prairies which are higher, wetter, and generally west of the cactus-acacia grassland.) Doubtless the other 23 species (including the Prairie Falcon (*Falco mexicanus*), White-tailed Hawk, (*Buteo albicaudatus*), two species of meadowlarks, and nine species of sparrows) are adapted to a ground cover of grass. Of these, at least four species are common breeding birds on irrigated croplands on the desert, as for instance around Torreón, Coahuila, but do not breed in shrub desert. These are Barn Swallow (*Hirundo rustica*), Cliff Swallow (*Petrochelidon pyrrhonota*), Western Meadowlark (*Sturnella neglecta*), and Lark Sparrow (*Chondestes grammacus*).

There has been little study of winter birds in the southern part of the desert. My one field trip in the dry season was in January-February 1964. Then I made a winter bird-population study on the same plot which served for a breeding-bird census area 6 months later. Total density was slightly less than half that of the breeding season; species number was only one less (22 instead of 23) but with a few changes, viz.: Present in winter in small numbers but absent in summer were Great Horned Owl, Elf Owl, Blue-gray Gnatcatcher (*Polioptila caerulea*), and Ruby-crowned Kinglet (*Regulus calendula*); present in summer (including visitors breeding near the plot) but not in winter were Common Nighthawk, Poor-will, Lucifer

Hummingbird, Cassin Kingbird, Ash-throated Flycatcher, Mockingbird, Scott Oriole, Brown-headed Cowbird, and House Finch. Apparently, the southern part of the Chihuahuan Desert is not an important wintering ground for species other than permanent residents.

At the level of subspecific differentiation, I have studied specimens of all 39 of the southern desert breeding birds. Eleven species have racial differentiation approximating the entire Chihuahuan Desert or a part of it; of these, seven have races whose ranges approximate the southern segment of the desert or that area plus the cactus-acacia grasslands directly west. These latter are: Poor-will, Ladder-backed Woodpecker, Bewick Wren, Cactus Wren, Crissal Thrasher, Black-tailed Gnatcatcher, Black-throated Sparrow. Of these, I regard four races as very distinct, or well-differentiated — Poor-will (*P. n. centralis*), Ladder-backed Woodpecker (*D. s. giraudi*), Cactus Wren (*C. b. guttatus*), Crissal Thrasher (*T. b. dumosum*) — the other three as quite distinguishable.

Conservation of most species of the desert avifauna is no problem. In fact, at least 16 species are increasing westward, with cactus-acacia shrub encroaching on overgrazed, eroded grasslands. There *is* a serious problem, I think, with some of the fragile grassland species, resulting from overgrazing, overplowing, and accelerated erosion. These species, such as Grasshopper Sparrow (*Ammodramus savannarum*), Cassin Sparrow (*Aimophila cassini*), Worthen Sparrow (*Spizella wortheni*), need major help. And a few desert species, such as Lucifer Hummingbird and Pyrrhuloxia, seem to need very natural vegetation. In the same category are the three desert woodpeckers, which require large yuccas and acacias, now becoming scarce from cutting, budding, plowing, overgrazing, and accelerated erosion. I wonder if anyone can predict the results, after 15 years, of fencing off a few hundred acres of desert from goats and destructive human activities?

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Distributional Relations of Breeding Avifauna of Four Southwestern Mountain Ranges

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The desert mountains of the southwestern United States and adjacent Mexico are similar to oceanic islands in certain respects, in that the more or less mesic and/or boreal environments found at higher elevations are surrounded and isolated by a sea of lowland desert. Alden H. Miller (1955), in his analysis of the avifauna of the Sierra del Carmens of northern Coahuila, was one of the first biologists to draw this analogy in a specific way. More recently, MacArthur and Wilson (1963, 1967) have generated a great deal of interest in island biogeography. Studies testing their ideas have been conducted on a variety of animals under a variety of conditions, including aquatic arthropods in caves (Culver 1970), montane mammals of the Great Basin of North America (Brown 1971), and Andean birds in isolated paramo habitats (Vuillenmier 1970).

Diamond (1973), extending and testing the theories of MacArthur and Wilson, characterizes the "fundamental law" of island biogeography as follows: (1) species diversity increases with island area; (2) species diversity decreases with distance from the colonization source; and (3) species diversity increases with increasing altitudinal relief. These patterns are thought to be maintained by recurrent colonization and extinction of species on a given island. For example, on a small island extinction should be more frequent than on a large one, in part because populations of the species present are smaller. Brown (1971) found that montane mammals did not follow the predicted pattern. Rather, he concluded that, in the animals he studied, recurring colonization is virtually nonexistent and differences in numbers of species are related to the area of the island and to differential extinction.

We have looked at the breeding avifaunas of four southwestern mountain ranges with these "laws" in mind and have attempted to offer explanations for variations from the predicted pattern.

In addition, we consider the ecological effects that similar species exert on each other, i.e., effects of competition and the phenomenon of ecological release as illustrated by Miller (1955) in his study of the birds of the Sierra del Carmens.

THE MONTANE ISLANDS

The breeding avifaunas (above 1676 m [5500 ft] elevation) of three mountain ranges in western Texas—the Guadalupe, Davis, and Chisos—and one in northern Coahuila, Mexico—the Sierra del Carmens—are considered here (Fig. 1). These four ranges lie within coordinates $28^{\circ}45'$ and $32^{\circ}15'$ by $102^{\circ}30'$ and $104^{\circ}55'$. Each range is characterized briefly.

The Guadalupe Mountains, the northernmost area under consideration, are formed by a long north-south range of Permian limestone (King 1948) in southeastern New Mexico and adjacent Texas. The northern Guadalupe are lower in elevation and drier than the southern half of the range which forms a magnificent escarpment at its southern end. From north to south, the range ascends gradually to 2667 m (8749 ft) at the summit of Guadalupe Peak. The eastern slope is heavily dissected by many canyons, while the western escarpment is very steep with open alluvial fans. Approximately 168 km² (65 miles²) lie above 1676 m (5500 ft) elevation.

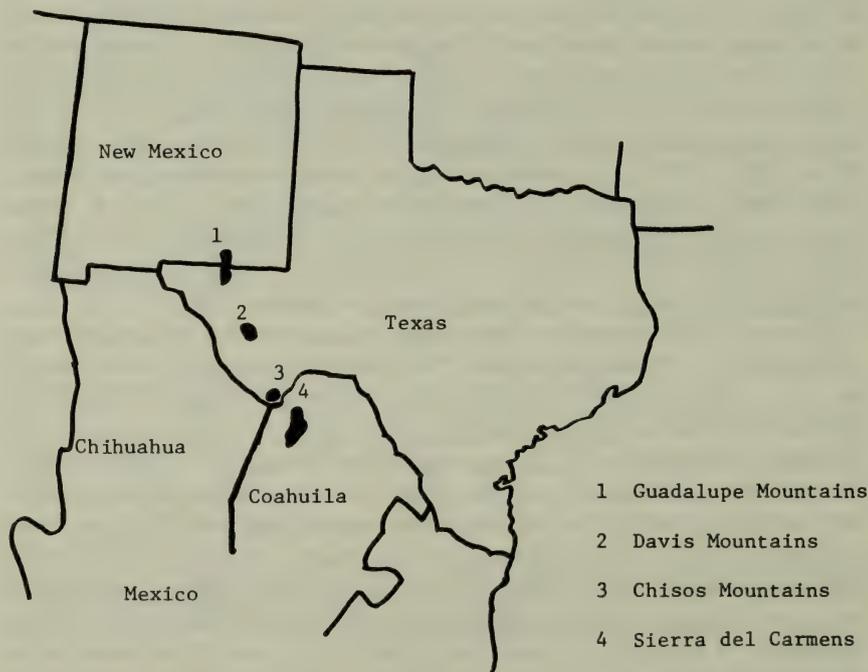


Fig. 1. Map showing the breeding avifaunas of three mountain ranges in western Texas. (1) Guadalupe Mountains, (2) Davis Mountains, and (3) Chisos Mountains—and one in northern Coahuila, Mexico, (4) Sierra del Carmens.

Vernon Bailey (1905) was first to analyze the Guadalupe vegetative zones. Burleigh and Lowery (1940) summarized earlier work and discussed faunal areas, including an annotated list of the known avifauna. Gehlbach (1963, 1965, 1967) and Potter and Robinson (1968) reported on the Guadalupe vegetation, and Newman (1971, 1974) summarized the avifauna in the highlands.

The Davis mountains lie only 160 km (100 miles) southeast of the Guadalupe. They are of igneous origin, and form rolling hills and open, grassy valleys at mid-elevations, and rocky canyons and jagged peaks in the highlands. The highest peak is Mount Livermore (2546 m [8352 ft]), and Pine Peak and Mount Locke are over 2073 m (6800 ft) in elevation. Approximately 182 km² (70 miles²) lie above 1676 m (5500 ft) elevation.

Hinckley (1944) described the vegetation of the Mount Livermore area and summarized earlier botanical studies. The area's avifauna has been partially studied. Smith (1917) reported on a few species, and Popper (1951) discussed sightings on Mount Locke. More recently, a county checklist was prepared by Espy and Miller (1972).

The Chisos Mountains which form the core of Big Bend National Park lie about 160 km (100 miles) southeast of the Davis Mountains, and are the southernmost mountains within the United States. The Chisos are an igneous mass of intrusive and extrusive rocks that rise out of the desert lowlands to 2388 m (7835 ft) elevation at the summit of Emory Peak. The Chisos peaks, canyons, foothills, and alluvial fans are more rugged than the Davis Mountains, but less than 16 km² (10 miles²) lie above 1676 m (5500 ft) elevation.

McDougall and Sperry (1951) discussed the plants and vegetative zones in the Chisos, and Wauer (1971, 1973) analyzed the avifauna and related vegetative zones.

Sixty-four kilometers (40 miles) southeast of the Chisos Mountains, the Sierra del Carmens form an impressive mountain system containing several peaks of over 2438 m (8000 ft) elevation. The northern half of the del Carmens consists of tilted limestone layers below. The Maderas del Carmen section lies in the southern half of the range from Pico Centinela (2626 m [8615 ft]) south and including a southwestern mountain regarded by Smith (1970) as Sierra de la Encantada. The Maderas del Carmen is of igneous origin. The western escarpment is steeply faulted and forms magnificent cliffs and deep canyons. The highest of these peaks is Loomis Peak (2731 [8960 ft]). The eastern slope is gradual and contains numerous rather gentle but dissected canyons. Approximately 299 km² (115 miles²) lie above 1676 m (5500 ft) elevation.

This section of Mexico has been neglected by researchers. The vegetation and climate of Coahuila was discussed by Muller (1947), and Miller (1955) reported on the avifauna and plant zones of the Sierra del Carmens.

THE VEGETATION

All four mountain ranges contain similar vegetative zones. Grasslands form a distinct belt around the mountains, starting at about 1067 m (3500 ft) and blend-

ing into the pinyon-juniper-oak woodlands that occur on the ranges between approximately 1372 and 2438 m (4500 and 8000 ft). Forest-type vegetation occurs only on the highest peaks, in cool canyons and highland depressions, and on upper north slopes.

Table 1 includes characteristic, dominant trees and shrubs of the four mountain ranges.

Several of the dominant trees and shrubs are common to all four mountains: ponderosa pine, alligator and one-seeded junipers, banana yucca, palmella, sotol, lechuguilla, chinkapin, Gambel's and gray oaks, netleaf hackberry, apacheplume, mountain mahogany, catclaw, cat's-claw mimosa, evergreen and fragrant sumacs, bigtooth maple, Texas madrone, and goldeneye.

The Guadalupe Mountains appear to contain the southernmost population of Rocky Mountain juniper and New Mexico agave that suggest affinity to the Navahonian Province of Blair (1950). Sotol, lechuguilla, evergreen sumac, and Texas madrone reach the northern edge of their range within the Guadalupe.

The Davis Mountains contain no unique dominants, but are the southern extension of sacahuista and Parry agave. Five species reach the northern end of their range there: Mexican pinyon, Emory, whiteleaf and Chisos red oaks, Mexican manzanita, and scarlet bouvardia.

The Chisos Mountains contain no unique dominants, and do not serve as the site for the southern limits of any dominant trees or shrubs. Arizona cypress, drooping juniper, beaked yucca, bear-grass, Havard agave, dwarf oak, Gregg ash, and mountain sage are of Mexican affinity and reach the northern edge of their range in the Chisos.

The Maderas del Carmens contain two dominant species, Coahuila fir and an agave, that are not known to occur within the northern three mountain ranges. Southwestern white pine is common in the Carmens and Guadalupe but does not occur in the Davis and Chisos mountains. This may be related to the higher elevations and greater mountain masses of the two former ranges. This might also explain the relative density of chinkapin oak, which is common in the Guadalupe and Carmens but sparse in the Davis and Chisos mountains. However, whiteleaf oak and Mexican manzanita occur only within the Carmen and Davis mountains although they are sparse in the latter area. There is no known case where a dominant species occurs only in the Guadalupe and Chisos mountains.

THE AVIFAUNA

The breeding avifauna of the four mountain ranges generally conform to vegetative zones and are closely related to the divergent habitats within the various units. Table 2 includes the 99 species known to breed within the four areas; 49 have been reported to breed in all four units.

Twelve bird species breed in the Guadalupe Mountains and are not known to nest within the other three areas. Nine of these utilize the forested areas in the highlands and upper canyons: Hairy Woodpecker, Olive-sided Flycatcher,

TABLE 1. Characteristic trees and shrubs.

| | Guad. | Davis | Chisos | Carmen |
|---|-------|-------|--------|--------|
| Ponderosa Pine (<i>Pinus ponderosa</i>) | X | X | X | X |
| Pinyon (<i>P. edulis</i>) | X | | | |
| Mexican Pinyon (<i>P. cembroides</i>) | | X | X | X |
| Sw. White Pine (<i>P. strobiformis</i>) | X | X | | X |
| Coahuila Fir (<i>Abies durangensis</i>) | | | | X |
| Douglas Fir (<i>Pseudotsuga menziesii</i>) | X | | X | X |
| Arizona Cypress (<i>Cupressus arizonica</i>) | | | X | X |
| Alligator Juniper (<i>Juniperus deppeana</i>) | X | X | X | X |
| One-seeded Juniper (<i>J. monosperma</i>) | X | X | X | X |
| Drooping Juniper (<i>J. flaccida</i>) | | | X | X |
| Banana Yucca (<i>Yucca baccata</i>) | X | X | s | X |
| Beaked Yucca (<i>Y. rostrata</i>) | | | s | X |
| Palmella (<i>Y. elata</i>) | X | X | s | X |
| Bear-Grass (<i>Nolina erumpens</i>) | | | X | X |
| Sacahuista (<i>N. micrantha</i>) | X | X | | |
| Sotol (<i>Dasylirion</i>) | X | X | X | X |
| Lechuguilla (<i>Agave lecheguilla</i>) | X | X | X | X |
| Havard Agave (<i>A. havardiana</i>) | | | X | X |
| Parry Agave (<i>A. parryi</i>) | X | X | | |
| New Mexico Agave (<i>Agave neomexicana</i>) | X | | | |
| (Coahuila) Agave (<i>A. sp.</i>) | | | | X |
| Hop-Hornbeam (<i>Ostrya</i>) | X | X | X | X |
| Chinakapin Oak (<i>Quercus muehlenbergii</i>) | X | s | s | X |
| Gambel Oak (<i>Q. gambelii</i>) | X | X | s | X |
| Gray Oak (<i>Q. grisea</i>) | X | X | X | X |
| Arizona White Oak (<i>Q. arizonica</i>) | s | | s | X |
| Dwarf Oak (<i>Q. intricata</i>) | | | X | X |
| Netleaf Oak (<i>Q. rugosa</i>) | | s | s | X |
| Emory Oak (<i>Q. emoryi</i>) | | X | X | X |
| Whiteleaf Oak (<i>Q. hypoleucioides</i>) | | X | | X |
| Chisos Red Oak (<i>Q. gravesii</i>) | | X | X | X |
| Netleaf Hackberry (<i>Celtis reticulata</i>) | X | X | X | X |
| Apacheplume (<i>Fallugia paradoxa</i>) | X | X | X | X |
| Mt. Mahogany (<i>Cercocarpus montanus</i>) | X | X | X | X |
| Catclaw (<i>Acacia greggii</i>) | X | X | X | X |
| Whitethorn Acacia (<i>A. constricta</i>) | X | X | X | X |
| Cat's-Claw Mimosa (<i>Mimosa biuncifera</i>) | X | X | X | X |
| Evergreen Sumac (<i>Rhus virens</i>) | X | X | X | X |
| Fragrant Sumac (<i>R. aromatica</i>) | X | X | X | X |
| Bigtooth Maple (<i>Acer grandidentatum</i>) | X | X | X | X |
| Texas Madrone (<i>Arbutus xalapensis</i>) | X | X | X | X |
| Mexican Manzanita (<i>Arctostaphylos pungens</i>) | | s | | X |
| Gregg Ash (<i>Fraxinus greggii</i>) | | | X | X |
| Mountain Sage (<i>Salvia reglia</i>) | | | X | X |
| Scarlet Bouvardia (<i>Bouvardia ternifolia</i>) | | s | X | X |
| Goldeneye (<i>Virguiera stenoloba</i>) | X | X | X | X |

X=present s=sparce

Nomenclature according to Correll and Johnston (1970), *Manual of the Vascular Plants of Texas*. Texas Research Foundation, Renner, Texas.

TABLE 2. Breeding avifauna.

| | Guad. | Davis | Chisos | Carmen |
|---|-------|-------|--------|--------|
| Turkey Vulture (<i>Cathartes aura</i>) | X | X | X | X |
| Goshawk (<i>Accipiter gentilis</i>) | | | | X |
| Sharp-shinned Hawk (<i>A. striatus</i>) | X | | X | X |
| Cooper's Hawk (<i>A. cooperii</i>) | X | X | | X |
| Red-tailed Hawk (<i>Buteo jamaicensis</i>) | X | X | X | X |
| Zone-tailed Hawk (<i>B. albonotatus</i>) | p | X | X | X |
| Golden Eagle (<i>Aquila chrysaetos</i>) | X | X | X | X |
| Prairie Falcon (<i>Falco mexicanus</i>) | X | X | X | |
| Peregrine Falcon (<i>F. peregrinus</i>) | X | X | X | X |
| Kestrel (<i>F. sparverius</i>) | X | X | X | X |
| Montezuma Quail (<i>Cyrtonyx montezumae</i>) | X | X | X | X |
| Turkey (<i>Meleagris gallopavo</i>) | X | X | | X |
| Band-tailed Pigeon (<i>Columba fasciata</i>) | X | X | X | X |
| White-winged Dove (<i>Zenaida asiatica</i>) | | | X | X |
| Mourning Dove (<i>Zenaida macroura</i>) | X | X | X | X |
| Yellow-billed Cuckoo (<i>Coccyzus americanus</i>) | X | X | X | X |
| Screech Owl (<i>Otus asio</i>) | X | X | X | X |
| Flammulated Owl (<i>O. flammeolus</i>) | X | X | X | X |
| Great Horned Owl (<i>Bubo virginianus</i>) | X | X | X | X |
| Pygmy Owl (<i>Glaucidium gnoma</i>) | | | | X |
| Elf Owl (<i>Micrathene whitneyi</i>) | X | X | X | X |
| Spotted Owl (<i>Strix occidentalis</i>) | X | | | |
| Saw-whet Owl (<i>Aegolius acadicus</i>) | X | | | X |
| Whip-poor-will (<i>Caprimulgus vociferus</i>) | X | X | X | X |
| Poor-Will (<i>Phalaenoptilus nuttallii</i>) | X | X | X | X |
| Common Nighthawk (<i>Chordeiles minor</i>) | X | X | | X |
| White-throated Swift (<i>Aeronautes saxatalis</i>) | X | X | X | X |
| Lucifer Hummingbird (<i>Calothorax lucifer</i>) | | | X | X |
| Black-chin. Hummingbird (<i>Archilochus alexandri</i>) | X | X | X | X |
| Broad-tailed Hummingbird (<i>Selasphorus platycercus</i>) | X | X | X | X |
| Rivoli's Hummingbird (<i>Eugenes fulgens</i>) | X | p | X | X |
| Blue-throated Hummingbird (<i>Lampornis clemenciae</i>) | p | | X | X |
| Common Flicker (<i>Colaptes auratus</i>) | X | X | X | X |
| Acorn Woodpecker (<i>Melanerpes formicivorus</i>) | X | X | X | X |
| Hairy Woodpecker (<i>Dendrocopos villosus</i>) | X | | | p |
| Ladder-backed Woodpecker (<i>D. scalaris</i>) | X | X | X | X |
| Cassin's Kingbird (<i>Tyrannus vociferans</i>) | X | X | | |
| Ash-throated Flycatcher (<i>Myiarchus cinerascens</i>) | X | X | X | X |
| Say's Phoebe (<i>Sayornis saya</i>) | X | X | X | X |
| Western Flycatcher (<i>Empidonax difficilis</i>) | X | X | X | X |
| Western Wood Pewee (<i>Contopus sordidulus</i>) | X | X | | |
| Olive-sided Flycatcher (<i>Nuttallornis borealis</i>) | X | | | |
| Violet-green Swallow (<i>Tachycineta thalassina</i>) | X | X | X | X |
| Steller's Jay (<i>Cyanocitta stelleri</i>) | X | X | | |
| Scrub Jay (<i>Aphelocoma coerulescens</i>) | X | X | | |
| Mexican Jay (<i>A. ultramarina</i>) | | | X | X |
| Common Raven (<i>Corvus corax</i>) | X | X | X | X |
| Mountain Chickadee (<i>Parus gambeli</i>) | X | X | | |
| Black-crested Titmouse (<i>P. atricristatus</i>) | | X | X | X |
| Plain Titmouse (<i>P. inornatus</i>) | X | | | |
| Bushtit (<i>Psaltriparus minimus</i>) | X | X | X | X |

TABLE 2. (Continued)

| | Guad. | Davis | Chisos | Carmen |
|--|-------|-------|--------|--------|
| White-breasted Nuthatch (<i>Sitta carolinensis</i>) | X | X | X | X |
| Pygmy Nuthatch (<i>S. pygmaea</i>) | X | X | | X |
| Brown Creeper (<i>Certhia familiaris</i>) | X | | | |
| House Wren (<i>Troglodytes aedon</i>) | X | | | |
| Brown-throated Wren (<i>T. brunneicollis</i>) | | | | X |
| Bewick's Wren (<i>Thryomanes bewickii</i>) | X | X | X | X |
| Cactus Wren (<i>Campylorhynchus brunneicapillum</i>) | X | X | X | X |
| Canon Wren (<i>Catherpes mexicanus</i>) | X | X | X | X |
| Rock Wren (<i>Salpinctes obsoletus</i>) | X | X | X | X |
| Mockingbird (<i>Mimus polyglottos</i>) | X | X | X | X |
| Curve-billed Thrasher (<i>Toxostoma curvirostre</i>) | X | X | | X |
| Crissal Thrasher (<i>T. dorsale</i>) | | X | X | X |
| Robin (<i>Turdus migratorius</i>) | X | | | |
| Hermit Thrush (<i>Catharus guttata</i>) | X | X | | |
| Western Bluebird (<i>Sialia mexicana</i>) | X | X | | X |
| Blue-gray Gnatcatcher (<i>Poliopitila caerulea</i>) | X | X | X | X |
| Phainopepla (<i>Phainopepla nitens</i>) | | X | X | |
| Black-capped Vireo (<i>Vireo atricapilla</i>) | | | X | X |
| Hutton's Vireo (<i>V. huttoni</i>) | X | X | X | X |
| Gray Vireo (<i>V. vicinior</i>) | X | X | X | X |
| Solitary Vireo (<i>V. solitarius</i>) | X | X | X | X |
| Warbling Vireo (<i>V. gilvus</i>) | X | X | X | |
| Orange-crowned Warbler (<i>Vermivora celata</i>) | X | | | |
| Virginia's Warbler (<i>V. virginiae</i>) | X | | | |
| Colima Warbler (<i>V. crissalis</i>) | | | X | X |
| Olive Warbler (<i>Peucedramus taeniatus</i>) | | | | X |
| Yellow-rumped Warbler (<i>Dendroica coronata</i>) | X | | | |
| Grace's Warbler (<i>D. graciae</i>) | X | X | | |
| Painted Redstart (<i>Setophaga picta</i>) | | | X | X |
| Eastern Meadowlark (<i>Sturnella magna</i>) | | X | | |
| Scott's Oriole (<i>Icterus parisorum</i>) | X | X | X | X |
| Brewer's Blackbird (<i>Euphagus cyanocephalus</i>) | X | X | | |
| Brown-headed Cowbird (<i>Molothrus ater</i>) | X | X | X | X |
| Western Tanager (<i>Piranga ludoviciana</i>) | X | p | | |
| Hepatic Tanager (<i>P. flava</i>) | X | X | X | X |
| Summer Tanager (<i>P. rubra</i>) | X | X | X | X |
| Black-headed Grosbeak (<i>Pheucticus melanocephalus</i>) | X | X | X | X |
| Blue Grosbeak (<i>Guiraca caerulea</i>) | X | X | X | X |
| House Finch (<i>Carpodacus mexicanus</i>) | X | X | X | X |
| Pine Siskin (<i>Spinus pinus</i>) | X | X | | p |
| Lesser Goldfinch (<i>S. psaltria</i>) | X | X | X | X |
| Rufous-sided Towhee (<i>Pipilo erythrophthalmus</i>) | X | X | X | X |
| Brown Towhee (<i>P. fuscus</i>) | X | X | X | X |
| Rufous-crowned Sparrow (<i>Aimophila ruficeps</i>) | X | X | X | X |
| Gray-headed Junco (<i>Junco caniceps</i>) | X | | | |
| Yellow-eyed Junco (<i>J. phaeonotus</i>) | | | | X |
| Chipping Sparrow (<i>Spizella passerina</i>) | X | X | | |
| Black-chinned Sparrow (<i>S. atrogularis</i>) | X | X | X | X |
| Totals | 81 | 71 | 63 | 73 |

p-probably

Brown Creeper, House Wren, Robin, Orange-crowned and Yellow-rumped warblers, Western Tanager, and Gray-headed Junco. Virginia's Warbler prefers grassy slopes beneath stands of Gambel's oak. Spotted Owls have been recorded at rocky places in the higher canyons and the Plain Titmouse breeds within the pinyon-juniper woodlands.

The Davis Mountains have only two bird species not known to breed in the other mountains, Eastern Meadowlark and Brewer's Blackbird. Nine species appear to be restricted to the Guadalupe and Davis mountains: Cassin's Kingbird, Western Wood Pewee, Steller's and Scrub jays, Mountain Chickadee, Hermit Thrush, Grace's Warbler, Pine Siskin, and Chipping Sparrow. Two species, Black-crested Titmouse and Crissal Thrasher, reach the northern edge of their range in the Davis Mountains.

The Chisos Mountains have no species not known to breed in the other three mountain areas. Two species which breed in the Chisos and north are not known to nest in the Carmen Mountains: Prairie Falcon and Warbling Vireo. Four species reach the northeastern edge of their range in the Chisos: the Lucifer and Blue-throated hummingbirds, Mexican Jay, and Painted Redstart. The Black-capped Vireo does not nest in the Davis and Guadalupe mountains but its breeding range extends northeast to Oklahoma.

The Carmen Mountains possess five breeding birds not known to nest within the northern three mountains: Goshawk, Pygmy Owl, Brown-throated Wren, Olive Warbler, and Yellow-eyed Junco.

RESULTS AND DISCUSSION

Species Diversity and Island Size

Based on present knowledge of the breeding birds of the four ranges, it appears that there is, at best, a loose correlation between island size and number of species. The Guadalupes, third in size and second in maximum elevation, contain the greatest number of breeding species, 81, whereas the largest and highest Maderas del Carmen massif and the smaller Davis Mountains contain about 73 and 71, respectively. The Chisos, smallest and lowest of the four with 63 species, has about 15% fewer species recorded than the nearby Carmens, despite the intensive field work done in the Chisos Mountains (Wauer 1971, 1973).

The Chisos Mountains, however, possess the highest ratio of avian species, 6.300, in comparison with the ratios of 1.246 for the Guadalupes, 1.014 for the Davis, and 0.634 for the Carmens. Table 3 illustrates this ratio. We believe that this phenomenon is largely due to geographic location and diversity of habitats.

Species Diversity and Altitudinal Relief

Insofar as maximum elevation is related to habitat diversity (i.e., one high peak might provide less montane habitat than two or more mountains of slightly less altitude), it appears that again the predicted relationship is indicated, but does not entirely fit the pattern. The Carmens contain several peaks of over 2438 m (8000

TABLE 3. Species diversity index.

| Mountain Range | Approx. Sq Mi | No. of Breeding Bird Species | Ratio |
|----------------|------------------|------------------------------------|-------|
| Carmens | 115 | 73 | 0.634 |
| Davis | 70 | 71 | 1.014 |
| Guadalupes | 65 | 81 | 1.246 |
| Chisos | 10 | 63 | 6.300 |

ft) and have extensive stands of coniferous forest, as compared to the other three ranges. The Guadalupes, however, do harbor a large area of montane forest. In short, the Guadalupes, with fewer high peaks and associated vegetation than the Carmens, have a greater number of species. The Chisos, least in elevation, also hold the fewest breeding birds, while the Davis Mountains, third in elevation, are also third in species diversity.

Species Diversity and Distance from the Colonization Source

This component of the fundamental law of island biogeography is likely the most important of the three in explaining the avifaunal patterns of the islands here considered. "Colonization sources" are larger areas which might provide immigrants or potential colonizers to the desert mountains. In the present case, there are three such basic sources: from the north, the southern extensions of the Rocky Mountains in New Mexico; from the west, the Sierra Madre Occidental; and from the south and southeast, the Sierra Madre Oriental.

The richest avifauna, in the Guadalupes, is also closest to a source of colonization—the Sacramento Mountains a few miles to the northwest. Most or all of the species confined as breeders to the Guadalupes or to the Guadalupes and Davis mountains have breeding populations in the nearby Sacramento Mountains (Hubbard 1970). These are: Spotted Owl, Common Nighthawk, Hairy Woodpecker, Cassin's Kingbird, Western Wood Pewee, Steller's Jay, Scrub Jay, Plain Titmouse, Mountain Chickadee, Brown Creeper, House Wren, Robin, Hermit Thrush, Orange-crowned Warbler, Virginia's Warbler, Yellow-rumped Warbler, Grace's Warbler, Western Tanager, Gray-headed Junco, and Chipping Sparrow. All of these species are distributed widely throughout the western United States.

The Davis Mountains, located about 240 km (150 miles) north of the Sierra del Carmen, and 160 km (100 miles) southeast of the Guadalupes, support a fauna equivalent in numbers to that of the Carmens. Eleven species appear to be derived from the north, while the Davis Mountains are the northern edge of the range of one species, the Black-crested Titmouse.

The Chisos Mountains have several essentially Mexican species, all of which occur in the nearby Carmens (White-winged Dove, Lucifer Hummingbird,

Blue-throated Hummingbird, Mexican Jay, and Painted Redstart). The low number of breeding avifauna of the Chisos can be explained largely on the basis of limited habitat.

The Sierra del Carmen provides the strongest case for the effects of isolation, as Miller (1955) clearly described. Although this is a large massif, about 32 km (20 miles) in length, with extensive belts of pine-oak and coniferous habitats, the avifauna clearly is depauperate as compared, for example, to the Chiricahua Mountains of southeastern Arizona, which are roughly similar in size and diversity of habitats. The Chiricahuas contain many species of Mexican affinity that are absent from the Carmens. The fact that they are less than 160 km (100 miles) north of the Sierra Madre Occidental in Chihuahua probably explains this comparatively rich avifauna, which is in large part composed of species derived from that major mountain system. In contrast, the Carmens lie 320 km (200 miles) east of the Sierra Madre Occidental and likewise are 320 km (200 miles) northwest of the Sierra Madre Oriental.

The absence of such southern species as the Coppery-tailed Trogon, Whiskered Owl, Arizona Woodpecker, Bridled Titmouse, Grace's Warbler, and Red-faced Warbler, as well as breeding populations of the widespread Hairy Woodpecker, Steller's Jay, Scrub Jay, chickadees of any type, and Yellow-rumped Warbler, is striking. To a field ornithologist familiar with the mountains of the southwestern United States and adjacent Mexico, these absences are perhaps more interesting and anomalous than any other aspect of the avifaunal characteristics of the Maderas del Carmen.

This lack of certain species has allowed development of the phenomenon known as ecological extension or ecological release, in that a species may occupy habitats from which they normally are excluded by one or more other species. A second feature of this unbalanced avifauna is a great increase in numbers of individuals of certain of those species which have expanded their ecological "spheres" as a result of the absence of competitors.

Miller (1955) described four cases of ecologic expansion in the Carmens: (1) altitudinal spread of *Dendrocopos scalaris* in the absence of *D. arizonae*; (2) altitudinal spread of *Parus atricristatus* in the absence of *P. wollweberi*; (3) expansion in numbers of *Peucedramus taeniatus* and *Setophaga picta*; and (4) altitudinal spread and possibly increased numbers of *Aphelocoma ultramarina* in the absence of *A. coerulescens* and *Cyanocitta stelleri*.

We will confine our attention here to the jays. Mexican Jays occupy the lowest extensions of oaks, the top of Loomis Peak, and all intervening habitats. Additionally, due perhaps to their generalized mode of life, they are abundant. This altitudinal and ecological spread reflects an ecological potential elsewhere unrealized (e.g., Chiricahua Mountains) and sheds light on the effects that other similar species may have via competition. For example, in southwestern New Mexico and Arizona, Steller's Jays and Scrub Jays occupy habitats which in the Carmens are held by Mexican Jays.

Although Mexican Jays are the sole jay occupant of the Maderas del Carmen

during the breeding season, it is almost certain that both Scrub and Steller's jays reach these mountains in autumn of many years and overwinter there. (This is true for the nearby Chisos Mountains where only Mexican Jays are known to breed.) Thus isolation cannot be the only explanation for this exclusive occupancy by Mexican Jays. Several behavioral and ecological characteristics exhibited by these jays probably prevent colonization of the Carmens by Scrub or Steller's jays. Mexican Jays are actively aggressive toward the other species. Scrub Jays housed with Mexican Jays in a large aviary were actively supplanted and even pursued by the latter species; in contrast, intraspecific aggression between Mexican Jays was comparatively rare. Similarly, free-living Mexican Jays appear to respond aggressively toward Scrub Jays (Ligon unpubl. observ.).

In addition, Mexican Jays, unlike Scrub and Steller's jays, are communal (Brown 1974; Ligon and Husar 1974), thus any would-be "colonizer" Scrub or Steller's jay must contend with a large number of highly aggressive potential competitors which also are larger in size and which belong to well-organized social units. Mexican Jays thus apparently present an ecological-behavioral blockade too great to allow colonization by either of the other jay species.

In certain other instances of ecological replacement, isolation per se may be the overriding factor, e.g., absence of chickadees and the Bridled Titmouse, and the (presumably) resultant expansion of the niche of the Black-crested Titmouse.

CONCLUSIONS

The isolated mountain ranges of the southwestern United States and Mexico provide what has been referred to as a "natural laboratory," in that various combinations of plant and animal species occur in different areas and the effects of one, or several, species on others can be ascertained. These natural experiments provide some of the most compelling evidence supporting the concept of competition and the manners by which it contributes to the organization of ecological communities. For these reasons, as well as for esthetic ones, the montane habitats of this region deserve careful study and preservation.

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Temporal Changes in Northern Chihuahuan Desert Bird Communities

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The Jornada del Muerto plain occupies a long, roughly north-south basin east of the Rio Grande in New Mexico, near the northern edge of the Chihuahuan Desert. It contains vegetation variously classified as desert scrub, desert grassland, and shrub-steppe. In portions of the southern end of the Jornada, in Doña Ana County, north of Las Cruces (32° 30'N, 106° 45'W), considerable ecological study has been carried out, primarily by workers from New Mexico State University and the U.S. Department of Agriculture. Since 1970, especially intensive effort has been put forth as part of the Analysis of Ecosystems section of the International Biological Program. These studies have included censuses of birds, conducted throughout the year on a monthly basis on study plots in three major ecosystem types: a creosotebush (*Larrea divaricata*)-dominated bajada (Fig. 1); a small playa with tobosa (*Hilaria mutica*) and vine mesquite grass (*Panicum obtusum*) on its floor and tall mesquite (*Prosopis glandulosa*) and other shrubs around its fringe (Fig. 2); and an area of yucca (*Yucca elata*)-black grama (*Bouteloua eriopoda*) grassland (Fig. 3). Hereinafter these three study areas will be referred to as the Bajada, Playa, and Grassland areas. In addition to the plot censuses, we have conducted monthly roadside bird counts along a route confined to yucca-grassland vegetation. Detailed measurements have also been made in the same period on the same sites of various abiotic factors, vegetation, invertebrates, and other vertebrates. Altogether, the data collected afford a valuable resource for examining the interactions of various biotic and abiotic components of the ecosystems of the northern Chihuahuan Desert. Results of these various efforts are included in reports of both the Desert and Grassland Biome programs of the IBP and many of them are in some stage of preparation for publication in the open literature.

Our own studies on the birds are among the few regular, long-term, year-round studies of quantitative aspects of bird communities of grasslands and desert scrub. The main body of our results is included in two papers, one primarily on

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Fig. 1. Bajada study area, facing east toward the San Andres Mountains across the floor of the Jornada basin. Creosotebushes in foreground. Photograph by W. G. Whitford.



Fig. 2. Playa study area, showing fringe of shrubs in foreground (creosotebush, *Yucca elata*, *Ephedra*, and leafless mesquite) and in far background. Grass on playa proper is primarily *Panicum obtusum*. Photograph by W. G. Whitford.



Fig. 3. Grassland study area. Prominent plants are *Yucca elata*, *Sporobolus flexuosus* (clumps of grass in foreground), and *Gutierrezia sarothrae*; grasses in background include tobosa and black grama. Photograph by C. H. Herbel.

numbers and biomass of the birds on the three areas, but also describing the areas and the methods of study (Raitt and Pimm in press), and one on the energetic impact of the birds on the ecosystems (Pimm et al. unpubl. data). In addition to the features of general ecological interest emphasized in those papers, our findings provide implications of some importance to the conservation of Chihuahuan Desert birds and their habitats. These implications stem largely from observed and measured or inferred temporal changes in the bird communities on the Jornada.

DYNAMICS OF JORNADA BIRD COMMUNITIES

Avifaunas of the Three Areas

A first step toward understanding of the dynamics of the Jornada bird communities is to examine the species composition of the three areas, including changes throughout the year (Table 1). Several salient features may be noted in these lists. The breeding avifaunas of all three areas are similar and consist of species characteristic of southern North American desert scrub avifaunas generally, although as Dixon (1958) and Raitt and Maze (1968) have pointed out,

TABLE 1. Regular and common bird species occurring on three Jornada study sites in summer (S) and winter (W)^a.

| | Grassland | | Playa | | Bajada | |
|--------------------|-----------|---|-------|---|--------|---|
| | S | W | S | W | S | W |
| Turkey Vulture | | | | | | |
| Golden Eagle | X | | X | | X | |
| Swainson's Hawk | X | X | X | X | | |
| Ferruginous Hawk | | X | | | | |
| Marsh Hawk | | X | | X | | |
| Prairie Falcon | X | X | | | | |
| Scaled Quail | X | X | X | X | | |
| Mourning Dove | X | X | X | X | X | X |
| Roadrunner | X | X | | | | |
| Burrowing Owl | X | | X | | | |
| Nighthawk species | X | | X | | X | |
| Western Kingbird | X | | X | | | |
| Say's Pheobe | | X | | | | |
| White-necked Raven | X | X | | | | |
| Horned Lark | | X | | X | | |
| Verdin | | X | | | X | X |
| Cactus Wren | X | X | X | X | X | X |
| Mockingbird | X | | X | X | X | X |
| Crisal Thrasher | | | X | | X | X |
| Black-tailed | | | | | | |
| Gnatcatcher | | | | | | X |
| Loggerhead Shrike | X | X | X | X | X | X |
| Meadowlark species | X | X | X | X | X | X |
| Scott's Oriole | X | | X | | X | |

^aSummer is defined as May-July, winter as November-February. All raptors of regular occurrence in the particular season are included; nonraptors are included if (1) they were recorded in two or more months of the particular season in each year, and (2) if their average density for the season was greater than 5 per km² each year.

TABLE 1. (Continued)

| | Grassland | | Playa | | Bajada | |
|------------------------|-----------|---|-------|---|--------|---|
| | S | W | S | W | S | W |
| Brown-headed Cowbird | | | | | | |
| House Finch | | | | | X | |
| Lark Bunting | | | | X | X | X |
| Cassin's Sparrow | | X | | X | | |
| Black-throated Sparrow | X | | | | | |
| Sage Sparrow | | | | | X | |
| Brewer's Sparrow | | X | | | | X |
| | | X | | X | | X |

breeding bird faunas of the northern Chihuahuan Desert scrub are depauperate compared to those of the Sonoran Desert. Webster (1964) found a much richer breeding avifauna in desert scrub in Zacatecas. The Bajada area, which bears "typical" Chihuahuan desert scrub dominated by creosotebush, was somewhat poorer in species and exhibited less seasonal turnover of its avifauna than the other two areas. The bird species on the Bajada in the nonbreeding season remained primarily those typical of desert scrub. In contrast, the breeding species of the Playa and Grassland plots were replaced in the nonbreeding season by avifaunas rich in species that breed primarily in true grasslands to the north and east. In an analysis to be published elsewhere (Pieper et al. unpubl. data), we used a principal coordinates multivariate statistical method to compare the similarities of the avifaunas of the three Jornada areas in the breeding and nonbreeding seasons with each other and with those of some other North American desert scrub and grassland areas. The results confirmed the generalizations stated above. Based on the three principal components there were three clusters of similar avifaunas: (1) a group of avifaunas of Sonoran desert scrub and desert grassland areas, very rich in species; (2) ones of shortgrass and tallgrass true prairies, poor in species; and (3) Chihuahuan desert scrub and desert grassland *breeding* communities, somewhat intermediate in species richness. The Jornada desert grassland *winter* community was a part of the second cluster rather than the third. The results of Webster (1964) in Zacatecas were somewhat similar to ours: little turnover between summer and winter in a desert scrub area, with considerable turnover in a grassland avifauna.

Seasonal and Annual Variation in Density and Trophic Representation

In our analysis of seasonal and annual shifts in numbers and biomass (Raitt and Pimm in press), we subdivided the birds into various ecological categories but found that a simple subdivision into insectivores, seed-eaters, and raptors permitted the most meaningful analysis. In the present analysis, the same categories will be used, but raptors will receive only slight attention. Figure 4 shows monthly mean numbers per square kilometer for the Bajada and Grassland sites for the insectivore and seed-eating groups. Insectivores were dominant in the breeding season on both sites and on the Playa also. They were also dominant on the Bajada at other seasons; seed-eaters have not been numerous on the Bajada at any season. By contrast, seed-eaters have been dominant on the Grassland site in the nonbreeding season and, in fact, their densities have been so high as to bring overall numbers in the nonbreeding season to much higher levels than those of the breeding season. In regard to the relative importance of seed-eaters and of nonbreeding season versus breeding season, the Playa birds resembled those of the Bajada in 1971 but since then have resembled those of the Grassland.

Insectivore densities have changed from year to year in correlation with their food supply, but annual differences have not been striking. Seed-eaters, on the other hand, have fluctuated widely on both Grassland and Playa sites in the three

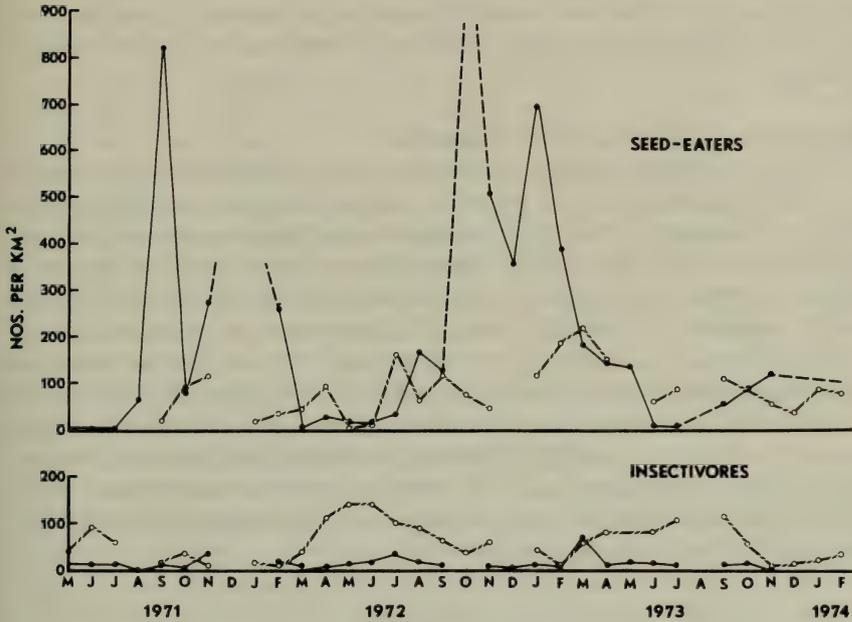


Fig. 4. Changes in density of seed-eating (upper) and insectivorous (lower) birds on the Bajada (open circles, diagonally broken line) and Grassland (solid dots, solid line) sites from May 1971 to February 1974. Dashed lines are interpolations for missing Grassland data, based on results of roadside censuses in grasslands.

winters of our study. In these year-to-year comparisons for the Grassland, we have relied somewhat on data from roadside counts as they better reflect the relative numbers of large wintering flocks of seed-eaters and they help fill in gaps in our Grassland plot censuses. Grassland seed-eaters were numerous in the fall of 1971, but numbers dropped off rapidly and remained at moderately low levels until the following autumn. In the nonbreeding season of 1972–1973, the flocks of seed-eaters arrived in the fall, as in 1971, and remained until spring (roadside counts and Playa censuses revealed both an earlier arrival and a later departure than did the Grassland plot counts). In 1973–74, the fall-winter flocks failed to appear in our censuses altogether.

The most important species of these nonbreeding seed-eaters were Lark Buntings, Horned Larks, Mourning Doves, Brewer’s Sparrows, Sage Sparrows, and other emberizines.

Causes of the above variations between areas, between seasons, and between years are discussed in Raitt and Pimm (in press). Food availability seems clearly to be the principal proximate cause of the variation, with weather variation playing an important indirect role. Favorable growing conditions producing high crops of seeds have been correlated with high densities of seed-eaters on Grassland and Playa study areas (1972–73), whereas in dry years (1971–72, 1973–74)

with concomitantly low seed availability, numbers of seed-eaters have been low and flocks of important seed-eaters have been absent from the Jornada for most of the year.

Ecological Impact of the Bird Communities

The above findings, in combination with data on breeding and molting and on variation in populations of food organisms and potential competitors, provide the means for estimating the energetic demands of the Jornada birds throughout the period of the study. Our analysis of these demands is not yet complete, but it appears as if the birds seldom, if ever, have been very important among the various groups of consumers in energetic impact on the rest of the ecosystems. This is not to say that the birds are not important in the systems but rather that their importance lies in effects more subtle than that of total energy demand. One example of this importance is in the effects of feeding by large flocks of Lark Buntings, which have markedly altered the local density and dispersion of annual plants in preferred foraging areas. We will not pursue this topic in more detail, for our focus of interest in this paper is more on the importance of the Chihuahuan Desert to birds than the converse.

IMPLICATIONS FOR CONSERVATION AND LAND USE

Importance of Chihuahuan Desert Grasslands

The principal first order implication of our findings on the seasonal use of the Jornada by birds is that the Jornada, and areas like it in at least the northern Chihuahuan Desert, is a very important wintering ground for North American grassland birds. Mourning Doves, Horned Larks, Lark Buntings, Brewer's Sparrows, longspurs, and other emberizines are all important components of breeding avifaunas of shortgrass prairies and other mid-continent communities. In some years, at least, very large numbers of birds of these species spend the nonbreeding period on the grasslands of the Jornada and other portions of the Chihuahuan Desert. In the Big Bend region of Texas, Wauer (1973) reports that migratory periods are the times of greatest abundance of these species, but he also indicates that large flocks may spend the winter in years following seasons of high precipitation. Migrant species were also very numerous on Webster's (1964) Zacatecas grassland plot. For some of the above species, such as the Lark Bunting, the Chihuahuan Desert grasslands constitute the principal wintering grounds. At densities of over 100 per km² (260 per miles²), hundreds of thousands of Lark Buntings must have spent the major portion of the nonbreeding period of 1972-73 in Doña Ana County alone.

But 1972-73 was a relatively favorable year for seed production and seed-eaters in our region. In 1971-72, the flocks of Lark Buntings and of other nonbreeding seed-eaters arrived in some numbers in the autumn but many left soon, presumably after food became depleted. In 1973-74 such flocks failed to appear at all.

What are the implications of this striking variation between years? Two alternative, but by no means mutually exclusive, answers appear probable: (1) favorable years on the Jornada are favorable elsewhere on the Chihuahuan Desert, with resulting high winter survival of wintering populations of these species—the converse is true of years of low seed availability; (2) the effects of unfavorable conditions on the Jornada—or in any other comparable portion of the Chihuahuan Desert—in any given year are offset by the occurrence elsewhere in this vast region of areas with higher seed availability. Highly mobile flocks of these birds simply move through the region until they find those areas with sufficient seeds. Of course, it is possible that in some years the correct answer is alternative 1 while in others it is alternative 2. The actual outcome in a given year probably depends on the nature of regional climatic variation, i.e., on the degree of uniformity of regional rainfall patterns, for it is almost certainly rainfall which primarily governs annual seed production in arid and semi-arid regions (as shown, for example, by data from Jornada IBP sites).

We need to know a great deal more about regional patterns of bird density, seed production, and climate before we can determine and understand the relative frequency of these two outcomes. However, there is evidence of regional variation in both climate and wintering bird numbers. Everyone who lives in the Chihuahuan Desert knows that rainfall may vary greatly between even narrowly separated localities. For example, 19.6 cm (7.7 inches) of rainfall were recorded in 1974 through August at the weather station at New Mexico State University, while the El Paso, Texas, station, about 64 km (40 miles) away and at nearly the same elevation, recorded only 10.2 cm (4.0 inches) in the same period (in September, late in the growing season, El Paso received heavy rainfall but the example still suffices). It would seem that variation of that magnitude would almost certainly result in significant variation in availability of food for seed-eating birds. As to regional variation in density of wintering birds, in the winter of 1973–74 very few Lark Buntings appeared on the Jornada, but casual observations in the vicinity of Torreón, Coahuila, in December and in the states of Chihuahua and Durango in October and April indicated that sizable flocks were, indeed, wintering in Mexico and that the dearth of these birds in our region was not universal throughout the Chihuahuan Desert. Thus we conclude provisionally that outcome 2 does occur and may even be usual. If this is true, then most of the grasslands of the Chihuahuan Desert may be necessary to support the North American grassland bird populations over a series of winters. Each set of local habitats may be able to support bird populations only in certain favorable years, but in any given year there will be sufficient number of them in favorable condition to support the entire set of populations.

Another set of relationships about which we need more information is that between quality and quantity of the winter range, winter survival rates, and overall status of grassland seed-eating bird species. Our argument here rests on the assumption that the winter range is important in the economy of these species. Fretwell (1972) supported this assumption, and for the present we rely

upon his views and on the obvious fact that deterioration and shrinkage of their wintering habitats would, ultimately at least, have serious detrimental effects on the survival of the species.

Relation to Land Use and Conservation

If our preceding conclusions are valid, then conservation of Chihuahuan Desert grasslands is essential to the welfare of a number of North American grassland bird populations. Furthermore, extensive areas of such grasslands spread over broad regions are necessary as insurance that in each year sufficient wintering habitat of sufficient quality will be available in spite of drought and consequent low seed availability in some portions of the region.

It should be emphasized that desert scrub will rarely if ever support high densities of the birds in question. We point this out because very large portions of the Chihuahuan Desert are covered by this unsuitable type of vegetation, and because the desert grassland that formerly clothed many areas of the Chihuahuan Desert has been replaced by desert scrub. The causes of this replacement are somewhat controversial but that it has occurred on a very large scale in the northern Chihuahuan Desert appears certain (Gardner 1951; Buffington and Herbel 1965; York and Dick-Peddie 1969; Pieper et al. unpubl. data). If, as seems likely, grazing by cattle has been a causative factor in the replacement of grassland by scrub, then it is probably still occurring; and it probably is not confined to New Mexico, where it has been best documented, but is common over much or all of the Chihuahuan Desert. It is partly because of this replacement that we have not stressed conservation of desert scrub birds. They are perhaps no less important than grassland birds as a resource, but their future seems assured for the present because their habitat is widespread and probably increasing. On the other hand, to emphasize the point, the wintering habitat of grassland birds has shrunk drastically in the recent past and probably will continue to do so.

Replacement of grasslands by scrub because of overgrazing (or protection from fire, or deterioration of the climate, or whatever cause) is not the only danger to the habitats in question. Cultivation, as in the valleys of the Rio Grande, Rio Conchas, and Rio Nazas, and urbanization have also resulted in loss or degradation of grassland habitats.

Our ultimate point is that protection and preservation of lowland grasslands in the Chihuahuan Desert region, whether they be desert grassland plains, playas, or riparian grasslands, are relevant beyond immediate, local considerations, however important. The future of a number of continental bird populations may depend upon their success.

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Effects of Habitat Attrition on Vireo Distribution and Population Density in the Northern Chihuahuan Desert

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INTRODUCTION

The Chihuahuan Desert encompasses an arid region including southern New Mexico, much of west Texas to just east of the Pecos River drainage, south to include the eastern two-thirds of Chihuahua, and much of the states of Coahuila and San Luis Potosí and northwestern Hidalgo, as well as parts of Durango, Zacatecas, and Nuevo Leon (Jaegar 1957; Shelford 1963). This area is essentially the Chihuahuan biotic province of Dice (1943).

The effects of drought on arid country vegetation are well known. Much of the vegetation of lower elevations—the mesquites, acacias, cacti, and yuccas—survives prolonged drought reasonably well. At higher elevations, drought seems to affect productivity substantially and in some years may appreciably alter the composition of local biotas. Habitat attrition as a function of clearing for agricultural purposes or overgrazing by domestic stock likewise has severe effects on local faunal composition. Drought in combination with man-produced habitat changes may operate synergistically to eliminate some kinds of animals more or less permanently from affected areas, contingent in part upon the adaptive plasticity of the animals in question. In the northern parts of the Chihuahuan Desert and in areas adjacent to the desert proper, the distribution and concomitantly the numbers of some kinds of birds have doubtless changed in response to the above factors.

More than a hundred species of birds breed within the Chihuahuan Desert, but I will be concerned with only six members of the passerine family Vireonidae. Included are the Gray (*Vireo vicinior*), Solitary (*V. solitarius plumbeus*), Hutton's (*V. huttoni* ssp.), Bell's (*V. bellii* ssp.), Black-capped (*V. atricapillus*), and Warbling (*V. gilvus* ssp.) vireos.

It has been amply demonstrated (Barlow and Johnson 1968; Barlow 1967; Wauer 1973; Van Tyne and Sutton 1937) that all of these species breed locally within an area from extreme northern Coahuila to southeastern New Mexico. The

breeding status of the Solitary and Gray vireos south of the Sierra del Carmen in southern Coahuila is not clear. I have studied all six vireos elsewhere in their ranges.

VIREO HABITATS

By now in the present symposium it hardly bears repeating that a diverse ecology characterizes habitats in the northern desert. These habitats range from relatively low-lying, drainage-favoring plant communities of creosote bush and succulent desert, to grasslands, to mixed deciduous-coniferous forest at higher elevations in the relatively isolated mountain ranges. In the Chisos Mountains and environs within Big Bend National Park, Wauer (1971) has identified six distinctive plant associations divided among five floristic formations. Those relevant to vireo distribution are: the Arroyo Mesquite-Acacia Association 540–1220 m (1782–4026 ft); the Deciduous Woodland Association 1128–2380 m (3722–7854 ft) which interdigitates with the Pinyon-Juniper-Oak Woodland Association between the same elevations—contingent upon exposure; and the Cypress-Pine-Oak Association 1770–2195 m (5841–7244 ft). Recognition of these associations is useful for the present discussion because the habitats they comprise are often depleted, modified, or lacking outside the protected environment of Big Bend Park.

Of the six vireos in question only *Vireo bellii* breeds regularly below 760 m (2508 ft). This species prefers riparian scrub, associated with permanent streams or rivers. Ingress by this vireo into the creosote-succulent desert faciations has been facilitated by the presence of mesquite and willow oases, associated with natural springs, seeps, and playas, and also with wells and ponds near human habitation. Patches of such habitat are fairly widespread in Big Bend Park where protection from grazing and other forms of habitat destruction has contributed to the maintenance of substantial populations of Bell's Vireo.

Territory size in this species ranges from 0.20 to 1.2 ha (0.5 to 3 acres) (pers. obs.). In the desert in 1968, 10 territories found averaged 0.04 ha (1 acre) (range 0.20 to 0.60 ha [0.5 to 1.5 acres]) in area. Although *V. bellii* is gregarious and a relatively few acres may support 3 or 4 pairs, single pairs may be found in as little as 0.2 ha (0.5 acres) of mesquite and willow. This species seeks arthropods on small-leaved deciduous foliage and on twigs and small branches from just above ground level to ca. 5 m (16.5 ft), with most activity under 3 m (9.9 ft). Soft bodied prey is favored.

The Gray Vireo occurs in the Deciduous Woodland Association in Big Bend, especially nesting in Gregg's ash (*Fraxinus greggii*) and evergreen sumac (*Rhus virens*). Near Las Cruces, New Mexico, on the western side of the Organ Mountains (pers. obs.), *V. vicinior* has been found in streamside hackberry (*Celtis*) and Graves oak (*Quercus gravesi*). Gray Vireos occur east of the park in the Pecos River Canyon near its junction with the Rio Grande. This vireo has also been reported from canyons in the Texas part of the Guadalupe Mountains (Burleigh and Lowery 1940) in mixed Pinon pine (*Pinus edulis*), juniper (*Juniperus*), and

madrone (*Arbutus*). In Arizona, Gray Vireos frequent dwarf conifer forest, as well as the other habitats already mentioned (Barlow et al. 1970).

Gray Vireo territories that I have found (Barlow 1967; pers. obs.) were from 2.4 to 8 ha (6 to 20 acres) in area. Outside the desert, in central Arizona, I noted a singing male every 300 m (990 ft) for a distance of 15 km (9 miles) on the south side of the Bradshaw Mountains, Yavapai County. Within the desert in 1968, five pairs were located in the Basin in the Chisos. Leaves, twigs, and branches in both deciduous and coniferous growth (averaging 5 m [16.5 ft] in height) are searched for arthropods. Foraging occurs between ground-level (rarely) and 5 m (16.5 ft), with most occurring below 3 m (9.9 ft).

Habitat requirements of the Black-capped Vireo have been assessed by Graber (1961). She found that low, predominately deciduous growth dominated by oak, not necessarily associated with permanent water, characterized localities in which this species occurred throughout its restricted breeding range (at present central Oklahoma south through the Edward's Plateau in Texas west to Big Bend and south to central Coahuila where it occurs locally from 300 m to 1830 m [990 to 6039 ft]). *V. atricapillus* has demonstrated habitat co-occupancy with Gray, Bell's, and White-eyed (*V. griseus*) vireos (Barlow 1967; Graber 1961). In Big Bend, the Black-capped Vireo is found in the Deciduous Woodland Formation where it occasionally overlaps with *V. vicinior*.

A Black-capped Vireo territory studied in the Chisos in 1967 (Barlow 1967) comprised 1.6 ha (4 acres). Graber (1961) reported territories averaging between 1 and 1.8 ha (2.5 and 4.6 acres) in her study area in Caddo County, Oklahoma. Usually several pairs frequented patches of suitable habitat (Graber 1961). Foraging behavior and food preferences are similar to those of *V. bellii*. Food is sought mostly under 4 m (13 ft).

The largely sedentary Hutton's Vireo inhabits both the Pinyon-Juniper-Oak Woodland and the Cypress-Pine-Oak associations in the Chisos Mountains. This is the only place in the northeastern sector of the desert in which *V. huttoni* is known to breed. This species has been reported from the Davis and Guadalupe mountains in autumn (Smith 1917; Burleigh and Lowery 1940); however, these records probably pertain to wanderers, as there is no evidence that breeding populations occur in either of these mountain ranges.

Two territories in the Bradshaw Mountains, Yavapai County, Arizona, were respectively 1.36 and 1.68 ha (3.4 and 4.2 acres) in area. The only territory that I found in the Chisos comprised about 1.6 ha (4 acres). Habitat requirements are not so stringent as those of the other woodland-dwelling species, i.e., *Vireo solitarius* and *V. gilvus*. Several pairs of *V. huttoni* are usually found in preferred habitat. Hutton's Vireo is an insectivorous arboreal forager seeking prey on foliage and twigs between 1.5 and 18 m (5 and 59 ft), but with most activity below 10 m (33 ft).

Vireo solitarius plumbeus breeds irregularly in the Chisos in wet years in the Cypress-Pine-Oak Woodland Formation (Wauer 1971). This form is a fairly common breeding bird in the Davis Mountains where a preference is shown for

mixed strands of ponderosa (*Pinus ponderosa*) and pinyon pine which have some deciduous undergrowth present. In parts of its range, *V. s. plumbeus* also breeds on intermontane plateaus above 920 m (3036 ft) in riparian woodland along permanent streams. Here this bird is syntopic with *Vireo gilvus*. I have not found Solitary Vireos breeding in such deciduous habitat in the northeastern sector of the desert. I am uncertain whether populations in the desert lack this habit or if suitable deciduous habitat has simply been destroyed.

Solitary Vireos seen in the Davis Mountains had territories of about 2 ha (5 acres) in area in open pine forest with some deciduous understory. This insectivorous species forages throughout the arboreal canopy mostly between 3 and 20 m (10 and 66 ft), but takes more food from the surfaces of larger branches than do any of the other vireos in this study. Throughout the range of this species in the most favored locales single pairs may breed successfully in a few acres of coniferous forest, but in Arizona single pairs have also been found in isolated cottonwood groves.

The Warbling Vireo occurs in deciduous enclaves in the Cypress-Pine-Oak Association in the Chisos. In these mountains this species is of irregular occurrence as a breeding bird except in wet years, thus resembling *V. s. plumbeus* in this regard. In the Davis Mountains we have found Warbling Vireos in poplars in association with streams. The two territories of this species that I have studied in the west were both 1.2 ha (3 acres) in area. This arboreal insectivorous species primarily forages in the outer canopy, mostly between 3 and 12 m (10 and 40 ft). Single pairs are frequently found in small groves of deciduous trees.

DISCUSSIONS AND CONCLUSIONS

Among the six species discussed, the habitat requirements of *V. atricapillus* seem the most stringent. Habitat features acceptable to Black-capped Vireos are largely determined by climatic, edaphic, and topographical parameters and by secondary factors including fire, grazing, and human disturbance (Graber 1961). Graber has shown that this species has retreated from peripheral parts of its range because of drought and grazing.

I have made several detailed searches in Texas in what appeared to be suitable habitat and failed to find any birds. Between 4 and 8 May 1969, R. D. James and I drove approximately 1600 km (1000 miles) over roads in Kimble and Gillespie counties, Texas, searching for Black-capped Vireos by using playback of taped conspecific song. We found birds at only 13 of 200 sites. Localities inhabited by vireos were characterized by deciduous scrub having leafy growth to ground level. Where goats were pastured, a browse line to 1.5 m (5 ft) above the ground had been produced. Virtually all avian habitat associates of *V. atricapillus* in the places lacking goats (and hence a browse line) were also present in goat-browsed habitat.

Within the desert, Black-capped Vireos have apparently disappeared from localities at which they once occurred. For example, this species has been reported from the Glass Mountains in northern Brewster County by Van Tyne and

Sutton (1937). Neither I nor Graber (1961) were able to find this vireo in that area between the early 1950s and the late 1960s. The sensitivity of *V. atricapillus* to even slight habitat change has been shown by Graber (1961) and reconfirmed by my own field work.

The distribution and numbers of *Vireo vicinior* have been poorly understood. In fact, this species has been listed on the first "blue list" printed in *American Birds* (Anonymous 1972). This list comprises species "giving indications of non-cyclical population declines or range contractions." However, within the desert there is a good indication that the Gray Vireo has extended its range. The first specimens for Texas were taken in the 1930s from the Chisos and Glass mountains (Van Tyne and Sutton 1937). Then Burleigh and Lowery (1940) found this species in canyons in the southern Guadalupe Mountains at the north end of the Trans-Pecos. Subsequently, the Gray Vireo has been seen in summer in the Pecos River Canyon and eastward. Likewise, *V. vicinior* recently has been found breeding in the Sierra del Carmen in extreme northern Coahuila (Barlow and Johnson 1968) and wintering in Big Bend Park (Barlow and Wauer 1971). Gray Vireos have also been recorded in Texas in the Sierra Vieja Mountains, Presidio County (Phillips and Thornton 1949) and in the Davis Mountains (J. Scudday pers. comm.) However, I have been unable to find this species in marginally suitable habitat in accessible parts of the Del Norte Mountains.

This species tolerates a broader range of habitat types than any of the other five vireos. Often it occupies the least hospitable mountain slopes and canyon walls where cattle seldom graze. The range of the Gray Vireo is largely west of the major areas where goats are raised commercially. Even though Gray Vireos are often found in very arid habitats, the 35 territories which I have seen in Texas and Arizona since 1967 have been near a water supply available during at least part of the breeding season. The continued presence of this species would be threatened by prolonged drought or by the clearing of preferred habitat. The latter seems to have obtained in the Del Norte Mountains in Brewster County. Due to the size of the territories in this species, fairly large tracts of undisturbed habitat, in comparison to the requirements of other vireos, would need to be preserved to benefit individual pairs.

Except in the Guadalupe Mountains, Warbling and Solitary vireos do not have large populations in the northeastern part of the desert. They are restricted to islands of forest habitat growing in the mountains. No breeding populations were reported from the Sierra del Carmen by Miller (1955), although he may have missed later arriving summer residents because he worked there only in April. In the Davis and Guadalupe mountains both species are probably present every year, but they breed sparingly in wet years in the Chisos. So drought conditions would limit their numbers and result in their absence in very dry years. Removal of phreatophytes—especially cottonwoods (*Populus*)—certainly has caused the disappearance of Warbling Vireos locally in Brewster and Jeff Davis counties (pers. obs.)

Hutton's Vireo populations would be decimated if the pine-oak woodland

which they prefer was to be destroyed on a large scale by logging or fire. Perhaps this might happen in northern Mexico; however, the only large population in Texas seems safe within the confines of Big Bend Park.

Bell Vireos seem relatively safe. Overgrazing may have caused their numbers to decline on some ranches. I have thought, for example, that more birds should occur along Calamity Creek in central Brewster County. Only direct pressure would jeopardize this species.

The Black-capped Vireo may be of uncertain status throughout its breeding range because of limited tolerance for habitat alteration. Concern has been sufficient in Texas so that the species has recently been placed on the rare and endangered list there. *Refugia* such as provided within the protected areas of Big Bend Park eventually could become critical to the survival of this species north of Mexico if its numbers diminish further in other parts of Texas. It is hoped that in adjacent parts of Coahuila that some acreage can be set aside for a park in which actual or potential local breeding populations of all six vireos could receive needed protection.

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Changes in the Breeding Avifauna within the Chisos Mountains System

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Big Bend National Park is located in southwestern Texas within the great southern arch of the Rio Grande, half-way between El Paso on the west and Laredo on the east. All of the park is within Brewster County. Within this great bend is an environment of arid lowlands, alluvial washes, rolling foothills, and a mountain range—the Chisos—that rises to 2388 m (7835 ft) elevation. The Chisos Mountains form a montane island that is the southernmost in the United States and the only mountain range in the continental United States totally within a national park. Approximately 104 km² (40 miles²) of the Chisos Mountains lie above 1067 m (3500 ft). The physiographic and climatic factors of the area were summarized by Wauer (1971).

The vegetative composition of Big Bend National Park was mapped by Warnock and Kittams (1970), and the ecological associations were discussed by Wauer (1971, 1973a). Four major biotic units can be identified: riparian, desert, grassland, and woodland. Riparian vegetation makes up only a minute part of the park's flora, occurring along the Rio Grande and adjacent drainages and at isolated desert springs and tanks. Desert makes up 49% of the park's vegetational composition. Forty-nine percent is grassland, and only 2% is woodland. About 320 ha (800 acres) of the woodland may be considered forest-edge type habitat.

My residency within Big Bend National Park from August 1966 through July 1972 allowed me the opportunity to investigate thoroughly and to evaluate the park's avifauna and related ecological associations. I was able to review all earlier data published on the West Texas avifauna and vegetation, and to make certain determinations on their relationship. Considerable data are summarized in Wauer (1973a), including information obtained by several ornithologists from the 1901 Biological Survey (Bailey 1905), Van Tyne and Sutton's work in the 1920s and 1930s (1937), and later studies.

VEGETATIVE CHANGES

The earliest description of the area's vegetation was done by an early rancher, James G. Gillette. Gillette (1933) was foreman of the G-4 Ranch (the area's first



Fig. 1. The Chisos Mountains from the west side. Major peaks (left to right) include Pulliam Ridge, Crown Mountain, Casa Grande, Toll Mountain, and Emory Peak.

ranch, located between the western half of the Chisos Mountains east to Terlingua) and in 1933 wrote the following:

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

Ranches encircled the Chisos Mountains by the 1920s. The best cattle feed was within the belt of grasslands situated between the desert and woodlands. By the mid-1930s, extensive portions of the Big Bend country showed evidence of overuse (Wauer 1973b). When lands were purchased for the national park in 1941 and 1942, landowners were given free grazing privileges that extended to June 1944. A total of 3880 cattle, 9000 sheep, 25,700 goats, and 310 horses was being grazed on the area when land purchasing took place (Prewitt 1947). In

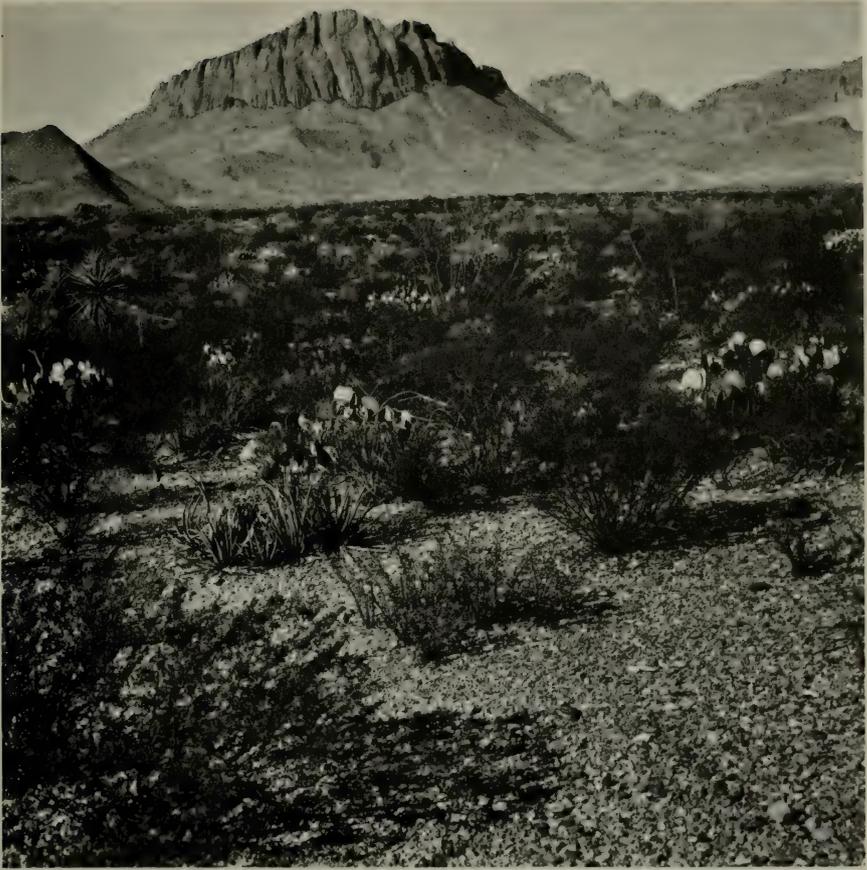


Fig. 2. Desert and grassland vegetation surround the Chisos Mountains. This view is looking west toward Nugent and Crown mountains.

1944 a total of 19,000 to 25,000 cattle, 6000 to 8000 sheep, and 15,000 to 18,000 goats, and about 1000 horses was removed from the area (Wauer 1973b). The 2 years of free grazing devastated the vegetation and changed habitats in every case. To make matters even worse, the drought years of 1947 through 1951 furthered the deteriorating conditions (Ross Maxwell pers. comm.).

The removal of livestock from Big Bend National Park started a vegetation recovery trend that has been documented. In 1948, the Soil Conservation Service established twelve 300-cm (10-ft) transects, four each within the desert, grassland, and woodland. Warnock (1969) located and surveyed ten of the transects in 1956 and 1969. Table 1 (Baccus 1972) summarizes his findings. A significant increase of ground cover resulted in all study areas. The increase from 1956 to 1969 was greater than from 1948 to 1956, probably as a result of the drought

TABLE 1. Vegetation development of ground cover on plots established by SCS.

| Plot | Altitude (ft) | Percent Ground Cover | | |
|---------------|------------------|----------------------|------|------|
| | | 1948 | 1956 | 1969 |
| Panther Pass | 5800 | 0.34 | 3.81 | 2.60 |
| Green Gulch | 4200 | 0.13 | 0.52 | 1.23 |
| Green Gulch | 4200 | 4.30 | 3.62 | 6.67 |
| Green Gulch | 4200 | 0.38 | 0.63 | 1.51 |
| Burnham Ranch | 3800 | 1.39 | 3.16 | 5.05 |
| Tornillo Flat | 2800 | — | 0.05 | 0.10 |

Compiled by Baccus (1970)

during the earlier period. The Burnham Ranch, located along the desert-grassland ecotonal zone, exhibited the greatest increase of ground cover, 72% during the 21-year period.



Fig. 3. Laguna Meadow contains the best example of the Chisos Mountains chaparral.



Fig. 4. Pinyon-juniper woodland in Green Gulch, Chisos Mountains.

In 1955, Texas A and M University personnel established 77 random transects in the park. Thirty-five were surveyed by Warnock in 1967 (1967a) and are summarized in Table 2 (Baccus 1972). These data show that the grassland slopes had the greatest increase in average ground cover, although a substantial increase in grasses was evident for every plot. The average ground cover increase from 1955 to 1967 for the grasslands (453.3) was almost two times the increase for the woodlands (276.3) and the desert (272.4). Not only did grasses increase in areal coverage, but they became the dominant plants within the zone of vegetation that had previously been desert or desert-grassland ecotones. Warnock found that 73% of the woodland transects indicated substantial changes in community vegetation; e.g., slight changes in tree composition and significant increases in grass cover.

AVIFAUNAL CHANGES

Avifaunal abundance and distribution within the Texas Big Bend area were summarized by Van Tyne and Sutton (1937) who utilized all available earlier

TABLE 2. Summary of floral changes from 1955 to 1967 on plots established by Texas A and M University^a.

| Plant Formation | No. of Plots | Average Total Ground Cover in 1955 | Range of Total Ground Cover in 1955 | Average Total Ground Cover in 1967 | Range of Total Ground Cover in 1967 | Increase in Average Ground Cover From 1955 to 1967 | No. of Plots with Grass Increase |
|-----------------|--------------|---------------------------------------|--|---------------------------------------|--|--|-------------------------------------|
| Woodland | 11 | 289.5 | 22.5-480.0 | 565.8 | 81.5-1848.5 | 276.3 | 8 |
| Grassland | 14 | 188.8 | 25.5-338.5 | 642.1 | 332.0-1168.6 | 453.3 | 14 |
| Desert | 10 | 227.6 | 13.0-629.5 | 500.0 | 34.0-1140.0 | 272.4 | 6 |

Compiled by Baccus (1970)

^aMeasured in hundredths of a square foot.

avian data. That publication serves as the principal basis for comparison with data accumulated by Wauer (1973a). The discrepancies in avian abundance and distribution assumedly can be attributed to the vegetative changes, which themselves are recognized as a result of climate, soils, temperature, precipitation, and utilization. The following species are examples of status changes.

Sharp-shinned Hawk—*Accipiter striatus*. The presence of this species as a nesting bird within the Chisos Mountains is an indication of a mesic forest condition. Nests were found in Boot Canyon in 1966, and on the north side of Mt. Emory in 1969 (Wauer 1973a). It previously had been recorded only as a migrant and winter visitor, but its presence as a breeding bird is of special interest because it is an indicator of conditions not previously recognized in the Chisos Mountains.

Swainson's Hawk—*Buteo swainsoni*. Van Tyne and Sutton (1937) regarded this bird as a regular nesting species throughout the lowlands of the Big Bend area. It still is a fairly common nesting hawk of the yucca-grasslands north and south of Big Bend National Park, but I did not record it nesting within the park during my 6 years of residency.

Montezuma Quail—*Cyrtonyx montezumae*. This grassland bird had not been recorded within the park for many years. Van Tyne and Sutton (1937) recorded it in 1933 but wrote that "local hunters and ranchers testified unanimously to the great decrease in the number of this quail in recent years in even remote areas. No adequate explanation of this decrease was offered but surely overgrazing, which now prevails in nearly every part of the country, must be an important contributing factor." The species was extirpated from the Chisos but continued to survive within the adjacent Sierra del Carmens to the south and the del Nortes, Glass, and Davis mountains to the north.

White-necked Raven—*Corvus cryptoleucus*. Van Tyne and Sutton (1937) reported this species as a common breeding bird of the yucca-grasslands and mesquite flats in the Big Bend area. Like the Swainson's Hawk, I did not find it nesting within the park, although it still is a common nester on mesquites and utility poles north of the park and south of the Rio Grande.

Curve-billed Thrasher—*Toxostoma curvirostre*. Only once during my 6 years of residency did I record nesting Curve-billed Thrashers within the park—at Panther Junction Residential Area in 1972 (Wauer 1973a). Van Tyne and Sutton (1937) reported the species to be common throughout the desert and grasslands of the park. It is still a common nesting species of the yucca-mesquite ranchlands north and south of Big Bend National Park.

Crissal Thrasher—*Toxostoma dorsale*. Van Tyne and Sutton (1937) reported this species present and breeding locally within the Chisos Mountains area, but I found it to be a common nesting bird of the chaparral zones that encircle the mountains.

Gray Vireo—*Vireo vicinior*. Van Tyne and Sutton (1937) did not report this species to nest in the park area, and recorded it only once. Wauer (1973a) regards

it as a "fairly common summer resident at suitable localities." Numerous nests were found within the lower chaparral zones between 1219 and 1676 m (4000 and 5500 ft) elevation.

Varied Bunting—*Passerina versicolor*. This species is locally common within the park vicinity, utilizing dense vegetation zones in the lower foothills for nesting; in wet years it nests in weedy patches along the Rio Grande. Van Tyne and Sutton (1937) found it nesting along the river and a few singing birds in the lower Chisos Basin. It apparently has increased within the park area in recent years.

Black-chinned Sparrow—*Spizella atrogularis*. Van Tyne and Sutton (1937) found the species nesting in the Chisos Basin but recorded it only twice. Wauer (1973a) regards it as a "fairly common summer resident at chaparral areas above 5,200 feet."

DISCUSSION

It is logical to assume that changes in the area's breeding avifauna are related to changes in the floral composition. It is also assumed that data available on avian distribution and abundance for the pre-Big Bend National Park period are valid for use in comparing with current avifaunal data. Five of the eight species discussed—Sharp-shinned Hawk, Crissal Thrasher, Gray Vireo, Varied Bunting, and Black-chinned Sparrow—have increased in abundance and distribution. Four species—Swainson's Hawk, Montezuma Quail, White-necked Raven, and Curve-billed Thrasher—have decreased in abundance and distribution within the park since the vegetation has begun to recover.

Nesting Sharp-shinned Hawks indicate the presence of a rather mesic association of conifers that seems inconsistent with the absence of other nesting species within the Chisos system that would normally share this association, e.g., Rufous-Hummingbird (*Selasphorus rufus*), Western Wood Pewee (*Contopus sordidus*), Olive-sided Flycatcher (*Nuttallornis borealis*), Steller's Jay (*Cyanocitta stelleri*), Red-breasted Nuthatch (*Sitta canadensis*), Hermit Thrush (*Hylocichla guttata*), Ruby-crowned Kinglet (*Regulus calendula*), Yellow-rumped Warbler (*Dendroica coronata*), Western Tanager (*Piranga ludoviciana*), and others. A few expected avian species do nest within the association, e.g., Broad-tailed Hummingbird (*Selasphorus platycercus*), Common Flicker (*Colaptes auratus*), Western Flycatcher (*Empidonax difficilis*), Violet-green Swallow (*Tachycineta thalassina*), White-breasted Nuthatch (*Sitta carolinensis*), and Black-headed Grosbeak (*Pheucticus melanocephalus*).

Vegetational development of the woodlands increased 195.4% from 1955 to 1967 (Warnock 1967a). Two of the transects utilized for the vegetative comparisons are located in the immediate vicinity of the Boot Canyon Sharp-shin nesting site. An examination of these two sets of data indicates that the greatest increase in ground cover was made by pinyon rice-grass (*Piptochaetium fimbriatum*), Mexican pinyon (*Pinus cembroides*), and Grave's oak (*Quercus gravesii*). The ground cover (in hundredths of square feet) on the two sites increased from 211.0

in 1955 to 680.2 in 1967, 322.0%. The change produced a habitat suitable for Sharp-shinned Hawk nesting.

Crissal Thrashers and Black-chinned Sparrows nest within a zone of vegetation in the Chisos Mountains that is dense and brushy in appearance and composed of low-growing trees and shrubs. Dominant species include Coahuila scrub oak (*Quercus intricata*), bear-grass (*Nolina erumpens*), mountain mahogany (*Cercocarpus montanus*), desert ceonothus (*Ceonothus greggii*), evergreen and fragrant sumacs (*Rhus virens* and *R. aromatica*), and silktassel (*Garrya wrightii*). Examples of this habitat are found in Blue Creek Canyon, along the Window Trail in Oak Creek, at various places in drainages along the southern side of the South Rim, at Laguna Meadow, and along the trail between the Chisos Basin and Laguna Meadow.

The best example of this habitat is at Laguna Meadow where a 1955 transect was established. An examination of that plot revealed that the ground cover increased from 282.2 in 1955 to 428.0 in 1967, 151.5% (Warnock 1967a). Major ground cover increases (more than 100%) were recorded for mountain mahogany, fragrant sumac, dwarf oak, desert ceonothus, and stipagrass (*Stipa tenuissima*). Warnock (1967a) wrote, "Comparing the 1955 photograph with the more recent one it becomes obvious that the grasses in the area were certainly more abundant in 1955, at this particular site. The brush has greatly increased. . . ."

The change in the vegetative composition of these units suggests the development of a Chisos Mountains chaparral. Comparing this formation with chaparral components in Arizona and northern Mexico supports this notion. Lowe (1964) summarized Arizona chaparral and pointed out that the "dominant plants are generally tough-leaved evergreens shrubs. Scrub oak (*Quercus turbinella*) is by far the most common dominant and it may account for over 90 percent of the stand in many areas." Dwarf oak accounts for 45.3% of the ground cover (not including grasses) on the Laguna Meadow site. Of 14 genera listed by Lowe (1964) to represent Arizona chaparral, 9 are represented in the Chisos chaparral. One notable exception is manzanita (*Artostaphylos*).

The increase in Gray Vireos may correspond to the development of the chaparral units. Several Gray Vireo nests were located in the Chisos Mountains (Wauer 1971; Wauer 1973a), and Gregg's ash (*Fraxinus greggii*) served as the nesting site in every case. This shrub is abundant within a zone of vegetation that circles the Chisos along the upper edge of the sotol-grasslands and just below the chaparral and pinyon-juniper woodlands. Very few data are available to serve as a comparison for the present status of this association. A comparative photographic analysis by Warnock (1967b) of views across the Chisos Basin taken in 1935 and 1955 reveals the decrease in cacti and lechuguilla (*Agave lecheguilla*) and increase in several woody plants including Gregg's ash. The immediate foreground of the photographs falls within an area that served as a territory for nesting Gray Vireos during 1967 and 1968.

Varied Buntings nest within a zone of vegetation that was categorized by

Wauer (1971) as arroyo-mesquite-acacia association. Suitable habitats occur below 1585 m (5200 ft) elevation in the Chisos foothills and may extend to the Rio Grande floodplain. Dominant plants include woody shrubs such as evergreen sumac, white-thorn acacia (*Acacia constricta*), Apache-plume (*Fallugia paradoxa*), skeleton goldeneye (*Viguiera stenoloba*), and short-thorn zexmenia (*Zexmenia breviflora*). Localized patches of bee-brush (*Aloysia gratissima*) dominate mesic pockets of dense shrubbery in numerous places in the lower Chisos Basin. These zones are particularly good sites for nesting Varied Buntings.

Warnock (1967b) reported that photographic comparisons of the lower Basin revealed that "brushy plants like *Acacia constricta*, *Rhus virens* and *Rhus trilobata* are more abundant." Other important plants recorded as increasing at this site include: skeleton goldeneye, white-thorn acacia, and Havard agave (*Agave havardiana*).

Another site commonly used by nesting Varied Buntings is the Old Ranch on Cottonwood Wash, 1082 m (3550 ft) elevation. Warnock (1967b) compared photographs taken in 1917 and 1967. He wrote about the 1917 conditions of the site: "The grasses throughout the area were heavily utilized and the creek bottom was eaten clean." In 1967, four-winged saltbush (*Atriplex canescens*) dominated the old fields: "Mesquite (*Prosopis glandulosa*) and tasajillo (*Opuntia leptocaulis*) are abundant along the creek bottom along with seep-willow (*Baccharis glutinosa*)." Other important plants include desert hackberry (*Celtis pallida*), skeleton goldeneye, bee-bush, shorthorn zexmenia, Texas persimmon (*Diospyros texana*), and Havard agave.

I want next to discuss four examples of decreases in avian abundance and distribution within Big Bend National Park. Three species—Swainson's Hawk, White-necked Raven, and Curve-billed Thrasher—are still common breeding birds on ranchlands surrounding the park. Yet their presence within the park, with one exception discussed previously, is restricted to migration, winter, and casual visitation.

Ranchlands outside of the park utilized by the above three species for nesting appear to have characteristics similar to the park lands prior to the removal of livestock. Apparently, the reason that they no longer nest within the park is due to the removal of livestock and the resultant increase in vegetative cover.

I will use two appropriate sites within the park for vegetative comparisons. Warnock (1967b) compared the vegetation in photographs taken in lower Pine Canyon in 1916 and 1966. The most striking changes were the decrease of sotol (*Dasylirion leiophyllum*) and increase in *Opuntia*, shrubs and grasses. Other important increases on this site occurred in *Ephedra*, Texas persimmon, Torrey yucca (*Yucca torreyi*), skeleton goldeneye, creosote bush (*Larrea tridentata*), ocotillo (*Fouquieria splendens*), *Mimosa* sp., range ratany (*Krameria glandulosa*), cat-claw (*Acacia greggii*), white-thorn acacia, and several species of grasses.

A transect located below the Window and evaluated by Warnock (1967a)

showed an increased ground cover from 338.5 in 1955 to 891.5 in 1967, 263.4%. More than 100% increase occurred in several grasses—*Boutelous eriopoda*, *B. hirsuta*, *Tridens muticus*, *Leptoloma cognatum*, *Heteropogon contortus*—and croton (*Croton pottsii*), (*Ruellia parryi*), and shortthorn zexmenia. Three species showed defined decreases in the 11 years: lechuguilla, sotol, and *Panicum hallii*.

Montezuma Quail had not been recorded within Big Bend National Park for more than two decades. "The overgrazing in the 1930s and early 1940s, plus the severe drought that hit the Big Bend area during the 1940s and 1950s, probably resulted in the extirpation of this species" (Wauer 1973a).

Vegetative recovery by the late 1960s suggested the feasibility of reestablishment of the species. Boot Canyon was one of the last areas in the park where this grassland quail had been recorded. The vegetation within a pinyon-juniper woodland transect in upper Boot Canyon increased from 229.0 in 1955 to 387.5 in 1967, 169.2%. Major increases occurred in pinyon rice-grass, sedge (*Carex planostachys*), *Poa involuta*, and Havard agave. The vegetation within a Boot Canyon site located along the drainage in mid-canyon increased from 188.5 in 1955 to 598.7 in 1967, 313.4%. Major increases occurred in pinyon rice-grass, Mexican pinyon, alligator juniper, Grave's oak, *Koeleria crisata*, *Muhlenbergia pauciflora*, *Cologania angustifolia*, tick-clover (*Desmodium psilophyllum*), and golden-eye (*Viguiera cordifolia*).

These data showed that the Montezuma Quail habitat had significantly recovered by 1967. Twenty-six birds were obtained from similar habitats in Arizona and released in the Chisos woodlands on 11 January 1973 (Wauer 1973c). Although no birds were observed for several months following their release, David Riskind and I found three singing males near the point of release on 16 and 17 May 1974, and I observed a lone male in upper Boot Canyon on 24 May 1974. Since these sightings represent the first in the Chisos Mountains for several decades, it is assumed that the reestablishment of the species was successful.

SUMMARY

The relative abundance and distribution of eight bird species of the Texas Big Bend country are described and related to documented vegetational changes. The development of a coniferous habitat now offers a suitable niche for nesting Sharp-shinned Hawks. The development of a Chisos Mountains chaparral and associated vegetation has allowed for an increase in breeding Crissal Thrasher, Gray Vireos, Varied Buntings, and Black-chinned Sparrows. The recovery of the Chisos grasslands has provided suitable habitats for the survival of Montezuma Quail. Vegetative recovery at lower elevations has changed the composition of the Big Bend Park desertlands so that the Swainson's Hawk, White-necked Raven, and Curve-billed Thrasher no longer breed there. The evolution of a chaparral association and related avifaunal changes implies that biotic changes are taking place within the Chisos Mountains system.

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The Significance of Wilderness Ecosystems in Western Texas and Adjacent Regions in the Ecology of the Peregrine

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The status of the Peregrine Falcon (*Falco peregrinus*) in the Chihuahuan Desert is, in my mind, a particularly relevant issue in our evaluation of the region's biological resources. It is a highly interesting species aesthetically and biologically. It has the widest range of any bird of prey, or almost any bird for that matter, being found practically everywhere in the world except Antarctica and New Zealand (Hickey and Anderson 1969). Except for the Gyrfalcon (*F. rusticolus*), it is probably the fastest of all birds. For the most part, the peregrine nests on large cliffs, commonly near water, and eats birds of all kinds. The northern populations migrate incredible distances, even over water, where they sometimes land on ships many hundreds of miles from shore. The hunting technique of the peregrine is to catch birds by direct pursuit.

During the early 1960s, the peregrine received a different kind of notoriety. It had become apparent that many formerly stable populations had declined, some to the point of extinction. In 1965, an international conference on the population biology of the peregrine was held at the University of Wisconsin to evaluate the decline and search for its causes.

The stability of peregrine populations had long been thought to be characteristic of the species since they had persisted throughout many periods of adversity. For instance, there was a bounty on peregrines in England during the war because they were intercepting homing pigeons carrying war messages. Despite many pairs being killed at their eyries, sites would be reoccupied the following spring. Yet, during the 1950s, peregrine numbers in many areas began to fall sharply.

PEREGRINES IN EUROPE

In Europe, for example, the peregrine now occupies a fraction of its former range. There were about 400 known eyries in Finland during the 1940s (Linkola

and Suominen 1969) and an estimated total breeding population of 800–1000 pairs. By 1965, only 15 eyries could be found. A similar reduction has occurred in other parts of Scandinavia (V. Jensen pers. comm.). In West Germany the situation has gone from 350 known eyries in 1950 to about 80 in 1965 (Mebs 1969). These are in the mountainous areas to the south. The numbers of pairs in France went down to about one-third of their former number, or to about 100 to 150 pairs; again, the peregrines survived in the mountainous districts. In Great Britain and Scotland at least 850 pairs existed in the 1930s, but by the early 1960s only about half of these remained and these were reproducing poorly (Ratcliffe 1969). The British workers began observing some very peculiar behavior. It appeared that the peregrines were eating their own eggs, but it was then discovered that the egg shells were very thin and were evidently breaking under the weight of the incubating female. A strong correlation was found between shell thickness and the amount of DDE (the stable metabolite of DDT) in the egg. By examining shell weights and measurements of peregrine eggs in museum collections dating back to the early 1900s, Derek Ratcliffe discovered a remarkable drop in eggshell thickness beginning in 1947 (Ratcliffe 1967). This is precisely the period in which DDT came into general use by the civilian populace. Ratcliffe's hypothesis, which has been repeatedly demonstrated by others in the literature, is that DDT and its stable derivatives inhibit the metabolism of calcium during the formation of the eggshell. Furthermore, the DDT compounds, as well as a number of other organic substances used in farming or industry, travel through the food web, being concentrated at each trophic level.

The geography of world decline is of special interest to this paper, since, as I will discuss momentarily, the Chihuahuan Desert is an area where peregrines continue to breed, and I will attempt to explain why this is so.

Where, geographically and environmentally, have the European peregrines managed to survive? Geographically, they have persisted in the highlands of Scotland, in the mountainous interior regions of Germany and France, and in Spain. It should be emphasized that ecologically the peregrine has survived in the pastoral areas of Europe and has become extirpated in areas of modern cultivation. The exception is the now nearly extinct population of Finland, but this was a migratory population which wintered in northern France and other cultivated areas of Western Europe (Linkola and Suominen 1969).

NORTH AMERICAN PEREGRINES

As in Europe, the peregrines of North America have experienced drastic losses during the past several decades. Again, let us look at the pattern of their decline.

In the early 1940s, in North America, east of the Rockies and south of the Boreal Forest, there were about 400 known eyries (Hickey 1942). Today there are possibly one or two (Berger et al. 1969; Cade and Fyfe 1970). Further north and west there continue to be some large populations of breeding peregrines. The Pacific coast of Canada and Alaska harbors numerous pairs of peregrines (*F. p. pealeii*), and the Aleutian chain has at least 300 pairs (Cade and Fyfe 1970).

These birds are reproducing normally since neither the peregrines nor the majority of their prey are migratory and thus have rather low levels of DDT (White et al. 1973). The falcons do have larger levels of polychlorinated biphenols (industrial plasticizers) than are found in some other peregrine populations, and the ecological pathway of these contaminants to the peregrine is unclear. PCB's have effects similar to those of DDT. Elsewhere in the North American Arctic and subarctic there are at least several thousand pairs (Fyfe 1969; Cade 1960). Pesticide levels are quite high in some populations of these peregrines (Cade et al. 1971). They are highly migratory and winter as far south as Argentina where DDT is heavily used. These are the birds which migrate through Texas in the fall and spring and can be seen in fair numbers along the coast (Hunt et al. 1975; Hunt and Rogers 1973; Rogers and Hunt 1975).

In the western continental United States the peregrine population has fared better than it has to the east. In California the population has declined about 85%, from about 100 pairs to about 16 known pairs (Bond 1946; Herman et al. 1970; Herman 1971). Peregrines do breed in Arizona, but it would be difficult to approximate their numbers (6 pairs?). The formerly healthy population of Washington and Oregon has been reported to have diminished to about 10–20% of its former size (Nelson 1969) and is perhaps even smaller (Steve Herman *in litt.*). Idaho had nine or ten known pairs and now has three and possibly a few more (Morlan Nelson *in litt.*). In Utah, there were 42 known pairs, but there has been about a 90% reduction (Porter and White 1973). Incidentally, DDT was still being used in Utah in 1970 and in Oregon in 1974 in connection with the "control" of Tussuk moths. There are no known eyries in Nevada at this time (Robert Oakleaf *in litt.*) but the population there probably was always small. The Rocky Mountain region from New Mexico to Montana has been surveyed recently by Enderson and Craig (1974). Eleven occupied sites were found of 33 eyries known to have been occupied in the past. This represents a decline to about one-third their former numbers. DDE concentrations in peregrine eggs from this region remain high. In New Mexico there are four known pairs of nesting peregrines (Frank Bond *in litt.*).

An overview of the peregrine situation in North America is similar to that in Europe. The peregrine has been lost in the areas of crop cultivation and has survived in the wilderness regions of the tundra, the boreal forests, the pacific maritime islands, and in the cordillera.

PEREGRINES IN THE CHIHUAHUAN DESERT

Now, let us consider the Chihuahuan Desert. First of all, the census technique of visiting sites where peregrines are known to have bred in the past is not applicable here. Generally, there is very little historical information to use in determining how the population has fared through the period of world decline. However, I believe that any student of the ecology of this species would agree that it was never a very common raptor in the area.

In 1901, a nest with young in the Chisos Mountains was observed by Vernon

Bailey and H. C. Oberholser (Kincaid 1974). This eyrie, or one of its alternates, is evidently still active as an adult, and young were seen flying roughly 6 km (4 miles) from the old site in July 1967 by Wauer (1973). Van Tyne and Sutton (1937) reported several sightings in the Big Bend of adult peregrines in the breeding season, including what was thought to be a mated pair. The cliff where the pair was sighted was occupied by Prairie Falcons (*F. mexicanus*) in the early 1960s and was apparently vacant of falcons in 1972. Peter Koch and Morlan Nelson told me of pairs of peregrines in the Big Bend Park which they had found during the 1950s, and these eyries are still active. Wauer (1973) reported observations of four pairs in the Big Bend National Park and has recently located a fifth pair near the park area. Pansy Espy and Jody Miller observed a pair at an eyrie in Jeff Davis County in 1969 and 1970, but the site was occupied by Prairie Falcons in 1974. In this case, the peregrines have likely moved to an alternate site, as they often do (Ratcliffe 1962). I saw a peregrine in 1974 in the vicinity of the former nest.

Elsewhere in Texas, peregrines are reported to have bred near Kerrville, near some bat caves in 1902 and 1908 (Kincaid 1974). It is not known if peregrines still nest in central Texas, but Stager in 1941 reported seeing peregrines feeding on emerging bats in this area during the peregrine breeding season, and similar observations were made in the late 1950s by Alexander Sprunt IV (pers. comm.). Very probably there are peregrines nesting in the Guadalupe Mountains as a bird was seen vocalizing at a cliff there at the appropriate time of year by G. A. Newman (Kincaid 1974) and Roland Wauer.

In eastern Mexico, the peregrine has been found nesting in Tamalipas (Cade 1969), in Coahuila (Ely 1962), and in Chihuahua (Wauer pers. comm.). Morlan Nelson (pers. comm.) has also seen breeding birds in the Sierra Madre Oriental but the extent of their occurrence there is not known.

On the basis of his observations in the Big Bend National Park, Wauer (1973) has estimated the total West Texas population to be about 15–25 pairs. Naturally, I became quite interested in the validity of this estimate since, if true, it represents a greater nesting density than anywhere else in the 48 states. California has about 16 known eyries, but they exist over a rather wide area.

There are five known pairs of peregrines within an 80 km (50 mile) circle in the vicinity of the Big Bend Park. For comparison, I sent out a questionnaire to some experts in some of the other western states. Frank Bond in New Mexico knows of three eyries in a 129 km (80 mile) circle, but that is the best I could find.

This past summer (1974) John Smith of the Endangered Species Office of the Texas Parks and Wildlife Department and I made an extensive airplane survey of western Texas for the purpose of finding suitable cliffs to check out on foot next spring. During these 38 hours of flying, we attempted to evaluate virtually every large cliff in West Texas in terms of its likelihood of supporting a pair of peregrines. Our evaluation included the size of the cliff, its elevation and directional exposure (see Porter and White 1973), the presence of potholes or ledges,

proximity to water, other aspects of the surrounding terrain, and the likelihood that a sufficient supply of prey was available. All of these considerations were made in the light of the characteristics of cliffs which actually do support peregrines in Texas and New Mexico.

Herman (1971) used a similar technique for surveying peregrine eyries in California, but his purpose in doing so was to determine whether or not the eyries were active. Our experiences indicated that this is not a good method for seeing either peregrines or Prairie Falcons, although we did observe one pair of peregrines at their eyrie from the air. James Enderson tells me that Prairie Falcons "hit the deck" when an airplane approaches and we had similar experiences. Strangely, this may not be the case with helicopters as Clayton White (White and Sherrod 1974) has experienced during his peregrine studies in Alaska.

Parenthetically, among the interesting things that came up in the aerial survey was that some cliffs appear to be perfect in every respect except they have no holes or suitable ledges for falcons to lay their eggs. Richard Fyfe has responded to this kind of problem in his area of Canada by digging artificial nesting holes in the cliffs, many of which have been immediately occupied by Prairie Falcons, Canada Geese (*Branta canadensis*), and one pair of peregrines. This method of increasing the amount of peregrine habitat might well be worth trying in Texas.

Returning to our evaluation of Wauer's West Texas estimate of 15-25 pairs, on the basis of the airplane survey, our own observations, and conversations with others, John Smith and I are of the opinion that Wauer's figure is about right.

DISCUSSION

Why have peregrines been able to survive in the Chihuahuan Desert? Cade (1969: 504) has written that the reason for the large peregrine population remaining in the North American Arctic is that the Arctic is a wilderness. I contend that the Chihuahuan Desert, even though it probably never had great concentrations of peregrines, is today even more of a wilderness than is the Arctic as regards the ecology of the peregrine. Most of the Arctic bird life upon which the peregrine feeds, as well as the falcons themselves, are migratory, living in the Arctic less than half the year, and spending the rest of their time in southern locations where they can pick up pesticides and other pollutants. The prey of peregrines in the Chihuahuan Desert is apt to be on the average much less migratory, and because the region is largely pastoral, there is little or no contamination, except locally.

Most of the mountain ranges are not high enough for heavy buildups of winter snow so, except along the rivers, there is not much cultivation for lack of irrigation water. Prey birds such as passerines, doves, and quail foraging in the periphery of such mountain ranges are likely to be totally uncontaminated. Birds adapted to mountain life, including the peregrine and much of its prey, are likely to migrate to and from mountainous areas, if at all. James Enderson informs me that adult peregrines in Colorado may remain near their eyries throughout the year.

Porter and White (1973:69) have made an interesting generalization. They write:

In the desert . . . the peregrine's role is the reverse of its role in the Arctic. The desert peregrine is forced into the role of a specialist because the harsh arid environment produces few of the prey species preferred by the peregrine, and because the prairie falcon competes more successfully for the peregrine's marginal food niche and its marginal nesting niche.

Perhaps some pairs of Chihuahuan Desert peregrines have survived because they happen to specialize on a few species of uncontaminated prey. I believe this is especially true at eyries in the higher elevations where peregrines likely feed on jays (sps.), woodpeckers (sps.), Bandtailed Pigeons (*Columba fasciata*), and other woodland species.

It can be generalized, in view of the details of world decline, that the safest kinds of prey birds for peregrines to eat are those which are granivorous, nonmigratory, and nonagricultural. Some prey species in the Chihuahuan Desert are at odds with some of these requisites, and may be hazardous to nesting peregrines. It is probable, for example, that bats form a significant part of the diet of some pairs, since bat predation by peregrines is a well-known occurrence (Stager 1941; Porter and White 1973; Dementiev 1957; Clunie 1972). Bats, being insectivorous and migratory, are likely to contain pesticides, and the concentrations need not be great to build up rapidly in the peregrine, perhaps only a few parts per million (Enderson and Berger 1968). We know that bat populations have declined in some places (e.g., Carlsbad Caverns) since the advent of the pesticide era, and that bats do contain DDT, and that they are common in the Chihuahuan Desert. Cliff Swallows would seem to be also at least a potential problem for peregrines. Enderson and Berger (1968) found several ppm of DDE in Cliff Swallows in the Arctic. Both Prairie Falcons and peregrines seem to take Cliff Swallows with regularity in Texas and New Mexico. One nest is directly over a large colony of Cliff Swallows, but admittedly, the falcons have raised young there in recent years.

Waterfowl and shorebirds along the Rio Grande and Rio Conchos may also be a hazard as they are known to contain many contaminants. There are two river eyries where young have never been seen, but a comparison of their productivity with the mountain eyries has not yet been carefully assessed. A full view of the extent of the Chihuahuan Desert peregrine population, its productivity, and food habits awaits a major field survey planned for the spring of 1975.

It is likely that the Chihuahuan Desert region, because of its ruggedness and remoteness, is a place where peregrines have escaped shooting. I believe, too, that the public is becoming generally less inclined toward shooting birds of prey. I regard falconry as a much overemphasized threat to raptors, at least in Texas, and have found among falconers some of the most valuable proponents of raptor conservation.

In conclusion, and to quote Roland Wauer, I would regard the Chihuahuan

Desert wilderness as one of the last strongholds of nesting peregrines in the continental United States. I think it important that whatever man does to change the Chihuahuan Desert, especially in the realm of agriculture, the welfare of the peregrine should be remembered, not only for the high aesthetic value of the species but because it is a valuable indicator, or perhaps it is a critical indicator, of the health and viability of the ecosystem.

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Summary of Avian Resources of the Chihuahuan Desert Region

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From the standpoint of its bird-life, the Chihuahuan Desert region cannot claim to be the richest, nor the most threatened, in Mexico or the United States. The title it still *can* claim is that of the least known region in spite of the fine work done by our panel of speakers in this symposium. Let us look at some of the reasons for this and try to maintain a balanced, general perspective.

The earliest explorations of North America for birds were made by Europeans. After the middle of the 19th century, North Americans took the lead. Both groups were particularly interested in the rich tropical and semi-tropical birds that were unlike those at home. They traveled by sea or by the few main roads and railroads in nearly all cases; an occasional explorer took up residence in the faunally rich coastal slopes. Veracruz, Oaxaca, and Sinaloa gained fame, and the peninsulas were explored.

But the Chihuahuan Desert held few attractions. Birds were few and unspectacular; generally, distances were great and transportation poor. Europeans felt the desert was far away and unrewarding. Americans wanted to get past it into richer fields as fast as possible. Only the methodical coverage of Salvin and Godman's collectors and later of Nelson and Goldman included this desert region.

Nor did they find much. To date, not one single species of bird has been found to be endemic to the Chihuahuan Desert region, and even endemic races or subspecies are very few. The closest approach to an endemic species is probably Worthen's Sparrow (*Spizella wortheni*) which is also found in Puebla locally.

What do we mean by "The Chihuahuan Desert Region"? This is no simple question. Drawing lines in nature is a thankless task. To the north and south, matters are fairly easy. Here in Texas and New Mexico, as the land rises northward, desert gives way to grassland and forest. Southward, the land becomes lower, in southern Zacatecas and northeastern Jalisco, and tropical vegetation comes in. To the west, the grasslands, woods, and forests of the great Sierra Madre Occidental border most of our region; in Arizona the land lowers westward, and the Sonoran Desert boasts a richer flora, notably of cacti. But to the

east and southeast arid lands stretch on, more or less, into Hidalgo, southwestern Tamaulipas, and Nuevo León. Gradually, where no mountains intervene, the vegetation becomes thicker, suggesting thorn-forest. All, or nearly all, of the characteristic species of Chihuahuan Desert birds reach northern Hidalgo.

Next to the desert itself, or what we call "desert" in America, grassland is the most abundantly represented vegetation type in our region. Such avifaunal richness as the North American grasslands possess, which is not great, is concentrated in summer far to the north of us. Most of the species reach our region, or its northern parts, in winter, but in the south our grasslands are pretty depauperate, even in winter.

Like any desert or semi-desert region, then, the faunal richness of the Chihuahuan Desert region depends on its special, isolated patches of more mesic habitat. These are of two kinds. First, there are mountains, such as the Chisos. Second, there are local springs, ponds, or intermittent water courses, or most exceptionally a real river like the Rio Grande. These oasis-like habitats are well known to American ornithologists. Local observers have watched some of them for years; in fact, there are permanent naturalists' headquarters in the Chiricahua and Chisos mountains, and an excellent book on the Big Bend area of Texas by Ro Wauer (1973). Certainly more work is needed in some areas; but even the most neglected of the higher United States ranges—the Animas Mountains—has been visited occasionally in recent years by Drs. Niles and Hubbard, in addition to the classic early explorations of Mearns and Goldman. Thus we have a fair knowledge of the birds of the northern and northeastern fringes of the Chihuahuan Desert region.

But what of the rest? South of the border, a very different situation prevails. One may travel past range after range of mountains, and arroyo after arroyo, in which no ornithologist has ever set foot. The few explored areas are lost in a sea of *Terra incognita*, ornithologically. And the results of the one long-range exploration, that of the Sierra del Nido, Chihuahua, remain unpublished as yet.

We should, therefore, bear in mind that many local populations—indeed the majority—of birds of the Chihuahuan Desert region remain to be studied. We may doubt that any new *species* of birds remains to be discovered in this area; but careful studies of adequate material, taken at the right time of year, would almost certainly show the existence of undescribed subspecies, whose distribution we cannot even guess. The more isolated and smaller a local population is, the better the chance of its developing distinctive characteristics. This means that there is a real danger of wiping out distinct subspecies before we can even guess their existence through overgrazing, spraying, woodcutting, and other uses and abuses of local spots of greenery.

A corollary to this danger is what I may perhaps call "taxonomic imbalance." Some wags claim that we ornithologists carve out new subspecies in order to avoid having too many specimens of the same bird! There is a grain of truth in this facetious charge, for no one can study material he cannot see. Since the specimens he does see are from the United States, our desert-region birds have

been generously subdivided into subspecies here, but not to the south. Yet, in some cases, their actual variation is the reverse; that is, they are relatively stable northward, yet vary greatly in central Mexico. The Red-eyed Towhee (*Pipilo erythrophthalmus*), including the so-called Collared Towhee ("P. ocai"), is a striking example of such a case. Another, currently under study by Dr. Hubbard, is the Rufous-crowned Sparrow (*Aimophila ruficeps*). Of the Horned Lark (*Eremophila alpestris*), long famous for its geographic variations in color, the whitest race, the reddest, and one of the blackest all occur in or near the Chihuahuan Desert region. What these cases all have in common is that careful studies have unearthed new races in central and northern Mexico in the past 25 years, while pointing to the probability that earlier-described races from the southwestern United States are not valid. This is what I mean by "taxonomic imbalance," whose extent we cannot gauge without further exploration.

Unless this taxonomic imbalance is corrected—and this means carefully planned, extensive explorations—we will not even know whether we are in *danger* of losing "biological diversity," as Dr. Stebbins puts it. Let us not forget that nature has labored for millennia to produce this diversity, this nice adjustment of life to environment. Wise men tell us that the time to protect an animal or plant is before it becomes rare.

To summarize, then, the Chihuahuan Desert region is a large one, but not especially rich in birds, as far as yet known. Only along parts of its fringes is it properly explored. New, and occasionally striking, subspecies continue to be found in Mexican areas in and near the region, which need well-planned study. Such a study is unlikely to be undertaken, however, by private museums or scientists because of the relatively limited number of species here, except for occasional laudable sallies like that reported by Hubbard and Crossin (1974).

We have no choice at present but to extrapolate ideas of the region's avifauna from those ecological and population studies which *have* been made. In so doing, however, let us strive to set these ideas in perspective and give our conclusions with a humility befitting our limited knowledge as of 1974, and with proper gratitude to those dedicated scientists who have enabled us to form any idea at all of the region's bird-life.

As a confirmed pessimist, I fear we have certain other factors bearing on conservation of birds. Bell's Vireos (*Vireo bellii*) may be safe physically, but probably need help from over-abundant cowbirds, which Hargrave watched wipe out his vireos at Benson, Arizona. Persistent pesticides are still used in our region and are used in quantity when people become alarmed, such as in encephalitis epidemics. The ecological danger of such use should be clear to informed persons by now, and is pointed out by Hunt in this symposium.

But the Earth's main problem is surely people pollution, compounded by ever-increasing travel. The pressure on birds is less direct than that on certain reptiles such as horned lizards and tortoises; it comes through removal of succulents and other vegetation and consequent depauperization of the flora. As Dr. Webster points out in this symposium, plant diversity is probably important to

birds. I would like to second his suggestion that a large area of southern Chihuahuan Desert be fenced off while it is still intact, and also that this be done in the various other plant associations as well. Dr. Raitt points out the need of extensive grassland preservation. As Dr. Barlow would point out, these fenced plots need protection against *both* man and his livestock and domestic animals.

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Panel Discussion
and
Keynote Addresses

Panel Discussion

Ro Wauer:—When Dave Riskind and I first began to establish a format for this symposium, it became very clear to us that a series of papers on a number of disciplines would be just that, unless the significant resources discussed could be further explored. And so we devised a panel of a number of disciplines that could dig into things, interact with an audience, and come up with some firm ideas about resource protection.

I could not think of a more appropriate individual to moderate this panel than Myron Sutton. He has been with the National Park Service for years. An Arizonan, he has worked at the Grand Canyon, Carlsbad, Montezuma Well, Walnut Canyon, and the National Capital Parks in Washington, D.C. Besides being a ranger and a naturalist in the Park Service, he has been involved in museum planning. He was an instructor at the Albright Training Center, Regional Interpreter with the Northeast Region, a long-range planner, and for the last 10 years he has been with NPS International Affairs. His new book, *Wilderness Areas of North America*, has just been released, and I quote from the book jacket:

Ann and Myron Sutton have studied hundreds of wilderness areas in nearly forty countries to update their knowledge of this continent. Ann, a geologist and native Illinoisan, and Myron, a botanist and native Arizonan, traveled more than 40,000 miles throughout North America. They hiked the major mountain ranges, penetrated remote forests, canoed on northern rivers, and dived along tropical reefs. Fluent in Spanish, they explored Mexico and Central America wild places with administrators, wardens, and biologists. Together, Dr. and Mrs. Sutton have written twenty books on the wild outdoors, including the Appalachian Trail, the American West, The Wilderness World of the Grand Canyon, The Life of the Desert, The Secret Places, The Wild Places in Yellowstone, and A Century of the Wilderness Ideas.

There is no better moderator than Myron.

Myron Sutton:—Thank you very much, Ro. After what we've heard in the last few days, I think someone should begin writing a book on the Chihuahuan Desert. It's a marvelous subject, and the information so nobly brought forward here certainly ought to be made available to other scientists around the world and to the general public as well.

One of the reasons for having this panel seems to be to determine just how long the Chihuahuan Desert will live. It's distressing to hear the number of springs that have dried and the number of species that are nearing extinction. Yet I think we can still be optimistic; the profound scientific information available seems to be sufficient to permit local, state, and Federal land-managing agencies and plan-

ning agencies to apply their skills to preserving what is left on both sides of the border.

During the last several days a number of comments have led into what this panel is all about. We heard about the hundred plant species that are endangered, as well as about endangered beauty. The latter certainly isn't scientific, but you know as well as I how many millions of people come to places like this for their sheer beauty. Dr. Hubbs and his colleagues talked about the serious problem of survival of fish fauna. One of Dr. Hubbs' remarks would do well as a theme for this panel, his observation that maintaining species by means of zoological parks is insufficient, that we ought also to maintain the natural environments and the natural habitats of these species. And as these distinguished gentlemen here will be able to demonstrate a little later on, that is not as easy as it sounds.

Dr. Morafka said that we, as biologists, are concerned with conservation—perhaps more profoundly concerned than any other discipline and any other group with the discipline. Dr. Conant described the loss of gallery forests due to the construction of dams, and the loss of frogs and turtles due to the introduction of exotic species. Dr. Scudday talked this morning on the loss of springs. To lose these parts of the ecosystem is to lose half a desert. So this afternoon we are going to discuss ways to preserve some of these priceless treasures that remain. As scientists, we sometimes tend to overlook how fabulous these things are. We've had photographers and people come into our national parks and other areas, and where we may see a herd of 25 deer scampering across the road and pay no attention to it, these other people go wild about that type of thing. So, sometimes it seems we are too close to realize what great treasures we are dealing with. And so preserving them, setting them aside, is something that must claim our attention, because internationally, as well as nationally, the philosophy is: You can hardly administer an area set aside for public benefit until you know what is in it. Any superintendent in any national park or forest or wildlife refuge is ill-prepared to make a decision until he knows on a scientific basis whether that decision will be right or which decisions to make. So, it is in that context that we proceed on the basis of the foundation of science to the preservation of areas.

This afternoon, the members of this distinguished panel invite you to question them.

I'm going to introduce them after which each of them will speak for 10 minutes or so on his particular discipline, his reactions to what has transpired, and about what he has heard this week. Put your thinking caps on because this is a participatory panel rather than one with talking limited to its own members. Your written questions will be brought up here for discussion by the panel, and we'll have an interchange. We would like some recommendations at the conclusion of this meeting. The procedure will be informal; the members of this panel will jot down recommendations of their own—ideas that have occurred to them and that they are uniquely qualified to make. But you, too, are qualified. As they speak, as you think, we would appreciate it if you would jot down *your* ideas for recommendations. We will collect the suggestions and then stay after class today and

go over them, distill them, and rule out the duplicates. This evening our distinguished banquet speakers will have an opportunity to comment on those recommendations. So, those recommendations will be transmitted back to you at the banquet and will become a part of the proceedings.

Now, let me go immediately to my left and introduce Lic. Horacio Gallegos Gamiochipi. Because so much of the Chihuahuan Desert is in Mexico, we probably have overbalanced this panel with too many Americans and not enough Mexicans. There may be reasons for that; the Chihuahuan Desert is a long way from Mexico City, and understandably, Mexican priorities, to a large degree, are where the population is. But we are gratified that they sent a man who equals at least a dozen of his colleagues and his countrymen. We have known very few people in international affairs who have been so dynamic, so successful in saving what is left in their country.

Horacio came to us about 2 years ago on a commission by his President, Luis Escheveria of Mexico, to learn as much as he could about the national parks of the United States. He went all over this country, specializing in the desert Southwest. He took thousands of photographs, gathered thousands of pages of United States policy, took it back to Mexico and distilled it, organized it, and put forward the proposal that a commission be established that would lead to preservation of parks and natural areas.

In the Ministry of Agriculture there is a fine parks division; and we, of course, have worked with them steadily over the years. Horacio decided he would create a commission that ultimately was titled CONOPAN, which means Comision Nacionales de Obras en Parques Naturales, or a National Commission for Public Works in Natural Parks, including developments, museums, and trails. The significant thing is that the commission has as its members many other departments of the government, such as the Ministry of Agriculture where national parks are, and so on. He will elucidate all this.

Farther on my left is Dr. Robert Linn of the National Park Service. Bob is a native of Ohio and got his degree at Kent State University and at Duke University with a Ph.D. major in plant ecology and a minor in forestry. I first met him in Isle Royale National Park where he was a ranger and later a naturalist. It was a tremendous inspiration to me to see what he did up there because that wilderness out in the middle of Lake Superior is very difficult for people to understand. It's a pleasant place, but it's one of those sites that needs to be interpreted. He not only did this from a scientific background, he also organized his own press, published his own nature trail booklets and informational pamphlets, and became a one-man bellringer for Isle Royale National Park.

As a result, the populace of this country has a much greater appreciation of Isle Royale. Bob went on to become Research Botanist in Washington and then Chief Scientist for the National Park Service, a post he filled from 1967 to 1973. All in all, he was in Washington for about 10 years. At present, he is a Senior Scientist assigned to Michigan Technological University at Houghton, Michigan, where he is a professor of biological science. But he still has his hands in many other

things, such as being a member of the Commission on Ecology of the International Union for the Conservation of Nature (IUCN). He's a Fellow of the American Association of the Advancement of Science, he received the Interior Department Distinguished Service Award in 1971, and he belongs to the Ecological Society, the Wilderness Society, and the American Bryological and Lichenological Society. So, for the utmost in science in our own national parks, here is the person in whom you can have a great deal of confidence and to whom you can direct your inquiries.

To my right again is Frank Blair. He doesn't really need much introduction. And yet it gives me a great deal of pleasure to recite again the accomplishments of a single individual who has advanced so tremendously the cause of science in this and other parts of the country. Frank got his degrees at the University of Tulsa, the University of Florida, and the University of Michigan. He has been at the University of Texas at Austin since 1946 where he is professor of zoology and director of the Brackenridge Field Laboratory.

Frank is a past President of the American Institute of Biological Sciences, past President of the Ecological Society of America, of the Society for the Study of Evolution, of the Southwestern Association of Naturalists, and of the Texas Herpetological Society. He is also a past Chairman of the United States National Committee for the International Biological Program, the IBP. And I've asked him this afternoon if he will share with us some thoughts on what the IBP is and what his role in it has been. He's a past Vice-President of the National Committee of the International Committee of the IBP, as well. Presently, he is Director of the Origin and Structure of Ecosystems Research Program, being accomplished by the United States section of the IBP. He is a series editor for publications of the United States contributions to the IBP and a member of the National Academy of Sciences and National Research Council International Environmental Programs Commission.

To Frank's right is Robert McIntosh, Assistant Regional Director of the Interior Department's Bureau of Outdoor Recreation. That agency serves as the federal focal point to assure prompt, effective, and coordinated action at all levels of government, city, state, and federal, for coordinating, planning, and financing public outdoor recreation. Bob's experience is in regional land use planning. He has been with the Bureau since 1967, involved in major efforts to plan new areas. These include the Alagash Riverway in Maine, the Tinicum Wildlife Refuge in Pennsylvania, the Gateway National Recreation Area in New York City, the Delaware Wild and Scenic River Study in New York and Pennsylvania. In 1970, he was granted a year's leave of absence from the Bureau of Outdoor Recreation to observe land use conditions in industrialized nations around the world, so he brings an international background to this meeting. Currently, he is directing the Bureau's Wild and Scenic River Study on the Rio Grande; and his office is in Albuquerque, New Mexico.

To my far right is John Henneberger, Associate Regional Director, Professional Services, of the National Park Service office in Santa Fe, New Mexico.

John comes to us with a considerable amount of experience in wild and wilderness territory. He was a Ranger at Crater Lake National Park, Grand Teton National Park, Joshua Tree National Monument, Yosemite National Park, and Olympic National Park. So, he knows the West from top to bottom. He also has been Superintendent of Scotts Bluff National Monument in Nebraska, a planner with the Western Regional Office, and Assistant Superintendent of Hawaii Volcanoes National Park. So, he knows the volcanic deserts as well as the Joshua Tree one.

He has worked in the Western Service Center as a Wilderness Coordinator and has appeared before Congressional Hearings. Perhaps one of his greatest contributions to society in general is putting forward the very complex projects of preserving some of the wilderness we still have in this country. It isn't as easy as it sounds. To John we owe a lasting vote of tribute for what he has done to save the beauty of this country. He is a graduate of the University of New Hampshire and Colorado State University; in fact, his thesis at that time was *Wilderness in the United States*.

Before we go into our presentations, I would like to set forth one pattern. This panel on the conservation of desert areas is part of a worldwide effort. Ten years ago, other countries in the world could not have cared less about the preservation of desert areas because they looked at desert areas as places that were relatively unused, unoccupied wastelands—certainly unfit and unworthy of attention. I was never able to understand how this attitude survived so long. But it has been fantastic how, in the last dozen years or so, countries around the world have galvanized to preserve not just beautiful tropical jungles and wildlife habitats in mountainous areas and spectacular scenery and so on, but have taken up preservation of deserts. Costa Rica is an example, with Santa Rosa National Park established to cover the dry Pacific Coast lowland forest on the western side of that country. Chile has three national parks already established or in the process of being established north of Santiago, verging on its magnificent desert. Ecuador has set aside almost the entire archipelago of the Galapagos Islands which has a number of fantastic desert ecosystems now being preserved by the government of Ecuador. In Argentina, the province of Chabu in Patagonia has established a geological reserve which looks just like our South Dakota Badlands. But it has thousands and thousands of square kilometers of petrified wood, and they are taking care of it very carefully.

In the Canary Islands of Spain there are three national parks. One of them does not have a single tree and little more than lichens, but it is a fascinating volcanic area. In the peninsula of Spain itself, Coto Dona Ana is an estuary at the mouth of the Savo River which is a marsh and tidal basin in a semi-arid condition. In Turkey and Jordan, at the request of those governments, we have had teams master-planning desert areas, for example, ancient Troy. This is not just a Troy, it's *the* Troy—the capital of the Hittite Empire. We have helped them prepare 11 master plans for the preservation of desert areas in Turkey, and the same in Jordan. The Israeli Government has a Natural Resources Department. I have

seen their magnificent publications on the flora of their desert. They're doing a fine job. And I need not tell you what is happening with the thousands and thousands of square miles of plains and dry forests and savannahs that are being preserved in many of the countries of Africa—some of the largest national parks in the world. Even in Alaska we are preserving some sand dune areas, some sand valleys, some colder deserts which are very significant in the makeup of that state's ecosystems.

In Mexico we are collaborating, as Sr. Gallegos will tell us, with various aspects of research in desert ecosystems. Four principal problems prevail in all of these desert areas. One is the exotic species, such as the 25,000 goats on James Island in the Galapagos Islands. You can imagine what the goats, pigs, rats, and wild donkeys do to the native species on those islands. Goats in Hawaii, goats in New Zealand—we have all those problems. A second problem is poaching. In Africa and the Middle East, particularly, poaching still is a problem. Human population explosions as well as animal population explosions still are a problem in a number of desert areas around the world.

A third problem is low priority or public indifference. We in the United States enjoy with pride the conservation organizations that are working to preserve some of these areas, but that does not happen everywhere in the world. So we are collaborating with many other countries in efforts to preserve desert and other types of areas.

That sets the background and tells us that we are in a worldwide effort here. Now I would like to turn the meeting over to this distinguished panel and start with their comments on their particular fields of interest.

First, Horacio, we would appreciate your comments on the status of conservation in desert work in the Republic of Mexico.

Horacio Gallegos:—Thank you, Mr. Sutton. Distinguished persons who are here, my English is not too good, but I want to try to speak in English; so, if you do not understand what I say, make a note and I will translate later. This Commission of Public Works in Natural Areas was born in the federal government of Mexico about a year and a half ago because we think there are so many areas that the Mexican Government or the people of Mexico must preserve and protect. We will have enough money in the Mexican government to buy such lands and pay to protect them. So, the difference between national parks and natural parks in Mexico is that we have not bought the land. We just left the land in the possession of the owners, but we make an agreement with them to protect the land and we make them the owners of the service for that reason.

In that way we are increasing our protection of our natural areas from 1½ million acres to 15 million new acres of natural area preserves in only one and a half years. This means a lot of work, no holidays for the staff, no Sundays, no nothing—only work. We are very proud of this staff working very hard. We are working in underwater parks to preserve the coral reef and the flora and the fauna of Costa Cozumel Island and Vera Cruz Reef, and the Acapulco Reef and the peninsula of Baja California. We have the cooperation of the Japanese under-

water parks personnel who come to Mexico and work with us in these studies.

We are trying to protect a lot of the seashores in Mexico to keep the beauty of them because in some—you have heard of Acapulco—the poor can not enjoy the beauty of the seashore because the Marriott, Western, and Hilton hotels are on the shores. But there still is time to preserve beautiful seashores, and we are selecting the most beautiful areas and protecting them for the people of Mexico.

In the cultural areas, there is another agency in the Mexican Government to protect the archeological sites, but they do not have enough money to develop and interpret the areas. They spend a lot of money to rediscover and protect the area—I mean take the dust and the earth from the pyramids—but they do not care about the visitors. We are in a big program to try to make the best interpretation in our cultural areas because we are trying to make the Mexican people proud of their heritage and their backgrounds. Two thousand years ago, we had a beautiful culture there—the Mayan, the Toltec, the Olmec—but now the Mexicans going to the pyramids only see stones. We want to interpret them to make the people feel proud of their background and then try to work like these ancient people to make the best country of Mexico.

We are working in three different deserts right now. With the help and collaboration of the University of Arizona and the University of California, we have been working in the desert of Baja California, which has one of the most beautiful desert flora I have ever seen.

But this unique flora in the park of Baja California has a big enemy right now—the tourists who come across the new highway, crossing the Baja California peninsula. We try to protect and interpret most of the desert there.

In the Pinacate area, another desert, we have been working almost 2 years, with staff of the National Park Service and the University of Arizona, to try to make a master plan for this park. It is unique, with beautiful craters of volcanic and geologic importance. We are working hard to declare it protected by the end of this year. That is why they announced to me a few minutes ago that National Park Service people have accepted an invitation to work with our staff in the Pinacate–Sonoran Desert Park. We are thinking of a common administration or International Park. But this will come later.

First, we need to make a master plan. In the International Park of the Rio Bravo south of Big Bend, and in Big Bend National Park itself, we are working, but not too hard, because we are waiting for the agreement of the two countries to cooperate in the preservation of such areas. I think, with the collaboration of Dr. Villa and the Instituto de Biología of the University of Mexico, I can increase my staff and send an expert to this area to work in collaboration with the people who want to join with our staff in the Mexican area. I think we have a promise—we chatted, Dr. Villa and I, last night—of the nice support of the university staff and my staff in working together in the Mexican areas south of Big Bend.

We are working southwest of the Sonoran Desert because I have instructions by my Secretary of State to develop a few parks on the new highway from Chihuahua to Sinaloa. There is a highway that crosses over the Cañon de Cobre

in Chihuahua, so I need to protect several areas along the highway. But they are very interested in protecting some part of the Chihuahuan desert. As you can see, we have so much work that we want to split it in ten pieces in order to work in all the areas that are not damaged or very quickly damaged. We are trying to do it as fast as we can because it is our duty; and we are trying to learn something—we have accepted and are very pleased with the studies you are making in our areas, and will combine them with studies by Mexican teams from the university or from the Agriculture Department so that we go faster. That way we can realize our ideas and our hopes. Thank you.

Myron Sutton:—Thank you, Horacio. We will now proceed to Dr. Blair.

Frank Blair:—I will make an effort to put together my own reactions to the discussions in the last 2½ days, try to make a few generalizations, and end with two recommendations that I would like to suggest in principle at least. First, I would like to direct my comments to the basic scientific value of the Chihuahuan Desert, and second, to the equally if not more important question of man's impact on this desert and what it may mean for the future of this arid land ecosystem.

Looking first to the scientific values of the desert, I think that the presentations we have heard have given an excellent overview of our present state of ecological, taxonomic, and biological knowledge of this desert. I know the number of workers is very impressive. I thought I was fairly cognizant of the work going on in this desert, but I will be frank to say I learned quite a lot here about who is doing what in this desert area. However, I am also impressed with how precious little we really know about the dynamics of ecological adaptation and of evolution in this desert; and I am also impressed by the enormous potential offered by this desert for elucidating these fundamental biological phenomena.

I think two main characteristics of this desert system have emerged here in the few days we have been meeting. I would like to emphasize these. One is the dynamic nature of the desert ecosystems in terms of their responses to climatic change, the movement about of various subsystems as the climate has changed through the Pleistocene, through the Holocene so that we are looking at a very lively, dynamic system. And it should be possible to appreciate, perhaps in a way that we could do in no other ecosystem, the operation of ecological and evolutionary processes.

The second, very obvious characteristic of this system in protecting the Chihuahuan Desert as a whole, is the enormous diversity of subsystems (less than ecosystems) that one encounters in this desert. In recent years I have been more involved in the Sonoran Desert and the Argentine Desert than I have in the Chihuahuan Desert, although I did start my desert experience right here in this part of Texas. By comparison, I am impressed with the enormous diversity present in this desert. Consequently, I feel that the Chihuahuan Desert comprises a really priceless natural laboratory—I think the words were used earlier today—in which natural ecological and evolutionary experiments have occurred through prehistoric and historic time and are still occurring. It is a natural laboratory that has been underexploited in terms of adding to our store of knowledge. I would

just mention two or three examples of what I mean. The aquatic habitats of El Bolson de Cuatro Ciénegas hold a record of some 70 million years of evolution and, as Dr. Minckley pointed out in his discussions, they also provide a present-day situation in which it is possible to follow evolution occurring in the cichlid fishes in that particular Bolson.

Another thing that impressed me as the discussions went on, particularly as the botanists showed the colored slides of the Chihuahuan Desert, is the opportunity to get at one of the most difficult kinds of evolutionary evidence—the evidence pertinent to rates of adaptive evolution. In my early career, one of the high points in my experience in the Chihuahuan Desert was in the Tularosa Basin of New Mexico where we were working on the problems of color adaptation of rodents to the soil. I must say I was amazed at the number of what we call white sands areas, gypsum sand dunes, the enormous number of these that our botanical friends have uncovered in the Chihuahuan Desert. Now, if we can date the age of these remarkable white areas and if, as no one has really done, we can measure some degree of adaptation of the terrestrial organisms and their color to these, we probably can get a better measure of rates of adaptation, rates of evolution than we have for almost any organisms.

And third, one of the really interesting scientific questions is the age of the deserts. I think those of you who were here for our opening session will recognize that there is anything but agreement on the age of the Chihuahuan or Sonoran deserts. I am personally involved in a program in which we are looking at the multi-deserts of Argentina and the Sonoran Desert; we still are a long way from an answer. But I think that scientific investigations here in the Chihuahuan Desert certainly will add to this knowledge. There certainly were some interesting contributions in the course of our discussions here.

Summing up, the Chihuahuan Desert merits the best treatment we can give it on purely scientific grounds—what it can contribute to our basic scientific knowledge.

Turning to the second set of ideas, just a few words about man's impact on the desert and the possible future of the desert. At the present time, the deserts of the world, the semi-arid and arid regions of the world are coming under increased pressure. These really are two major ecological formations that today are being threatened by the population explosion, by the need to find more living room, more places to produce resources that are required for this growing population; these are the tropical rain forests and the arid lands. The arid lands are coming under pressure everywhere as Myron Sutton has pointed out. It occurred to me that 3 weeks from today I will be on an airplane heading for a meeting in Mendoza, Argentina, along with the Director of our Desert Biome Program in the United States, to participate in a meeting something like this organized by the Argentinians. The major difference is that there will be more emphasis on development, on the ecological background, the limitations of the arid lands for development as their populations grow. This sort of pressure on the arid lands is occurring throughout the world. I would like to make a point that perhaps the

Chihuahuan Desert has suffered much less disastrous impact of man's activities than many of our global ecosystems. There has been significant impact as we have seen in the discussions here, but until recently the Chihuahuan Desert survived fairly well. My first experience in this desert was in 1937, in the Davis Mountains and the surrounding desert. The Big Bend National Park was being developed with a CCC crew. Going back through Marfa 10 years later, I saw no difference other than the dog that was sleeping in front of the barber shop had moved across the street.

But the situation is changing today as we heard from Dr. Scudday this morning. Water resources have been exploited with disastrous results. One of the real impacts on this desert is the promotion of so-called "ranchettes," where people are sold small parcels of desert land often without water, that will support no one. The result is disastrous impact on the desert. We are seeing real pressure on the desert today; basically it is a matter of short-term gains and very little consideration for the future. I heard a really terrifying idea this morning from Bob Burleson. He told me that sheep probably were going to be brought back into some areas of the state of Texas. Sheep have been phased out over the years. I was told yesterday that Jeff Davis County, for example, has virtually no sheep left in it, but now, with the high cost of feed, the trend apparently is back to sheep farming because the sheep, as long as they can find anything to eat, do not have to be fed the expensive food cattle demand. These are the kinds of things that are really disturbing when we think about actions with no planning.

I think we still have time to develop the scientific expertise to accommodate the Chihuahuan Desert's demands, developing needs within the ecological constraints offered by the desert without totally destroying it. There was one suggestion made by my colleague Tom Mabry concerning the possible source of many kinds of chemical compounds in *Larrea*, the creosotebush. As petrochemicals come in shorter supply, it may be a godsend to have this desert plant that is manufacturing hundreds of kinds of chemicals that may be useful to man. So, we may be doing creosotebush agriculture in the desert instead of trying to raise cotton by trying to find water for irrigation.

I would like to stress again and again the need for innovation in these marginal systems. I have been impressed traveling in the Chilean deserts by the pricklypear cactus agriculture that is practiced in areas with 7 or 8 inches of rainfall annually. This is a crop that is adapted to that particular climate. It is going to produce a crop come what may. We have never looked at these arid and semi-arid land organisms to see if they are useful to man as a crop that can be adapted to the environment rather than trying to find enough water to raise something like cotton that requires an enormous amount of water through irrigation agriculture in the desert. This point was beautifully made this morning by Dr. Scudday.

It is appropriate to mention here the International Biological Program and what this can mean for those concerned with research on the environment. As many of you know, this is an international program that has officially ended after 7 years

of research activity involving some 58 countries. Basically, what this program has done is set up a pattern of international communication and cooperation among scientists interested in the environment. The name is a misnomer. It is not an international biological program, it is an international *ecological* program. It has set the pattern for international cooperation at the nongovernmental level, and I don't think we need to tell any bureaucrat here that there are some advantages to working at the nongovernmental level as well as some disadvantages. This was the first real international science effort working from scientist to scientist; it has set a pattern for what we call integrated multidisciplinary research—team research on major environmental problems.

Under this program in the United States two efforts are pertinent to our discussion here. One has been the so-called Desert Biome Study, which is the integrated research on deserts. I am afraid I must admit that the emphasis has been on the Sonoran Desert and the Great Basin Desert, rather than on the Chihuahuan, although as you have heard from some persons like Dr. Raitt, there has been research in the Chihuahuan Desert itself. This effort is continuing and funded for 2 more years at least.

The other effort is what we have called the Desert Scrub Program. Under the Origin and Structure of Ecosystems Studies, which is a cooperative program with Argentine scientists, there are comparisons of the Argentine multi-desert with the North American deserts. The Sonoran Desert is its nearest counterpart, although there are similarities also with the Chihuahuan Desert. I think it will be a sad day if we are not able to build on this successful effort to cooperate internationally in approaching the big problems of understanding the environment and relating environmental understanding to resource development.

Finally, in implementing these two lines of thought, first about the scientific significance of this desert, and second, about the need of understanding the ecological limitations of this desert in anticipation of population pressures on it, I would like to offer two draft recommendations.

The first is that a binational committee of scientists be appointed by the appropriate governmental agencies of Mexico and the United States to identify areas of great biological significance in the Chihuahuan Desert that should be established as protected biological reserves. This committee should (1) set priorities for establishment of these areas based on their scientific significance and on their degree of danger of destruction; (2) funds for its work should be provided, and (3) it should report back to the sponsoring agencies within 2 years. This is one recommendation dealing with the essential need for preservation of certain unique and biologically significant areas. These are the kinds of things, with which the World Heritage Trust for the United Nations is concerned.

Second, I recommend that appropriate governmental and nongovernmental bodies of Mexico and the United States explore possibilities and mechanisms for a binational research program on desert ecosystems of North America along the lines of the present desert biome and desert scrub programs of the United States component of the IBP.

Myron Sutton: Thank you, Frank. With permission of the panel, I would like to insert as appropriate right here the information about the newest international project—the establishment of biosphere reserves. This is under the Man and Biosphere Program of UNESCO. Let me suggest that if you do not know about the Biosphere Reserve Program, you should find out about it as soon as possible because its force and vigor is sweeping the international scene. The best source of information about this is the Environmental Section of the Department of State, Washington, D.C., which is handling the United States recommendations for biosphere reserves. I will just say that a biosphere reserve is described as representative of a biome or a biome subdivision in which it occurs. The area may contain natural ecosystems that are relatively undisturbed by man, or ecosystems that have been modified by man, or it may contain both modified and natural ecosystems.

There are other categories and several purposes. One major purpose is to conserve genetic diversity through long-term protection of sufficient natural ecosystems so that a significant proportion of the earth's plant and animal species can continue to exist and evolve surrounded by and in harmony with man's changing civilization. And if I am not mistaken (I was out of the country while a meeting was held on this in Washington), the Great Smoky Mountains were to be proposed as the United State's first biosphere reserve because they are tremendous in genetic diversity and relatively well-preserved. It seems to me, this program has profound significance to preservation of parts of this Chihuahuan Desert. Next, Dr. Linn.

Robert Linn:—Thank you, Myron. You may wonder why I am here and sometimes I wonder myself, being from the south shore of Lake Superior. If I have any expertise at all, I expect that it is in the realm of politics that I escaped from about a year ago. From those wars and battles of 10 years in Washington, I have accumulated a few scars that probably will be with me the rest of my life. Perhaps I could explain some of these so that others may be saved from such fates. In the few hours of embarrassment after I finish I can be off back to El Paso and a plane and get back to my north woods home and not have to take any responsibility for what I say here today. So, I feel fairly free to say what I think after having sat through almost every paper that was given.

It strikes me that the big problem today, touched upon already by this panel, is the rising human population of the earth, the scarcity of food and water, and the shortage of energy. It seems to me that even the Chihuahuan Desert region cannot long escape the impacts of those facts.

One of the things that seems to have happened in the past 10 years is that whenever a unique natural, wild ecosystem was about to be ravaged by building a dam, creating an irrigation project, or digging on open-pit mine, the biologists and the conservationists could call foul but not, in addition to that, suggest what might be done. The day is rapidly approaching when biologists and conservationists dare not cry foul at every impingement upon the natural scene without at the same time bending their backs very hard to recommend positive things that

people on planet Earth can do to preserve those unique natural, wild places that we hold so dear. I do not know how you go about doing this, but for a long time we have been talking about regional plans and most of the time regional plans get entangled with Federal Government programs and local communities and people are very suspicious of Federal Government programs, at least in the United States—I do not know about Mexico.

This makes it very difficult to bring about a plan that will receive the majority of the people's blessing and that will work. But, it seems to me that the agony and the effort is going to have to be endured, otherwise I can see all kinds of things coming down the road to annoy you in many ways.

For example, in the conversion of vegetable protein to animal protein, about 80 to 90% of vegetable protein is lost. Now, that is a huge waste of protein in a protein-starved world. I do not know how long we are going to have nice, fat juicy beefsteaks on our tables—I cannot afford them myself anymore—without the rest of the world rising up and saying, "Look! You're creating a terrible waste." I don't know in what form that look is going to resolve itself, but when it does resolve itself what is it going to mean to the impact on marginal grasslands that may be present. For example, in the Chihuahuan Desert ranching is now going on and it may intensify. I do not know, but I think that probably you ought to find out.

In the realm of energy, I cannot think of many finer places than the Southwest of the United States; I would go to the arid lands of North America to capture solar radiation and send it on its way into a machine making electricity of some kind. I have no idea how that is done or how it will be done in the future, and I have no idea how much electricity one percent of the solar radiation falling on the arid lands of the Southwest would make, but I'll bet it's a lot. The time is coming when someone will try to do this and we had best keep up with the technology that is developing along these lines so that, when the time comes, there are no surprises. Whenever one is converting one form of energy into another, in the past at least, water has usually been involved in some way. I guess I would just say, "Let us beware."

How do you go about making a plan? As I said before, I do not know. But meetings of this kind could be the focal point of themes that would begin to develop the basis needed for making such a plan. After all, here are the experts in biota, and you could expand it to other things—the geology and the soils, etc., of the Chihuahuan Desert. Here is where you get the basic information for making a regional plan.

I have been to meetings of a regional nature before, and some of them work and some of them do not. For example, there is a Lake Superior Biological Conference that meets once a year and has for the past 11 years, and it works beautifully. It's much smaller than this—we are talking about a much smaller area. On the other hand, some years ago I was instrumental in the creation of such a symposium in south Florida when all the ruckus was going on about the shortage of water in Everglades National Park. From one source I would hear one set of facts

and from another source I would hear a conflicting set of facts and from another source I would hear yet another set of conflicting facts. And I said, "Well, why not bring all of these people together and let's talk about it." And we did that in a room about one-tenth the size of this one the first year. Finally, in about 5 or 6 years, it got overwhelmingly large in a room about twice this size, and it died. I do not know yet why it died. I think maybe it got too big. But there are other things in south Florida that may have been instrumental in this too, such as bitterness and divisiveness and people with their own special interests and a lack of love among the people that were involved. But I think that even though there are cultural, political, and social differences of great magnitude among the people that it would take to make a plan for the wise use and management of the Chihuahuan Desert, it would be well worth the effort. With great intellectual honesty, forthrightness, and fact-facing mixed with compassion, it probably could be done.

Myron Sutton:—Thank you, Bob. Mr. McIntosh.

Robert McIntosh:—Thank you, Mr. Sutton. I would like to start by making the audience aware of one thing. I notice from the vantage point of sitting up here that there are more people sitting right of center than left, and the individuals on the right of center are asking more questions than those on the left, so you liberals beware.

I would like to address my comments today basically to a system. That system is a political system with a political process. The subject area I will use as an example is Wild and Scenic River Study of the lower canyons of the Rio Grande. Back in 1968, the Congress, through Public Law 9542, decided that henceforth it would be a national policy to preserve and protect those rivers that were outstandingly remarkable and that contained recreation, geologic, historical, cultural, fish and wildlife, etc., values. In doing so, it named some nine rivers, called the Instant Rivers, that were automatically incorporated into the system. These rivers by chance were those that, to a large extent, already were either in state or Federal ownership. Consequently, the instantaneous action is one of putting up a new sign rather than planning acquisition, and so on. Some 27 other rivers also were named to be studied for their potential inclusion into the system. The lower Rio Grande with its canyons was one of those rivers. Now, I want to point out that we have established one thing. We have a system, a system by which various resource areas that fall into the specific category can be identified and included. I know of no desert system. I know really of no biological system. But precedent was set just last week; Congress acted, the President signed, and we now have a Big Thicket Biological Preserve. So we have a prototype in that particular case, but we do not have the system there.

The Wild and Scenic Rivers Act defined the study area from the west boundary of Hudspeth County to the east boundary of Terrell County in Texas—it further enjoined the Secretary of the Interior not to proceed further until he had the assurance and the agreement of the government of Mexico to conduct the survey. From 1968 until 1972 discussions were underway through the Department of

State identifying the areas of involvement, the management problems, and so on, related to such an international study and the potential inclusion of an area within a Wild and Scenic River system. This work was carried out principally by the International Boundary and Water Commission, which is headquartered in El Paso, and when the dust had settled, it was agreed that the first phase of this study would originate at the Chihuahuan-Coahuila state line of Mexico, which is basically the point of Big Bend in Mariscal Canyon downstream to Amistad Reservoir.

It was at that point that three basic decisions or agreements were made between ourselves and the government of Mexico through the International Boundary and Water Commission. The first was that we would conduct unilateral studies; that is, the government of Mexico would address the problems, the potential land and river uses, within the study area on their side, and we would do likewise.

The second agreement was that once those studies are completed, through the Boundary Commission, the findings and recommendations of those two efforts would be compared and analyzed and the appropriate recommendations or agreements would be made between the commissions or the two sections of the commission—the United States and Mexican sections—and that further recommendations, if appropriate, would be made to their respective governments. In the case of the United States, that in essence is saying that the Commission would recommend certain actions to the Department of State in line with agreements with the Department of the Interior, eventually through the President and on to Congress.

At this point, as many of you know, we have concluded the study on the United States side. Last spring public meetings were held here, in Alpine, and in Austin, in which we surfaced the basic alternatives we had explored and the criteria we had evaluated the river against, and asked for comments and reactions. A pleasant surprise, not always the case in a situation like this, was the attendance at these public meetings. It was very good, and the comments and feedback we got at the meeting and through the mail were very beneficial in pulling together the package from which we will develop our final recommendations.

Basically, we have identified three major recommendations. First, let me say that criteria have been established for inclusion of river areas in the Wild and Scenic River System, and without going into a lot of detail as to what they are, I will say that the Rio Grande meets those criteria. Based on that, we developed three major alternatives for inclusion of the Rio Grande in the Wild and Scenic River Systems. In the report that will be available shortly (in bureaucratic terms this could mean an infinite time), the very complex alternatives are developed. I will try to sum them up as three major ones.

One is that the river from the eastern or downstream end of Big Bend National Park, basically starting at Black Gap Wildlife Management Area to the Terrell-Val Verde line, be included in the system and be managed by the state of Texas. The second is that the Rio Grande from Chihuahua-Coahuila state line or Big Bend National Park downstream to the Terrell-Val Verde line be included, with

the Federal Government administering those lands it already does within Big Bend National Park under the Wild and Scenic River concept, and the State assuming the management downstream from Big Bend. The third alternative is that the Federal Government, probably through the National Park Service, administer the Rio Grande Wild and Scenic River from and within Big Bend National Park downstream to the Terrell-Val Verde county line. The Black Gap Management Area would be accepted within the Wild and Scenic River System, either as State property with a Joint Management Agreement to be managed by the Federal government, or accepted by donation to the Federal Government from the state of Texas.

Those are the three basic alternatives that we are dealing with; and I am happy to announce that next week this package will be aired for the Secretary of the Interior in Washington. We will be driving hard at that point to develop the final recommendations that will eventually go in two different directions.

One direction that to me is most exciting, is to the Department of State, then to the International Boundary and Water Commission for formal transmission to the Mexican section of that Commission. We could then start discussion and have their feedback as to their planning to date, their ideas, their efforts, and what their international cooperation can be with respect to the management of a Wild and Scenic River-oriented program on the canyons of the Rio Grande.

Second is the obvious direction which all actions like this must take—transmittal through the administration, which means the Office of Management and Budget, the White House, and Congress. Our international efforts or discussions in this program have focused in two different directions, the formal channels (through the Department of State), and a second and very beneficial one to our efforts—the work that Sr. Gallegos and Myron Sutton have had underway for several years. We in the Bureau of Outdoor Recreation have benefitted in understanding the programs and concepts and the philosophies of the Mexican people. The Wild and Scenic River Study is the first of its kind that involves an international boundary, and, consequently, the skids are not greased for this action as far as moving it through the political process.

In the final analysis, the decisionmaker on the U.S. side will be the Congress. It is paramount that the public understand the responsibility that it has to itself to provide appropriate, unemotional, well-informed information to the elected representatives of Texas, as well as those across the country, so that the most appropriate and desirable decision is made. I can only point out the fact that to most people who are not native to this area (and probably many who *are*) the Big Bend country means cattle, the Big Thicket country means timber, and so on. The discussions of the last 2 days pointed out the major biological characteristics of this region that are in great danger of extinction through the influences of man in the area. If we are going to attempt to direct ourselves into preservation, better understanding and use of these areas, then we must direct ourselves into first, realizing the political systems in which we are working. Then we must dedicate our own efforts, our own expertise, and our own desires into making things happen. Thank you very much.

John Henneberger:—My input will be brief, and it is mainly in the field of utilization of all the data that has been presented during the last 3 days. How can we use all this natural science data in future planning efforts in the Chihuahuan Desert region to establish parks, nature preserves, refuges, or other preserve units? I have had some valuable discussions with many of you on what we can do in this area. One possibility which Bob talked about is to pattern some type of area after the Big Thicket National Biological Preserve—a Chihuahuan Desert National Biological Preserve. This has some wonderful possibilities.

First, let me recap briefly some of the planning efforts in the last 30-40 years. Much of this effort evolves around establishing an international park on the Mexican-American border. My recap covers mainly my own knowledge of the National Park Service area. Others on the panel have had input into this recap through their areas of knowledge. Since the mid-1930s there has been a series of efforts to establish an international park in the Big Bend region. While these efforts were directed mainly toward establishment of parks on both sides of the Rio Grande, there also have been investigations on the natural, historic, and archeologic resources of the region to establish foundations for delineation of park areas and for gathering basic knowledge.

Some of the earlier efforts sound surprisingly similar to those currently underway. The history of planning the Big Bend area reveals a repeated pattern of initial enthusiasm for a joint Mexican-American study, creation of a joint commission, some field work, and then very little implementation. A formal Mexican-American commission was established in 1936 to formulate policies and plans for the establishment and development of international parks, forest reserves, wildlife refuges along the international boundary with final recommendations of the joint commission to be submitted to both governments for consideration and approval.

The joint commission inspected the Sierra del Carmen, Maderas del Carmen range, and some of the adjacent villages in Mexico. At another meeting in El Paso, east and west boundaries of a proposed International Park at the international line were agreed upon. There were several scientific photographic expeditions to the Sierra del Carmen region to study the natural history during 1935 to 1938. The meetings were held in Mexico City. Then World War II intervened and nothing further was attempted until interest was revived in 1944-45. A Big Bend National Park was authorized by Congress in 1935 and was established in 1944 after considerable planning and study.

Other park and preserve areas were established in the United States in Arizona, New Mexico, and Texas. Some of these national park areas besides Big Bend Park, are Guadalupe Mountains National Park, which was recent; Carlsbad Caverns National Park, which was before this period; White Sands National Monument, and, if you extend the Chihuahuan Desert into eastern Arizona, Chiricahua National Monument. There are a number of State areas such as Black Gap Wildlife Management Area and Davis Mountains State Park. In New Mexico, the Valley of Fires State Park lies above Alamogordo. Some more parks are situated near El Paso and some National Wildlife Refuges lie along the Rio

Grande. So actually quite a lot of preserve units already are protecting the Chihuahuan Desert environment.

In the 10 years after 1945 there was much discussion and many meetings on both sides of the border on international park proposals; again, interest flagged. During this period and in the last 10 years, Big Bend National Park personnel and others—many have presented papers here today—have done investigatory work in the Maderas del Carmens, Sierra del Carmens, and other areas gathering natural history data of the region. We have heard the numerous presentations in the last 3 days. Then the Bureau of Outdoor Recreation began its Wild and Scenic River Study of the Rio Grande. Bob made a fine presentation of where we stand on that. We are nearing completion of our end of that study, as he said.

Interest in an international park in the section of the Chihuahuan Desert and the Sierra del Carmen, Coahuila, Mexico; and at Big Bend National Park, Texas, United States, again came to the floor in 1973. A series of preliminary planning at Big Bend last January between Mexican and American management, planning, and biological scientists on the establishment of a joint planning group from Mexico and the United States was talked about; they would (1) inventory and quantify the physical, biological, and cultural resources of the region, (2) identify broad objectives for protection of natural, physical, and cultural resources of an international park, and (3) locate a proposed boundary for an international park in the Chihuahuan Desert region. Similar discussions on the establishment of a joint planning group for an international park in the Sonoran Desert took place at another meeting that was going on at the same time.

Sr. Gallegos has mentioned that progress on the Sonoran Desert seems to be going faster than on the Chihuahuan. The planning group would work out of Big Bend National Park and acknowledged experts of the region were to be included in the planning group. The group would initiate its work upon concurrence by each government. To date, we are still in the discussion stage of this joint effort.

This symposium is a fine start on inventorying the physical and biological resources of the region. It will be extremely useful in planning efforts leading to an international park or a national park on the Mexican side if this is the only feasible course, and to the establishment of other parks, preserves, and refuges on a national, state, or local level. Many of the papers presented covered broad areas on both sides of the border. The inventory and distribution material on the biological resources of the Chihuahuan Desert region compiled here provides a natural resources basic inventory of a greater scope than is available or is used when we study and establish most of our national parks. There is a wealth of material here. It should be used and I hope we can do so. Often we do not use this type of material when Congress sets the boundaries. They are set for political reasons, for land ownership, and for reasons that have no real validity in preserving natural values.

Dr. Villa's presentation on the major game mammals and their habitats in the Chihuahuan Desert region shows graphically that there are still significant, relatively untouched natural areas below the international border, adjacent to or

near existing U.S. parks and game management and potential wild river areas. An excitement was generated in the last few days, as well as a wealth of data that we can draw upon in the preservation of natural values in the Chihuahuan Desert region.

Myron Sutton:—Thank you, John. And I am sure Horacio and John will be more than happy to take up any individual sites with you while we are all together. I think we had better proceed with questions from the floor now because the number of questions which have arrived precludes long answers; in fact, we may not be able to get to them all. If your questions are not covered, do not hesitate to come up and talk to the person to whom it was intended. Perhaps we can give those questions priority which can be answered by several members of the panel. John, I will turn it over to you.

John Henneberger:—The first question is from Bob Burleson to Sr. Gallegos. "If Sr. Gallegos can tell us, I would like to know the aims and intentions of the Mexican government on what developments are planned for Boquillas, Coahuila, across from Big Bend."

Horacio Gallegos:—We need to study the whole area of the Boquillas del Carmen, Mariscal, and Santa Elena and how it can best be integrated with the area of Sierra del Carmen. But as soon as we finish the inventory there, and the park planners of our staff can work on that project, we can tell you about this question you ask me now. Sorry, we cannot tell you exactly what we are trying to develop in this particular area.

Myron Sutton: Are there plans to build a paved road up the east side of the Sierra del Carmen from El Melon on the Muzquiz-Boquilla road to La Linda?

Horacio Gallegos:—Yes, we are intending to do that on the west of the Sierra del Carmen to Boquillas and on the east to La Linda. And there is another road coming from Manuel Benavidez, Chihuahua to Boquillas to integrate the road No. 2 coming from Tijuana.

Dave Riskind:—Do you have any idea what the timetable is for the development of these paved corridors through the Chihuahuan Desert region? How quickly is this type of development likely to take place?

Horacio Gallegos:—I think the first road is coming from Muzquiz to Boquillas, because it is already planned. The next road is to La Linda so that people can go the easy way to the Sierra del Carmen on the way to La Linda.

John Henneberger:—This is for Dave Riskind from Dr. Schmidtly. "I understand that exotic mammals have been introduced in the Trans-Pecos Texas. I would like to know if the Texas Parks and Wildlife Department is assessing the impact of these introductions on the native fauna, such as the pronghorn. Are there any regulations which govern the extent of these introductions?"

Dave Riskind:—I can answer this question to a certain degree. I work with the Parks Division of Parks and Wildlife, but as I understand it the Wildlife Division is not taking an active part in introducing exotic mammals anywhere in the State. However, private citizens are getting into the exotic game business in a rather heavy way, particularly in central Texas. It is difficult to find a piece of land

where these things have not been introduced. A certain number of exotics have been introduced in south Texas. I am not sure what has been introduced in the Trans-Pecos. The general category of these things as labeled by the Parks and Wildlife Department is "textotics," and the Department, as best as I can figure out, has been forced to try to understand what some of these impact factors might be with the introduction of these animals. If that clarifies your question a little bit, I will let it go at that.

John Henneberger:—This one is to Bob McIntosh about the Wild River Study. "How will the private landowners along the Rio Grande be dealt with on the issue of the riparian rights. Are they fighting the establishment of this section of the river in the national system?"

Bob McIntosh:—If a Wild and Scenic River is established on the Rio Grande, the first action will be a Congressional one if it is to be managed by the Federal Government within the national system. If it is to be managed by the state of Texas and included in the national system it will require appropriate and similar action by the state of Texas. If either one of those actions takes place, the next step is that it will be named and designated in concept. If either one of those actions take place, then within a period of time following, normally 2 years, the administering agency—if it is Federal, the National Park Service; assuming it is state, the Texas Parks and Wildlife Department—will master plan the area. And under the concept in which we have developed the alternatives, two basic actions will take place—acquisition in fee of those areas that are critical for public use, and acquisition less than fee to protect the scenic qualities of the canyons throughout the length of the corridor.

As for dealing with the riparian rights of landowners, when the determination is made, the acquisition in fee will be needed in those particular locations. Then the landowners will be justly compensated for the rights that are required by the administering agency. In the case in which we have less than fee, depending on the riparian rights that are of specific interest to that landowner, they may or may not be purchased. An obvious question is water withdrawals, and I can foresee many cases in which that right will be allowed to continue under the numerous regulations in which that right had prior establishment as well as the international treaties between the United States and Mexico.

With the second question, as far as fighting the establishment is concerned, at this point I can only say, no. They are not fighting the establishment because the action has not yet taken place; and the landowners, although they are few in number in the river corridor along the study segment—they are few in number as opposed to the interest of the Wild and Scenic River program across the country—have a very strong vote with respect to their local representation in Congress, and their case will be heard through public meetings and so on.

John Henneberger:—Bob, there's another one here.

Bob McIntosh:—The question is, "We already are aware of problems produced by opening areas or making areas more accessible to public exploitation. Will the Scenic River Program produce more problems of exploitation (van-

dalism, trophy-taking, souvenir hunting, etc.)? Would it be possible to exclude commercial exploitation, concessionaires, etc., and regulate numbers of visitors?"

The first point is obvious and well recognized I think in all levels of government as far as managing the resources for recreation purposes. The intensity of mobility, leisure time, and so on that has developed since World War II has created this problem. As managers in the federal as well as other levels of government, we were unarmed and unprepared to handle such problems. But lately the requirements of the National Park Service and similar agencies at state and local levels to master planning their parks and similar management areas shows the intensity and the pressures of people have been recognized.

Carrying capacities for areas like Big Bend, White Sands, Rocky Mountain, Glacier, etc., are being developed. It is an art at this time, and we are trying to work it into a science. In the new areas, Wild and Scenic Rivers on the Rio Grande, it is a very real problem, but it is a problem that fortunately is being recognized before the area is developed, if it is going to be developed as a Wild and Scenic River. When the management agency goes in and does the master planning beforehand, that will be a very significant factor in the type of development, the placement of developments, and the management of that area.

We are moving again into a period in which we do regulate use of recreation resources. Carrying capacities on a river are a relatively simple determination in which you can control the density of use as it moves down or up through that corridor. It will be a strong and significant factor in the management of Big Bend. As far as controlling the developments of concessionaires, etc., is concerned, I cannot say whether they will or will not be there. Obviously, there will be pressure or interest from river trip-types, sponsored organizations to carry people through the Lower Canyons as well as the canyons within Big Bend as they exist today. But, again, they will be subjected to the basic management regulations that will be developed from the carrying capacity. So, although we are fearful and recognize the problems of exploitation by human recreation-type use, we recognize it and will manage for it.

John Henneberger:—This one is for Frank Blair on production of industrial chemicals. "The concept of production of industrial chemicals from the creosotebush as a substitute for petroleum-derived chemicals is indeed intriguing. But, would it provide more than just a drop in the bucket of consumer needs? I would like to hear a quantitative estimate or an educated guess as to how the annual production of chemicals from the creosotebush might compare with the production of petrochemicals in a typical recent year, say 1972."

Frank Blair:—Obviously, I cannot give a quantitative answer. I do not think there is any implication in Dr. Mabry's presentation that there is enough creosotebush in the world to replace the petrochemicals derived from petroleum. But I think the point was that some of the things the creosotebush is producing may well substitute as long as the demand is not enormous. I do not think there was intent to suggest that creosotebush would substitute for fossil fuel petroleum in any gross way.

John Henneberger:—This one is for Myron Sutton. “Who should initiate action toward establishment of a United States-Mexican Big Bend International Peace Park?”

Myron Sutton:—This has been discussed for so many years. The United States has been on record in the past in promoting such efforts and it is our feeling now that the Mexican Government should make these efforts. There are several opinions on it from the Mexican side. Some feel this would benefit most the American tourist, and, for that reason it is not a high priority around Mexico City. While there is something to that, there is something to the opposite side also. Our feeling is that it would be more appropriate if the Mexican Government were to make these initiatives or define a National Peace Park or adjacent parks side by side—that sort of thing. It would be more diplomatic and appropriate if we, having had our opportunity and having made the promotions in the past, were now to allow the Mexican government to work this matter into their general overall domestic and international priorities.

John Henneberger:—Bob Linn, we will let you handle this one. “How can we develop effective means for incorporating scientific expertise into the political system to prevent or at least minimize damage to natural ecosystems?”

Robert Linn:—Well, I am not sure I know. The point I tried to make is that if there is a plan for the management, use, preservation, etc., for a general region such as the Chihuahuan Desert region, that plan must be based upon these kinds of expertise and facts; and the plan itself then becomes part of the political system. I do not know if that answers the question or not. Does it? Bob Miller, you asked the question.

Bob Miller:—What I had in mind was that there have been decisions made in the past and there are decisions being made by independent agencies in both the United States and Mexico which have resulted in some unfortunate situations, and I was hoping that there could be developed some way of coordinating these plans, as they are proposed, with some overriding agency that would look over the proposed action and get scientific input as to whether they are in the best interest of the nations concerned.

Robert Linn:—We do not have that kind of ability at this point. I think that the creation of the Environmental Quality Council and the Environmental Protection Agency are two examples of an effort that was made. I do not think that effort has come up to maybe even 30% success, but if a plan is made for an area that has the facts, that has the proposals to develop certain kinds of things that can be done without ruining the environment of the area, and this plan is put into such a thing as the Council on Environmental Quality’s bureaucracy, and that bureaucracy must approve the other agency’s proposed projects and programs for the area, then perhaps you have a handle on it—something like this. But at the moment, I would agree with you. There really is not a 100% effective way of doing this.

Myron Sutton:—I might add a footnote to that by quoting our latest giant effort in the establishment of some sort of a joint park in the Big Bend and Pinacate areas. This proposal went from the Secretary of the Interior to the

Secretary of State, which in a way constitutes what you were asking about—some supernational body that reviews these proposals. The Secretary of State's legal and environmental departments looked at it as well as various other divisions; and then the matter was transmitted to the United States Embassy in Mexico City. It went through the various sections of the embassy—a note or some other means of transmitting it to the Department of Foreign Affairs of the Mexican government was prepared. That was done in this particular case. The Mexican Government discusses and considers the matter at that high level. Next they go down to their technical bureaus, presumably to discuss the technical aspects, then come back to the American Embassy with a response, which is communicated back to the Department of State in Washington, and then to us. In this case they felt that at the moment there is not sufficient research material available to entertain the proposal for an international park. And so, step by step, we get closer to success; this is the existing procedure for that sort of thing.

John Henneberger:—This one I will address myself. "What is the feasibility of a system of biological preserves consisting of small areas similar to the Big Thicket, small gypsum areas where there are unique floral elements that would be ideal candidates?" One of the concerns that I got out of this symposium is that we possibly can establish the Big Thicket National Biological Preserve concept in the Chihuahuan Desert area, not only on this side of the border, but south of the border. As I said, we have very significant natural phenomena already preserved in Big Bend, Guadalupe, and Carlsbad; we could add to this existing system. The important national natural values could be administered by the National Park Service. Let us face it. The days of Big Bend National Park establishment are over. You are not going to get 500 or 600 thousand-acre parks on the mainland of the United States anymore. You might in Alaska, and the last hurrah is going on there about setting aside such large areas. But we could add small significant areas to the system, and we might even add them to existing parks as detached units. So, this is something we could explore. There are all sorts of areas already identified—some were identified in these papers—in the Del Carmens and the Grassland Preserve, and somebody told me that the state of Texas has 800,000 acres in west Texas already under its administration. Possibly units out of that acreage could be added to a biological preserve. There are all sorts of possibilities, and I intend to pursue them when I get back to Santa Fe.

The next question is along this same line. "What in your collective opinions would be the minimum area as to percentage of total necessary to remain undisturbed to meet purely scientific needs?"

Frank Blair:—Let me respond to that. I think we cannot establish any firm and absolute limits. There are ecological principles concerning the size of an area that will maintain itself. As one example, the Nature Conservancy in central Texas has bought one acre of land which surrounds the mouth of the cave that has a unique biota in it. It is somewhere between the size of the cave mouth and many, many sections. It depends entirely on the local situation. I do not think there is any absolute answer.

John Henneberger:—There is a whole series of questions here that are in the same vein. “What proportion of the Chihuahuan Desert region in both the United States and Mexico is under the jurisdiction of public agencies? What degree of control exists over these lands?”

Well, that is where we have to go from here—studies to identify land ownerships and values on the land. That is where we have to start getting money and do the basic research.

Dave Riskind:—I think all of us are fairly familiar with state and Federal lands over which agencies have some control. What about in Mexico? What kind of control does the Mexican government have over any unit of land in Mexico? I would be particularly interested in finding out this if Horacio could address himself to it.

Horacio Gallegos:—The federal government in Mexico controls all the land or the uses of the land, and our constitution says that everything in the soil or all lands belong to the federal government. And they give us uses. They can be for private, or they can be for the community, or for particular people. But in national parks, the land is federal—the same as in the United States. You are interested in the area of the Chihuahuan Desert, right? For example, what can we do in the Chihuahuan Desert? First, to make an exploration of the lands we need to protect and pay money for them. But if the area is too big, it is a lot of money to pay. So, the way we are thinking of doing it is to be involved with the people who have the land right now and make an agreement—it is not a very good agreement because it is going to be enforced by the government—to protect and preserve the area. We want to charge for entrance to the park and all the money will go to the poor people of the area. If we make trailer parks or cabins we are going to give the local people the trailer parks and cabins. We are going to train them to manage the areas in the service. Then, all the money will be coming to them to change their way of life. There are very poor people there so we are going to increase their economic, cultural, and social way of life. They will want to keep and protect the area, like a business, for future generations. We can enforce high standards because we are going to spend a lot of money, not to buy the land, but to increase the way of living of the poor people in the area. We are going to ask the people who have private ownership of the area, as we have always done in all the parks in Mexico, to donate the area for the park. If they do not donate it, we will let them stay in the area but force them to protect it like a reserved area.

John Henneberger:—This question is, “The renewable natural resources of the Chihuahuan Desert regions of Mexico and the United States need to be summarized and presented in socioeconomic as well as ecological terms in forms useful to the natural resources decision makers.”

This might be one of the recommendations rather than a question, but, Bob, you tell a little bit about the environmental assessments.

Bob McIntosh:—Realize two things within the systems in which we are working today. One, is the attempts made by the administration as well as certain members of the Congress to establish nationwide or national land-use planning. I imagine that if I polled the audience for their concept of what that term means, I

would have as many responses as there are people sitting out there. In essence, we are talking about identifying the potential, the values of the characteristic resources of the region, and identifying the losses or gains with respect to the decisions that are made in response to the specific character of that land. The work that is done or the potential of work that can be done with reference to the Chihuahuan Desert needs to be done in that light.

We do not have national land-use planning. We do not have national land-use thinking. The question was asked earlier, how we get scientific fact in the political process. The answer is elect those officials who will consider the values of the gains and losses with respect to the decision on land use! We have a humble attempt to try to incorporate such information into the decision-making process today. That is the Environmental Policy Act in which for every significant or every major federal decision, an Environmental Impact Statement must be prepared. This statement is not the decision-making document in the sense that it makes the recommendation, but it evaluates the recommendation in respect to the impacts, not only on the biological and natural resources, but also on the socioeconomic conditions that exist or are relevant to that particular action. The Congress passed that Act in 1969, it is still in force, and we are learning better every day how to handle it. Several states have followed. One specific example: the state of New Mexico passed a law 2 years ago to require such Environmental Impact Statements, and because of the burden of work and perhaps because of the evidence that was brought forward, the law was repealed. If we are dealing with a nation that is considering the potential impacts on our resources in those terms, then we are in serious trouble.

Myron Sutton:—I wish it were possible for the governments of Mexico and the United States to petition the United Nations to undertake a joint study of the Chihuahuan Desert. It is quite shocking to hear Dr. Phillips, of all people, say that so little is known of the birdlife of the Chihuahuan Desert. If UNESCO could undertake an international survey of this desert area, from the standpoint of picking up what is not known scientifically and converting it into information useful to managers, we might have the kind of overall survey of Chihuahuan Desert resources that so many speakers have sought.

Frank Blair:—If I may disagree with our moderator, I would much prefer to see Mexico and the United States attack this problem bilaterally rather than bring UNESCO into the picture. I think we would be much further along the way in 5 or 10 years than we would if we went through the international bureaucracy.

Myron Sutton:—I will have to agree with you there. Either way, it ought to be done.

It would be very difficult for this panel, some of the members of which are not skilled in this Chihuahuan Desert, to undertake an assessment of the priorities. Of course, the obvious suggestion is to establish a task force to do this, but you know what that does. Another suggestion, that might be just a little wild, would be to establish some sort of a Chihuahuan Desert coordinating council or private conservation council, if one does not exist already, that could use this as one of its major priorities to look over the whole desert area objectively, scientifically, and

from a management viewpoint, and determine what is deteriorating fastest. If the springs are going fastest, if Dr. Hubbs' fish are dying off faster than anything else, then let us go to fish. If Cuatro Cienegas is being eliminated faster than we think, let us see if the Mexican government—and they should certainly participate in all of these councils—could give priority to that. This takes quite a bit of attention, and the background presented at this symposium is really a fantastic step toward that kind of selection.

John Henneberger:—Last night we had some discussions about the Chihuahuan Desert Research Institute, which to me is a really fine vehicle for the identification of areas which should be preserved for further research, and I made an optimistic statement that possibly we could use National Park Service funds to funnel into the institute. I do intend to look into this when I get back to Santa Fe. There are vehicles to get funding, and funding is the key to further research. Does any panel member have any comments on that?

Dave Riskind:—I could interject something here although not particularly in relation to your statement. We are talking about establishing areas of priority, of high biological integrity, uniqueness, impairment—things of this nature. From the people in the audience right now you probably could get a very quick rundown on areas of extreme biological diversity, uniqueness, and so forth, and see how many of them overlap. I believe we could come up with a pretty clear indication of which areas need to be protected throughout this region. I know that Dr. Hubbs and Dr. Miller could give you a pretty specific rundown on the areas in which the ichthyofauna is particularly unique or endangered or threatened. I think that Marshall Johnston, Dr. Warnock, and Mike Powell could tell you the areas that are vegetationally unique. I believe we can move in this direction now and try to establish some of these critical areas that need to be set aside or that are biologically unique or interesting.

Myron Sutton:—Sr. Gallegos just mentioned to me that, in his opinion, after the Sierra del Carmens study, Cuatro Cienegas is the next priority.

Dr. Villa:—In regard to that question, I can tell you that the Mexican government established the National Commission of the Desert in Mexico. This commission is part of the government action in order to protect the northern part of the country. We have other institutions engaged in joint efforts to establish a means for protection. Under the constitution, the property and land is of great importance and the Mexican Government already is at work on the big problem of preserving these areas. Perhaps there will be some progress for establishing this cooperative effort between the biologists of the United States and those of Mexico.

Myron Sutton:—Thank you. I can assure you that we are in constant communication with the academic community and with the government of Mexico on these matters and so are the Fish and Wildlife Service and the Bureau of Outdoor Recreation and other parts of the Department of the Interior. We look forward to some splendid collaboration in the future. It will take time, of course, because we are not treating lightly matters of such importance.

First Keynote Address

BERNARDO VILLA-RAMÍREZ

Ladies and gentlemen, geography made the United States and Mexico neighbors. The desert has made us brothers. The principal motive for our being united here is the necessity of preserving the aesthetic values and natural resources, the instinct for survival, and the uniting in defense of humanity. The time has come to note that it was a mistake to have said in the past that the desert separates the United States and Mexico.

Today we can say that the desert unites us. A biotic province of much interest, the Chihuahuan Desert is common to both our countries, but the biggest part belongs to Mexico.

Man established frontiers. We are trying to break through them with understanding, with common interest, to save the human dignity, to shake hands over the Rio Bravo, and to establish there the fundamental purpose of what man can do and must do for the future—for the welfare of those people who are already in this world, of our children, and of our children's children.

This is a short summary of the findings that the scientists have made during this symposium. The amount of scientific and technical information I have heard is overwhelming. I am familiar with many of the people in the United States who have worked in the Chihuahuan Desert. I am also familiar with the Mexicans who have been interested in the study of this biotic province, and I share this interest. But to summarize this is very difficult because my capacity to assimilate everything said here is not enough!

There still is very much to be known. The way is not short, it is long. Behind us there are youngsters, like the students that accompany me today. They will help with this work, and side by side, as you say in English, we can do everything in order to preserve our natural resources. I hope that in the near future we will be working on the preservation of this natural resource with the enthusiasm and good spirit needed to pass on to future generations what we ourselves have inherited.

Gathered here are very important people. It has been a pleasure to meet with them. I have to acknowledge to those present my deep appreciation on behalf of those Mexicans who for a long time have been trying to do something for the preservation of this natural resource in the desert of northern Mexico. It is a pleasure to extend very deep appreciation to the people that organized this meeting:

David Riskind, Ro Wauer, all the people that have been working very hard in order to have this gathering here and to establish the best relationships on both sides in the hope of having this earth for us in the future. Thank you very much.

Second Keynote Address

BOB BURLESON

It is very difficult for me to follow Dr. Villa because he is a man who speaks with such conviction.

I would like to talk about the years I have spent in the Chihuahuan Desert and the things I have observed there, and about one aspect of the present situation facing the Chihuahuan Desert that perhaps has not been fully touched on in this meeting so far. Most folks here have been so concerned with the scientific aspects that the human, political, and cultural impacts in this area have been only incidental. It is my opinion that there is less time than we think to do something effective in the Chihuahuan Desert on both sides of the river; and because most of the Desert lies on the other side, we must be concerned also with Mexico, perhaps even more than with Texas. I believe that the pressures on the Desert right now, and that are quite obviously changing it day by day, are such that all of us ought to be aware of them and concerned with speeding up our timetable for doing something about it. So I want to talk about the political and cultural impact of humans on the Chihuahuan Desert as I see it today, and about some of the things that I think give urgency to the problems that have been discussed in this meeting.

I want to say at the beginning that, although I may have some things to say that may not reflect the highest credit on the government of Mexico, I have a sincere feeling of respect and admiration for Mexicans, the nation, the people, and the government; and particularly for those gentlemen and their wives who are here tonight. So, anything that I say must be taken in that light. I also have a lot of friends, I think, among the ranchers in the Trans-Pecos, and although I disagree strongly with some of their land-use practices, I want you to know that I do respect them and in many instances admire them.

First, let us take Mexico, since the biggest part of the land mass involved and some of the more interesting parts of the Desert are in Mexico. It may surprise some of you to know that there is a tremendous amount of activity going on—almost beaverish activity—in certain parts of northern Mexico. Road building is going at a faster pace than I have ever seen it in that part of the country. There are new roads being opened up everywhere. There are well-advanced plans for a new road from the Muzquiz-Boquillas highway straight up the east side of the Maderas del Carmen and Sierra del Carmen to connect with La Linda; and this, of

course probably will be a good, first-class road built up on a *bordo* or something similar to make it an all-weather road. This is going to open up the entire Sierra del Carmen region that is so much a key resource, biotically, not only to Mexicans but also to Americans who visit there. This island of mountains is a very important part of the country and the Desert. At the present time it is quite difficult to get there, and, except for those who live or work in the area, only a few people go.

The road is now being paved almost to Cuesta Plomo, the pass over the mountains from Muzquiz to Boquillas, and it soon will be brought on down into Boquillas where they already have built a new *aduanas* (customs) station. There is definite expansion on the Mexican side in anticipation of several events that I will mention a little bit later. All of these things are making for faster, easier access to the frontier, through Mexico, and they will result in more traffic, more use, and in faster ways to haul lumber, making timbering more attractive as an adventure in the mountains that still have timber on them.

Second, I would mention the fluorite mining activity in the Cuatro Palmas area and Agua Chile area near La Linda, across from Black Gap Wildlife Management Area and Big Bend National Park. The mining industry is very active, and a look at the roads and at the amount of vehicular traffic on them shows the results of the mining. Hundreds and thousands of acres that were scheduled originally to be included in the proposed international park actually are committed to a mining development as long as the resource lasts. And the same threat, as I will mention later, exists in our own parks on the American side of the river. These mining activities are going to continue. There is no way, economically, that the government of Mexico can afford to cease or limit the mining, so as long as the resource lasts there is going to be heavy mining activity and the pollution that is associated with it. It will affect the river. There are some discharges already from the Dow (now Du Pont) Fluorite works at La Linda that can be expected to increase, as can the traffic.

Another cause for concern is that the government of Mexico basically is committed to the idea of the *ejido* system of land use in the frontier area. I have seen the agrarians move in on formerly large holdings in this area right across from Big Bend National Park. There is continuous conflict between the agrarians and the large land holders who have—no matter whether they have been justified in it or not—held some of the high grazing land and some of the high mountain land in pretty good shape until very recently. I think this land long ago would have been grazed completely out of existence if it were in an *ejido*. Now the *ejidos* are moving into areas that were formerly part of the Rancho de las Norias, and there is a considerable amount of increase in this type of use of the land. It invariably and unavoidably will result in a dramatic decline in the vegetative quality and the type of environment that is there for plants and wildlife. I think it eventually will degrade the entire area if it is not stopped because under the present system, as I understand it, there is no way that any real, effective control of grazing practices can be imposed upon the *ejido* community. They basically are autonomous in this

respect; and there is no real regulation or effective control. It is a communal grazing approach that destroyed the land on the Indian reservations in the Southwest—and it is doing the same thing on every *ejido* along the northern frontier of Mexico where arid lands are overgrazed continually.

Another thing that bothers me is that it is a policy of the government of Mexico to try to develop the frontier and to encourage people to come to the frontier because of the serious population and economic problems in Mexico. That is one reason why the *ejidos* are created and are in existence in the area across from Big Bend National Park and the area of the proposed international park. This pushing of people into an area that has no economic base to sustain them is very much like our land speculators who divide into ranchettes land that should not have large numbers of people imposed upon it; it creates an artificial situation where we have people where people should never have been in quantity. It creates a demand for power resources and for services that necessarily are involved in feeding, clothing, and making a living. There is no resource base in northern Mexico to sustain these people, and they are living an impoverished existence on all of the *ejidos* that I know of. There are some who get more help from the government than others and some who probably are more successful than others, but it is a very precarious existence for most of them.

These problems are right there across the river and in the Chihuahuan Desert. The Mexican government has an almost insoluble problem with an explosive birth rate that even keeps ahead of the gross national product, so the government must make maximum use of every possible resource. We would be foolish to think that it can be changed without the very drastic changes that we need to make in our own country and are not making.

There are some other things that bother me and that must be counted into the equation when deciding what is to be done about the Chihuahuan Desert. One is the river—which has great historic value and over the centuries has drawn people like a magnet. I think it should be dedicated as a wild, free-flowing stream forever in the section of the Chihuahuan Desert through which it passes. This river is Conchos water that comes out of Mexico. It is controlled to a large extent by dams that are on Mexican property and that belong to the people of Mexico. It is entirely possible that future water-use demands in the valley of the Conchos, and the application of agricultural chemicals that will end up in the river through the return water, may reduce the flow of the Rio Grande to the point where it no longer is a wild and scenic river; this activity also may reduce the quality of the water below the point where it could be used for that. These are definite possibilities. If they occur, we in the United States probably would be to blame because we have done the same thing to Mexico on the Gila, the Salt, and the Lower Colorado. We are as guilty of ruining the water we send to Mexico as Mexico is of ruining the water she sends us. There is a possibility that one day we will be out of water on the Rio Grande except under a controlled-release situation. These things have to be considered and are extremely important for all of us to know and be aware of.

In addition to the foregoing, there is a lot of commercial plant-collecting going on in northern Mexico because of the demands in the American market. It is a regular business backed up by U.S. dollars—people are buying the plants and are selling them to nurseries and literally wiping out certain types of plants in a given area. I have seen burro-loads of various species of cacti cross the river many times; and at different times I have seen perhaps an acre of cacti drying out on the ground along the river. The *Alpine* paper reported recently that one fellow ships 7000 cactus plants a month that probably come from the Chihuahuan Desert. This is a tiny fraction of the slow-growing plant life that actually is going into areas where it does not belong; and with the very slow, uncertain reproductive rate of many of these desert plants, I do not think that the desert can sustain this type of cropping. All of us should try to discourage anyone from using or landscaping with desert plants that come from the Chihuahuan Desert or from the Sonoran Desert area. These are the main things that concern me about the Mexican side of the river and the desert.

Let us now look at the United States side of the river because we have not done any better with our land stewardship than has Mexico. In fact, with the resources that we once had, we are far more guilty of land abuse than Mexico because we have a higher average education level in our population. We have a higher standard of living in our population, and yet we have abused the Trans-Pecos to the point where most of it is a tiny vestige of what it once was; and it is not just an increasing aridity of climate—that may be part of the problem—but primarily, it is abusive land-use management that has created or expanded the thorn-scrub and the creosote bush aspects of the desert. Man can help make a desert and help destroy one by his activities; we have done and are doing both so we are equally to blame.

One of the biggest threats to the desert over which we have some jurisdiction is the rural subdivision; the land speculator who buys large sections of land and chops them up and sells them to what I would call gullible people—not really criminally gullible, but people who do not understand what they are buying and what is happening. I hope, quite frankly, that there is a special hell for land developers!

It may surprise some of you to learn that one-fifth of Brewster County, the largest county in Texas, is in the hands of people who are development-oriented, either by options, by the right of ownership, through long-term contracts, or by some other sort of ownership. Nearly all of the lower river area, the Terlingua area and headed on up toward Presidio, is in the hands of people who basically have plans for long-term development—chopping the land into ranchettes for sale.

To some land this appears to be a salvation because it no longer will be grazed abusively; but even that is fallacy because in most instances, the subdivider continues to graze the land after he has sold it. Very few people can afford to build a fence around their acre and most land still is open range. In addition to this, there remains the strain on the water resource because these developments must have a

water supply. This comes from the river or from an underground system of some sort. The developments are going to be drawing on fossil waters. We have gotten into this trouble everywhere that there is any development of arid lands. It is a matter of withdrawing faster than the recharge—water that went into the ground over thousands of years can be drawn out in twenty or thirty. We are in trouble with this all over the nation, and yet we still persist in doing it with no regulation whatsoever. So, a deadly threat to the Chihuahuan Desert is the subdivider and real-estate speculator who make their profits and do not care what happens in the future. So, that is Number 1—that is our fault, all of our fault.

Another problem is the mishandling of public works projects such as Amistad Reservoir. Construction of this nature is a blot on the landscape and an eyesore to the whole area, and, from the air, unfettered developments along the shores of the reservoir make it look like an oozing sore. This will happen everywhere that we build a dam. The land speculator comes in, he is a booster for construction of the dam, and he sells his arid land for a high price.

On our side of the river we also have mining problems. For example, the Bureau of Economic Geology in a recent report on fluorspar states that they regard the reserves in Big Bend National Park as future potential reserves to be utilized, and that the fluorite is running out. There is not nearly enough to meet the demands right now. Economic pressures will be put on the National Park Service and the Texas Parks and Wildlife Department because the Black Gap area contains fluorite. Economic arguments will be advanced and pressures applied to open up these areas to mining, despite the fact that the mining is in violation of the present rules and regulations of both agencies. Moreover, a certain segment of the population, that does not realize the consequences, will demand the mining.

The idea that the tourist dollar is the most important thing in life is prevalent in certain segments of the Alpine community, and in many other places. The idea that any change is worthwhile if it brings in more people or encourages them to stay more than 24 hours in our town is something that I will not accept. It adds to the community and overburdens the natural resources that draw people here, so that those resources will be destroyed. And those who would build super highways into Big Bend National Park and Walt Disney-type developments to get more tourist dollars will destroy Big Bend National Park and the Chihuahuan Desert if they are not stopped. It will take a chorus of knowledgeable people who have something to say and can explain what the problems are—that means you who can communicate these facts to the public and make people aware of these fallacies.

Geothermal and solar energy also is becoming extremely dangerous in my opinion. Dr. Linn said that we ought to be planning to utilize the Chihuahuan Desert as a source of solar energy. I disagree. Those parts of the Chihuahuan Desert that are under protection now ought to be forever excluded from that type of use; drilling geothermal wells is a threat to the Rio Grande up above Big Bend National Park and perhaps to the park itself. It is one of the two or three areas in Texas where suggestions for development of geothermal power have been made.

We have got to keep track of these things because where there is geothermal or solar power water is used to generate steam or for cooling purposes. The water is not here unless it comes from deposits that may dry up the very springs that keep the Rio Grande running. There is a large influx of water into the Rio Grande around the Bullis Gap area from underground springs in both Mexico and Texas. It substantially increases the average annual flow of the river and tapping these resources could do exactly what has been done in the Comanche Springs–Leon Springs area. Tapping these deep water resources to supply a power plant or an irrigation project could ruin this valuable resource.

These things are our own fault. The Yankee dollar has caused damage in Mexico that the Mexicans themselves probably never would have caused without our encouragement, our buying, and our financing of the operations. The Sierra del Carmens were logged off completely 20 years ago by American timber people. There are proposals to cut it again in the next 5 or 10 years. This area is so diverse that it should be preserved as a national park; it is a part of Mexico's heritage that Mexicans are proud of. Nature has not repaired it fully and may never be able to do so.

There are some things that need to be discussed in regard to international dealings—particularly two proposals that affect the Chihuahuan Desert. One is the proposal to create a Wild and Scenic River on the Rio Grande, something that both governments should favor. This would do very little harm and would preserve a resource that ought to belong to both Mexico and the United States. There are a substantial number of Mexicans who now operate kayak clubs and canoe clubs just as we do. It is a growing sport in Mexico. I have seen these groups on Mexican rivers, and Mexicans will be more and more interested in river travel for recreation and for sport. So, the proposal is of benefit to both groups and involves very little in the way of economics when compared to the resource being saved.

The other proposal is for an international park. It has been under consideration since 1936. If the present trend in Mexico continues, abusive grazing, timbering, and agricultural practices will destroy the area of the proposed park in the foreseeable future. The park should be built now if it is ever going to be built. Señor Gallegos is working on a very interesting proposal to make this park a reality. He has some good ideas, and I certainly do not have enough knowledge to argue with him, except on one point. That is the idea of making a major border crossing in Big Bend National Park, because, at the present time, Big Bend National Park is the only segment of the U.S. Chihuahuan Desert that is really protected. A major crossing and development of a border city on the Mexican side would increase traffic that is unrelated to Big Bend National Park, create a demand for better roads and the possibility of hauling ore through that area, and increase the possibility of commercial traffic through the park to supply the frontier zone. All of this concerns me, and I think these factors argue against a crossing in Big Bend National Park. I would much prefer to utilize the La Linda route and to route the Mexican main highway up the east side of the Sierra del Carmen. This is the position that I think we should take. Never-

theless, it is a fact, as Senor Gallegos agrees, that this land will go under unless something is done. This proposal possibly is an effective way to get the project moving, but the bridge crossing in Big Bend National Park must be resisted to the last ditch.

What are some proposals for action that might come out of a meeting like this? I have a few here that I have listed.

1. Because there is a basic conflict between various agencies of the Mexican government in their approach to the frontier, there needs to be some attempt at a unified Mexican policy toward the frontier zone in the area of the Chihuahuan Desert, where it definitely is valuable from a scientific and recreational standpoint to both Mexico and the United States. The mining and timber industries and the development of the *ejido* system are in conflict with any proposal to create an international park without a coordinated policy that would allow a unified approach to the problem. I believe that it would take a coordinated, unified plan by the Mexican government for their area of the Chihuahuan Desert, at least that part near the river and near Big Bend National Park.

2. Out of this meeting should come a proposal for a complete scientific assessment—and a good one—of the entire resource of the Chihuahuan Desert, both in Mexico and in the United States. I think that was one of Dr. Blair's proposals and certainly it should be implemented. We need to have on our side of the river some effective land-use legislation to protect areas against ill-thought-out development and ill-conceived energy and water projects that would destroy the resource that in the long run is worth more than these projects.

3. We should move rapidly to protect certain areas of the Chihuahuan Desert that are still available on our side of the river. The Capote Falls area is one that occurs to me, along with the Sierra Vieja and the Sierra Diablo mountains—those areas that are a part and parcel of the Chihuahuan Desert and that are still available for acquisition by public agencies to be administered as public lands. These areas should be acquired with all haste because they are valuable, they are there, and they really do not have a high economic use right now.

4. It also is essential to preserve Big Bend National Park against a concerted effort to overdevelop it. There is considerable effort on the part of highway associations, chambers of commerce, and others who really have not quite thought out the implications of their plans, to overdevelop Big Bend National Park and build superhighways through it, a paved highway along the river, and make it an auto park. If there is one good thing that may have come out of the energy crisis, it may be to curtail some of the excessive tourism that threatens all of our parks with overuse.

5. We should work toward the implementation of the international park if it is possible to do so without binding ourselves to an international river crossing at Boquillas. A footbridge that could not be used by vehicular traffic would be tolerable, but any crossing that allows automobiles and trucks to cross would destroy Big Bend National Park. It also would encourage a demand for improvement of the type of roads that are in Big Bend National Park—to make them high-speed

roads rather than ones that lie fairly easily on the land as they do now.

I have spoken very positively. Obviously, I have given my own opinions. I believe in them. It does not mean I am right, and I certainly welcome criticism, comments, or any adverse or constructive remarks that anyone else has to make.



