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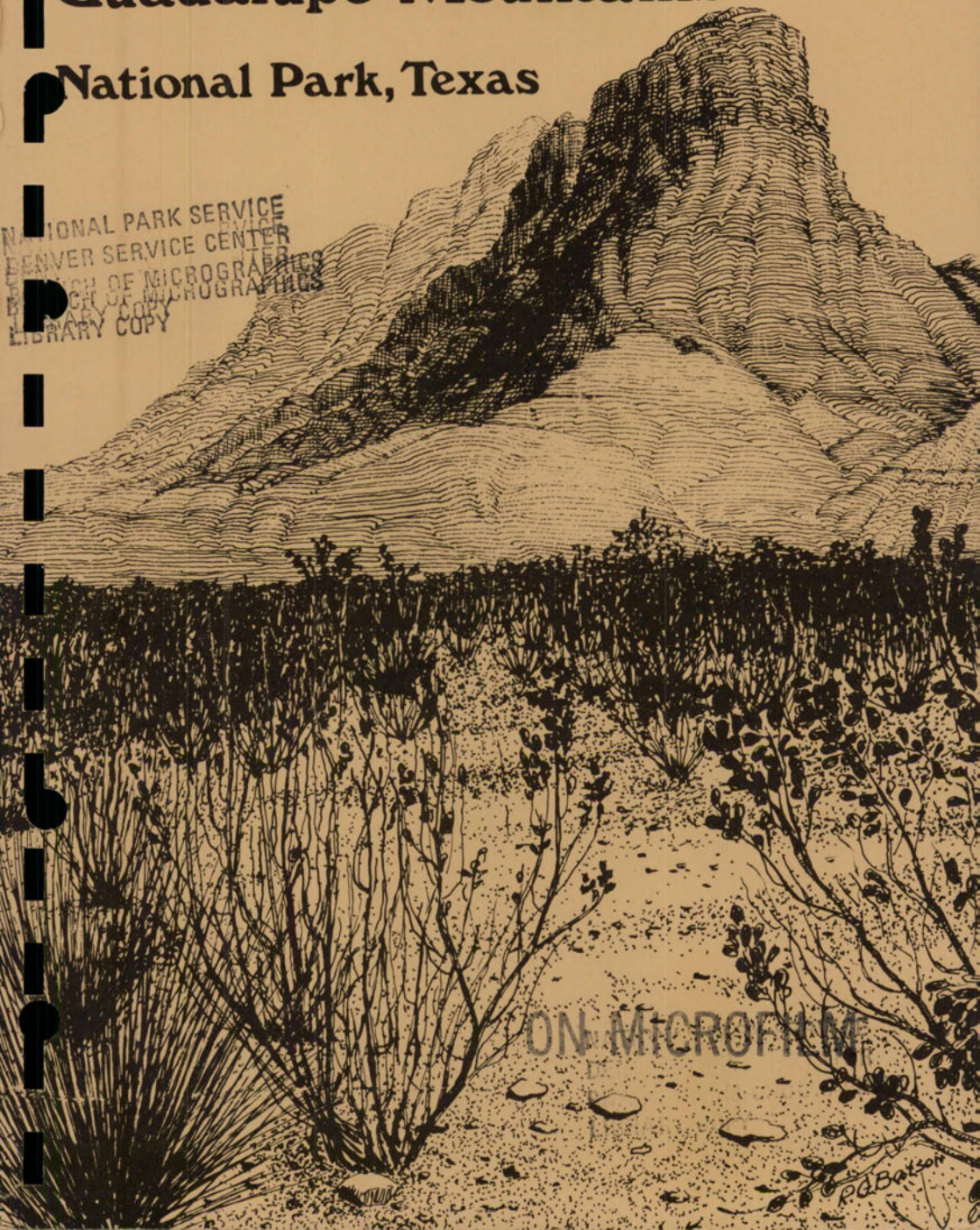


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# Biological Investigations in the Guadalupe Mountains National Park, Texas

Proceedings of a Symposium held at Texas Tech University, Lubbock, Texas • April 4-5, 1975

Edited by

**Hugh H. Genoways**

**Robert J. Baker**

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# *Editors' Note*

The Guadalupe Mountains National Park, which is located in Trans-Pecos Texas between Carlsbad, New Mexico, and El Paso, Texas, is one of the newest national parks being formed by the Congress in 1967. The Guadalupe Mountains and the associated Chihuahuan Desert included in the park represent a unique biological area in which a fragile biological equilibrium exists between the fauna and flora of the Chihuahuan Desert of the lowlands and the Rocky Mountains of the high elevations. The preservation of this area will depend upon sound management decisions.

This volume is the result of a symposium held at The Museum of Texas Tech University on 4 and 5 April 1975. The impetus for this symposium was furnished by our participation in a research project in the Guadalupe Mountains National Park. This work was funded by the Southwest Region of the National Park Service through Texas Tech University and administered by Mr. Roland H. Wauer. It became apparent to us that considerable scientific research was being conducted in the Park both by the staff of Texas Tech University and at other institutions. However, we believed that only limited communication was occurring between these scientists. We hope that the symposium and this volume will significantly enhance this scientific communication and will provide much of the baseline data necessary for the development of a master plan by the National Park Service for the Guadalupe Mountains National Park, Texas. Because the Carlsbad Caverns National Park, New Mexico, is geographically and physiographically closely related to the Guadalupe Mountains, we have included several studies that recently have been conducted there.

The research resulting in this symposium would not have been possible without the cooperation of the National Park Service. Mr. Roland H. Wauer, Regional Chief Scientist, Southwest Region, has been instrumental in initiating many of these research projects, especially those being conducted by personnel of Texas Tech University. Special thanks are due the personnel of the Guadalupe Mountains and Carlsbad Caverns National Parks, especially Donald A. Dayton, Superintendent; John Chapman, Area Manager; Gary M. Ahlstrand, Research Ecologist; Philip F. Van Cleave, Staff Interpretative and Environmental Services Specialist; and Roger Reisch, Park Ranger.

The symposium at Texas Tech University was sponsored by The Museum, the Graduate School, and the International Center for Arid and Semi-arid Lands Studies. We wish to express our gratitude to Dr. Craig C. Black, Dean J. Knox Jones, Jr., and Dr. Frank B. Conselman, respectively, of these organizations. The editors wish to extend their personal thanks to Dr. Craig C. Black, not only for his support of the symposium, but also for his support of our activities throughout our work in the Guadalupe Mountains National Park. We also gratefully acknowledge the editorial assistance and attention to detail of R. Laurie Hendricksen. Stephen L. Williams aided with some of the illustrative material. Many of the proper names used for specific localities are defined in the paper on mammals, whereas others may be found on the U.S. Geological Survey quadrangle map for Guadalupe Peak, Texas (1:62,500, 1933).

HUGH H. GENOWAYS
ROBERT J. BAKER

# *Welcome*

It gives me great pleasure to welcome participants and guests to Texas Tech University for this important symposium. The Guadalupe Mountains National Park provides a unique outdoor laboratory for biological investigations, which, of course, will provide the baseline data for the National Park Service in developing an interpretive program for public use of this area. Because investigators at Texas Tech University have played a major role in conducting biological studies in the park, it is especially appropriate that this institution take the lead in promoting an interchange of information for the benefit of the scientific community and also the more pragmatic interests of the National Park Service.

In the past decade or so, we have experienced a trend in the biological sciences in this country toward concentration of investigative research in the several experimental fields. At the same time, there has been a tremendous increase in interest on the part of the general public in environmental quality, preservation of natural areas, and in public use of national parks, monuments, and other similar facilities. It occurs to me that it is paradoxical, given a clear "back to nature" movement within our society today, that few institutions of higher learning are emphasizing the training of environmentalists. I am pleased to note that at Texas Tech University there still is a strong tradition in field-oriented studies by professors and students in our Department of Biological Sciences, in several departments in the College of Agricultural Sciences, and in our Museum Science program. The location of a large, new museum at the University contributes materially to this thrust.

I congratulate the organizers of this symposium and express my gratitude to those of you who are participants and attendees for supporting their efforts. In perusal of the program, I note not only that the symposium will bring together a substantial body of information on one of our newest national parks but also that the subject matter underscores the significant, continuing, and pressing need for research and teaching at the university level in ecology, natural history, and systematics of plants and animals, and in related areas of the geosciences and anthropology.

I wish for you a most successful and productive conference.

J. KNOX JONES, JR.

# *Introduction*

The reality of this Symposium on the Biological Investigations in the Guadalupe Mountains National Park gives me a great deal of personal satisfaction. I am proud to be part of the program.

Guadalupe Mountains have been a national park only since 1966, and before that time the area received attention from only a few scientists. The greatest amount of study resulted from private exploration for oil and gas. Vernon Bailey's 1905 report represents the earliest biological survey of the Guadalupe Mountains. Barton Warnock spent considerable time studying the plant life of the area, particularly within the lower canyons. William Davis studied the mammals of the Guadalupes. Fred Gehlbach's investigations of the herpetofauna was the first ecological analysis of the region. Owen Lind's limnological studies in McKittrick Canyon are continuing.

Since 1966, the Guadalupe Mountains have become a scientist's beehive. Titles of papers to be presented at this symposium demonstrate that research in the area is as varied as the Guadalupe environments.

We in the National Park Service believe that the recent series of investigations initiated within the Guadalupes are the proper way to develop a sound research and resources management program for this park, and to provide resources information for park planners, interpreters, and managers.

Too often Federal bureaucrats expend energy and great sums of money planning park developments without due regard to the full protection of the area's resources that were the primary reasons for establishment of the park. Too often land management agencies place fragile and unique resources second to roadways, campgrounds, visitor centers, and other facilities. Too seldom do we attempt to understand fully the potential implications of a development within a natural system.

Our approach at Guadalupe Mountains National Park began with the development of research priorities. This list is included within a Natural Resources Management Plan that is revised annually. Copies of the 1975 Guadalupe Mountains National Park Natural Resources Management Plan are available. The plan, initiated by the park staff and coordinated by the Office of the Regional Chief Scientist, includes two major sections:

1. Project statements which identify the area's natural resource problems and requirements to comply with National Park Service natural science standards.
2. Five-year programs that include maintenance costs, man-year needs, research priorities, and cost estimates.

A Natural Resources Management Plan is prepared for every National Park Service area containing natural resources.

Research priorities for Guadalupe Mountains National Park include the following items:

1. Inventory of Flora;
2. Fire Ecology Study;
3. Inventory of Fauna;
4. Climatological Data;
5. Inventory of Significant Geological Features;
6. Vegetative Analysis;
7. Faunal Factors;
8. Data Analysis;
9. Human Intrusion on the Ecosystem;
10. Soils Inventory and Analysis;
11. Water Resources Analysis;
12. Inventory of Microorganisms; and
13. Ecosystem Analysis.

This list includes only those studies to be completed and new projects required to comply with natural science standards. A complete ecosystem analysis of the Guadalupe Mountains may take decades to complete. We do plan to reach the ecosystem analysis stage at a few of our smaller natural parks as other project priorities are completed. Southwestern areas such as Bandelier, Capulin Mountain, and White Sands may reach that stage of comprehension fairly soon.

The Guadalupe Mountains plan calls for an annual funding base of at least $25,000 for research. Admittedly, the funding of $25,000 annually to field a team of scientists to gather information on an area as diverse as the Guadalupe Mountains is not very much. However, the National Park Service will continue to fund for many years the work that Texas Tech and its associated scientists have started in the Guadalupe Mountains. We believe that our association with University-based scientists is the best possible route to the completion of a basic resources inventory, analysis of those resources, and the development of a management information system.

The first objective is to acquire a resources basic inventory. We are especially interested in those resources that are unique or of special visitor interest. We will hear about some of the floral and faunal resources in the papers to follow. It is imperative to establish environmental baselines for use in long-range monitoring. The vegetative transects and mammalian grids installed within the Guadalupe Mountains system will function as a future

warning system against environmental impacts. The quality of the baseline studies must be high.

There are cases when special emphasis on project continuity and coordination of data requires other than seasonally oriented studies. We believe that a resident research scientist is a necessary element of the Guadalupe Mountains National Park staff. Dr. Gary Ahlstrand is investigating fire management possibilities within the Guadalupes; he also advises the Park Superintendent on research priorities, evaluates project results, analyzes their implications in the potential role of fire in the ecosystem, and is developing a fire-management program based upon his research and related data. Fire in the Guadalupe Mountains ecosystem probably will command an important position in management guidelines for the retention of that natural system.

Human intrusion on the Guadalupe Mountains is another concern that is being addressed within all of the studies. Carrying-capacity determinations will be made on sound biological information that is obtained by scientists concentrating on their various disciplines. The assimilation of those data with park requirements will lead toward decisions that will cause minimal impact.

Computerization of all the data obtained through field studies and the laboratory began during the first funded year. A coordinate grid system of 31,377 cells was developed for the 77,500-acre park. The purpose of structuring a data bank is to describe each data cell as completely as possible in terms of physical, cultural, and natural resources. Data storage and retrieval must be compatible with the National Park Service computer program housed at NASA's Slidell Computer System in Mississippi.

The National Park Service Science Center near Slidell is responsible for developing a management information system. This involves integrating scientific expertise, archival materials, and computer sciences with management and planning activities. It is our intention that, within the decade, Washington, D.C., and regional offices and major parks will possess terminals so that park staffs can take advantage of activities currently underway to manage soundly and to interpret their areas.

An initial Management Information System is already in use for backcountry campground management at Great Smokies National Park. A similar system has been installed at Grand Canyon for river management. Time and money will be needed for all parks to join such a system. The Guadalupe Mountains National Park program is a beginning.

ROLAND H. WAUER

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# *Geology of the Guadalupe Mountains National Park*

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The Guadalupe Mountains National Park enjoys a worldwide reputation as a region in which a unique complex of geological phenomena may be viewed and studied. Rocks, ranging in age from possibly medial Precambrian to Holocene crop out in or within the near vicinity of the park. Geologists have pieced together a fairly complete history of the last one and one-half billion years through study of these rocks. Although the region has been viewed by geologists for over 100 years, detailed studies did not begin until about 50 years ago; the renewed interest was prompted by the exploration for and production of petroleum and natural gas in west Texas.

The Guadalupe Mountains National Park is situated within an area commonly assigned to the Trans-Pecos region of Texas. This, in turn, occupies a portion of a well-known geological province, the Permian Basin. Trans-Pecos Texas is a land of contrasts, both physiographically and geologically. The region contains numerous distinct mountain ranges and intervening basins (Fig. 1). Some ranges are folded and block faulted, the product of the late Cretaceous to early Cenozoic Laramide Revolution and middle-to-late Cenozoic block faulting. Accordingly, the region possesses affinities with the Rocky Mountains and the Basin and Range Province of western America. Several ranges are made up of thick accumulations of lava flows and pyroclastic ejecta. Finally, the region boasts remnants of the folded Marathon Mountains, the product of late Paleozoic orogeny in the Ouachita-Marathon geosynclinal belt. Elements of the structure and stratigraphy of all the above are involved in the reconstruction of the history of Guadalupe Mountains National Park. To turn attention to the region of the park, one first must view the area of the expanded Permian Basin (Fig. 2). This maze of paleotectonic features was in the process of formation during most of the Paleozoic Era, but the features did not assume their Permian form until during late Pennsylvanian and early Permian time. Orogeny and subsequent erosion during this latter interval produced numerous platforms, shelves, and basins which controlled the types of sedimentary rocks that

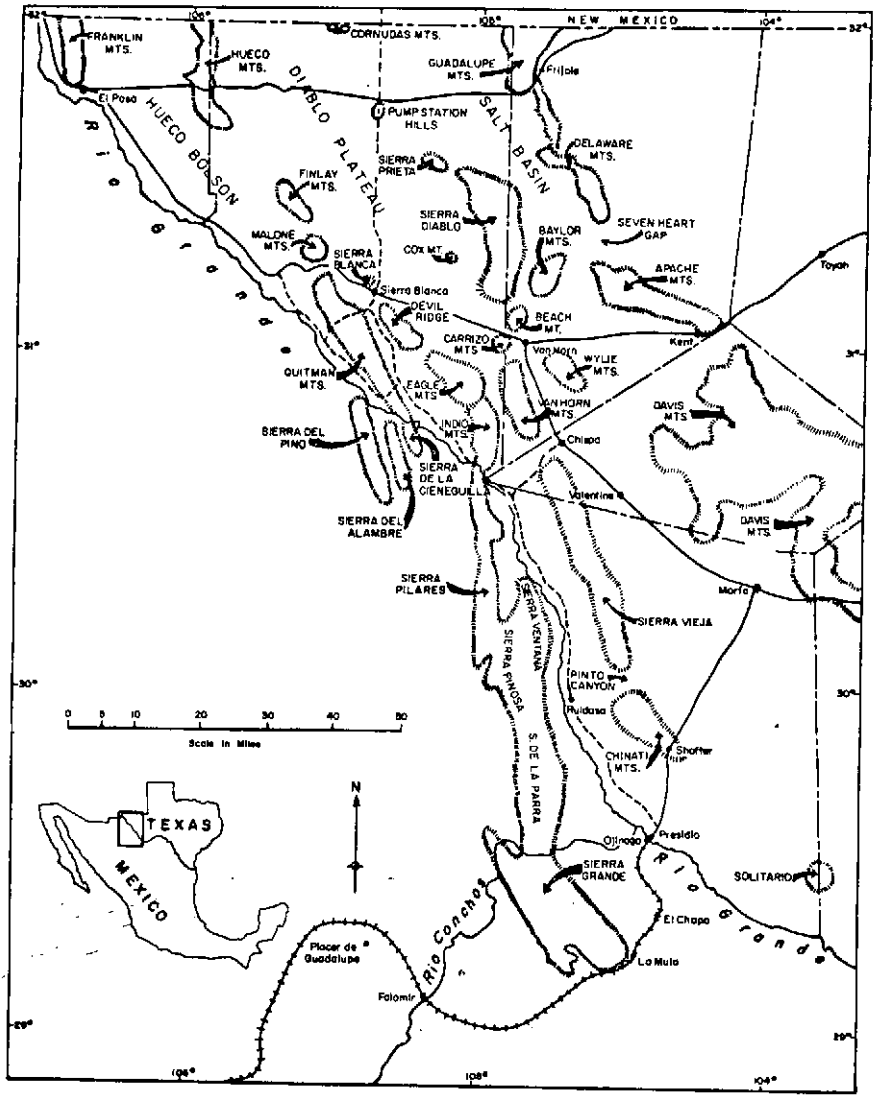


**Fig. 1.** Ranges and basins of part of Trans-Pecos Texas. After Permian Basin Section, S. E. P. M. 1975.

accumulated during the Permian Period (Fig. 3). With inundation of the complex topography by the early Permian sea evolved the possibility of deposition of sediments in such diverse environments as shallow-water platforms, back-reef lagoons, and deep-water basins. The margins of the shallow-water platforms afforded an opportunity for reef-forming organisms to flourish. Subsurface exploration has established the presence

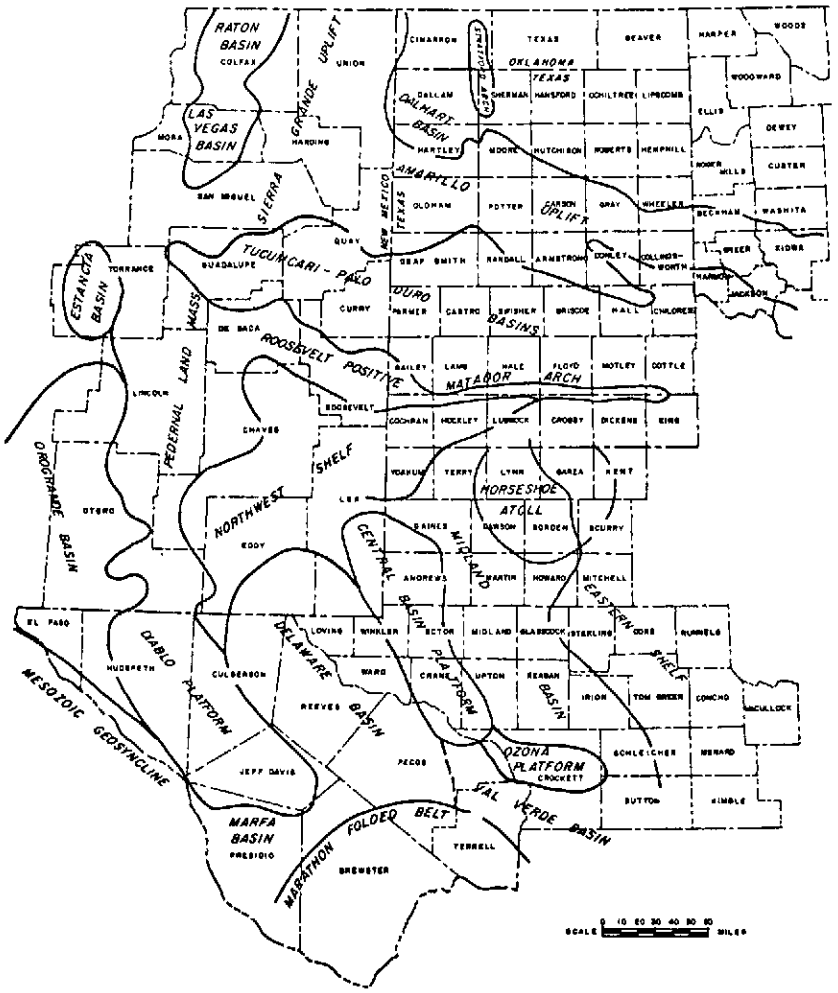


Fig. 2. Paleotectonic features of Permian Basin.

of a barrier reef along the margins of the Diablo Platform, the Northwest Shelf, the Central Basin Platform, and the Eastern Shelf. The entire North American continent records no barrier reefs of similar magnitude. Behind the reefs were wide, shallow lagoons in which carbonate, evaporite, and clastic sediments accumulated. Immediately seaward of the reefs were basins up to 2000 ft deep in which accumulated a thick sequence of predominantly clastic sediments which were transported down to the basin through submarine canyons and deposited as deep sea fans. On the slope between the reefs and the basin, accumulated piles of talus derived from the seaward face

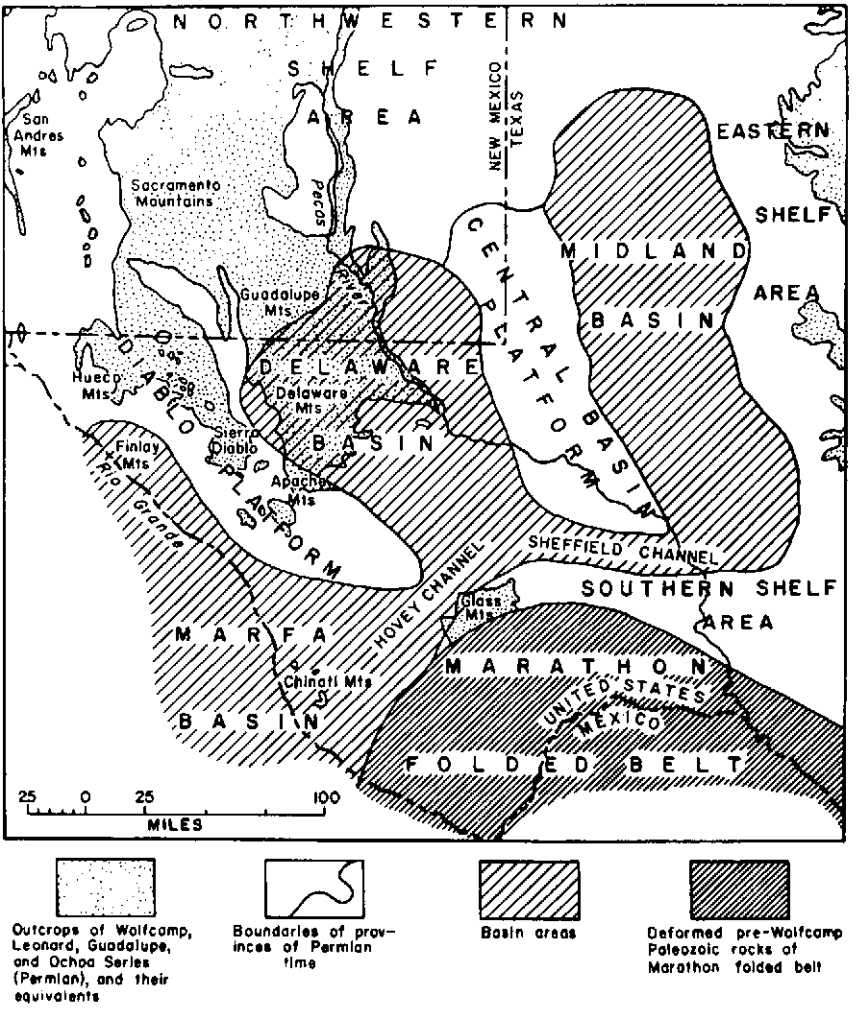


Fig. 3. Permian geological provinces of west Texas and southeast New Mexico.

of the reefs (Fig. 4). The back-reef lagoon, the reef, and the fore-reef talus constitute a stratigraphically restricted but complex relationship referred to as the "Permian Reef Complex" (Fig. 5).

The visitor to the Guadalupe Mountains National Park may view all the aforementioned environments of deposition via a leisurely walk through any of the major canyons which trend normal to the Guadalupe escarpment. For the motorist driving from Carlsbad, New Mexico, to Guadalupe Pass, the following applies. From Carlsbad to White City, one drives quite near the margin of the reef facies. From White City to Guadalupe Pass one travels

**Fig. 4.** El Capitan.

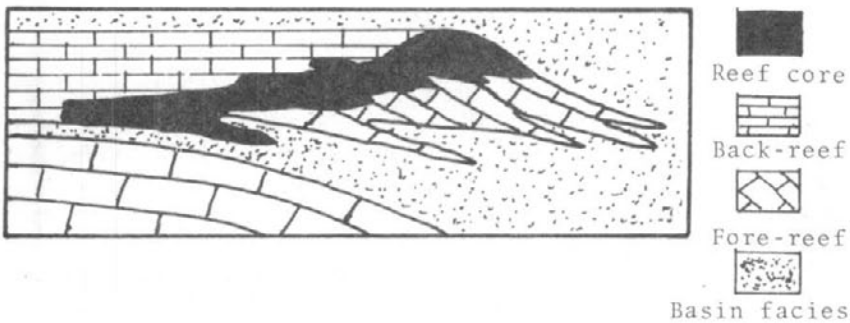


**Fig. 5.** Diagrammatic sketch of Permian Reef Complex.

over rocks which were deposited in the Delaware Basin. The most conspicuous unit, the Castile Gypsum, crops out in a road cut where the highway descends the Yeso (Spanish word for gypsum) hills to the flat area a mile north of the New Mexico-Texas state line. Farther east, in the subsurface, one would encounter extensive beds of halite (rock salt) with which are associated the potash minerals of the Carlsbad mining district. Both the gypsum and halite were formed as the result of evaporation of sea water. West of the highway, one cannot but be impressed by the precipitous Guadalupe escarpment. The top of the escarpment is formed by the Capitan barrier reef; the beds which slope steeply toward the valley floor are within the fore-reef talus

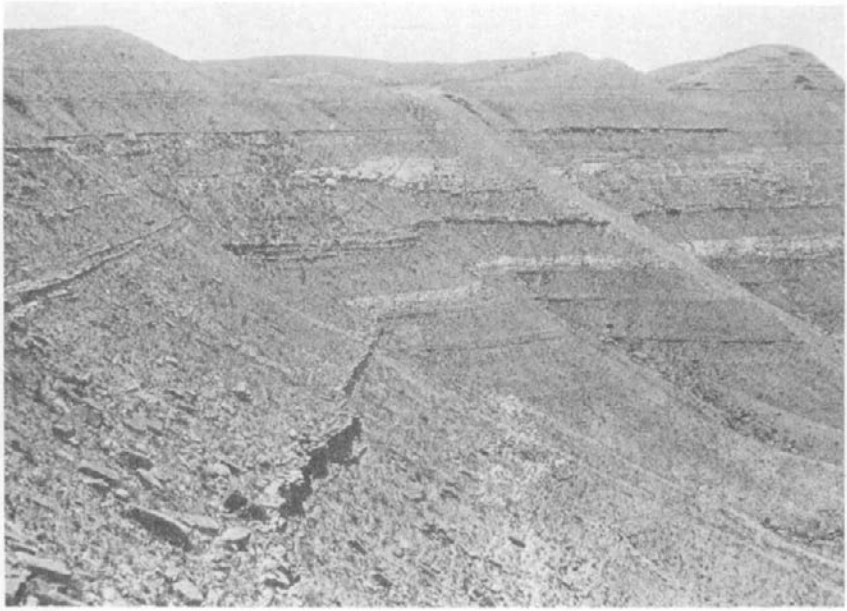

**Fig. 6.** West front of Delaware Mountains.

facies. The nearly horizontal beds near the highway are rocks of the basin facies. The rock in El Capitan was deposited near the margin of the reef barrier and the fore-reef talus. A glance to the southeast from Guadalupe Pass affords a view of the Delaware Mountains—a range made up of clastic rocks of the Delaware Basin facies (Fig. 6).

Specific aspects of the geology of the Guadalupe Mountains involve two separate studies. The first relates to the sedimentological history of the Permian Period as interpreted from the rocks in the immediate area. The second, mainly physiographic, concerns the late Tertiary and Quaternary history of the region. Following are brief discussions of the salient features of these two rather widely separated intervals of geologic time.

## PERMIAN HISTORY

The earliest events of the Permian Period are recorded in rocks of lower Permian (Wolfcampian) age. The first unit, the Hueco Formation truncates rocks of nearly all ages from Precambrian through late Pennsylvanian. The basal member, the Powwow Conglomerate, contains debris from nearly all pre-Permian units. Wolfcampian beds contain predominantly carbonate units across the platforms and clastic units in the basins. They do not, however, display the distinct differentiation into reef complexes evident in later Permian strata. One overriding characteristic of the Permian sea was the ten-

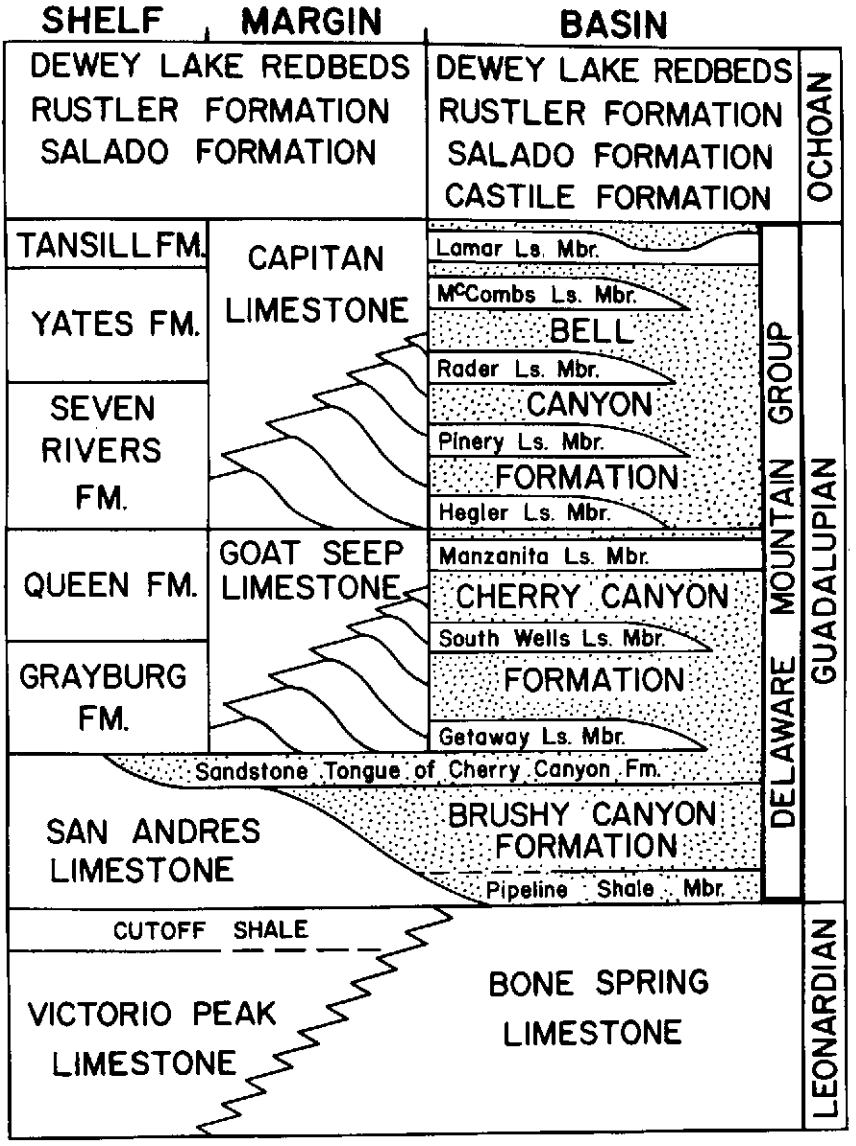


**Fig. 7.** Shelf, margin, and basin facies of Permian Basin.

dency, throughout Permian time, for the sea in the basin to become progressively smaller and deeper. The regression of the sea was not at a uniform rate, as many transgressive and regressive oscillations are recorded. Some of these sea-level fluctuations were undoubtedly of a eustatic nature and appear to

reflect sea-level changes because of multiple glacial cycles during the Permian Period.

At the beginning of the second Permian Epoch, the Leonardian, the contrast of shallow-water platform and deep-water basin topographies was well established and facies differentiation so characteristic of Leonardian and Guadalupian units became evident (Fig. 7). The first barrier reef of significant size, the Victorio Peak reef, developed along the eastern margin of the Diablo Platform. During growth of the Victorio Peak reef, a dark-gray to black limestone (Bone Springs Limestone) accumulated in the deep water of the Delaware Basin. This petroliferous unit may be seen in the first road cut as one approaches Guadalupe Pass from the south. Simultaneously, a lagoonal-arid coastal plain facies of gypsum, dolomite, and siltstone of the

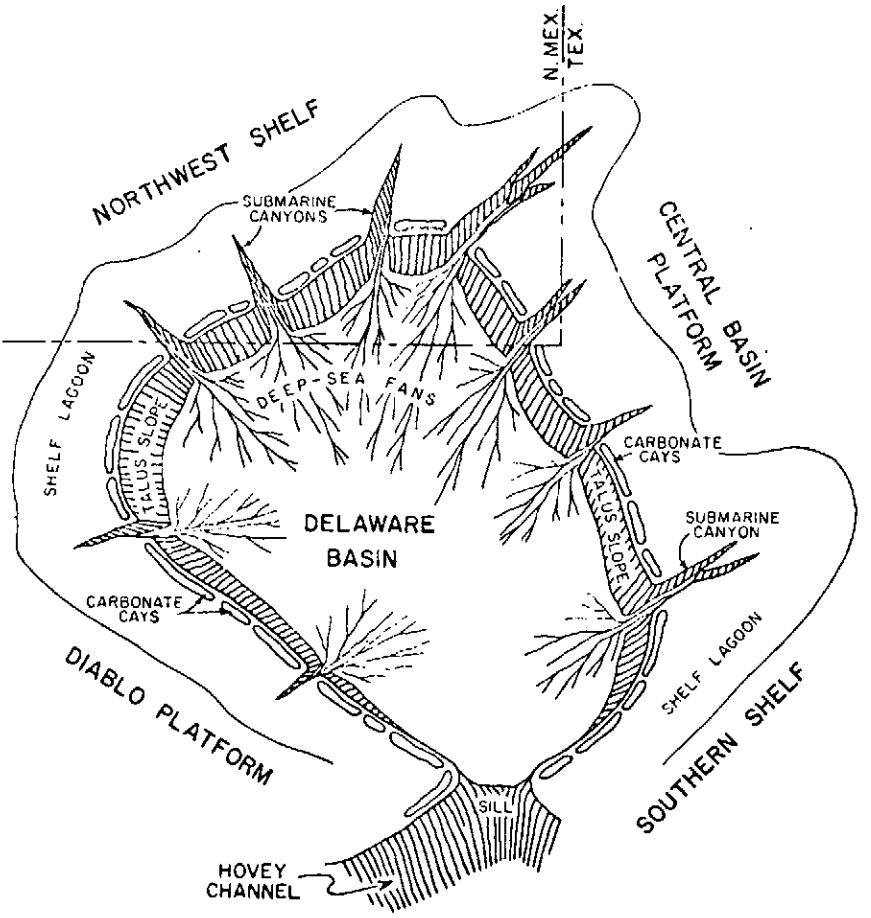


**Fig. 8.** Submarine canyons and deep-sea fans of Permian Basin.

Yeso Formation accumulated behind the Victorio Peak reef. The axis of the Victorio Peak reef lies several miles west of the axis of the first Guadalupian reef. Although outcrops of the Victorio Peak may be seen along the western side of the Guadalupe Mountains in Shirttail Canyon and Shumard Canyon, the best exposures are in Victorio Canyon in the Diablo Plateau about midway between Guadalupe Pass and Van Horn, Texas. Two distinct stages of reef growth are recorded during the Guadalupian Epoch—the first, the Goat Seep reef; the second, the Capitan reef. The Goat Seep reef lies several miles west of the Capitan reef. The spatial relationship between axes of the Victorio Peak, the Goat Seep, and the Capitan reefs attests to the general shrinking of the Permian sea and the consequent regressive (offlap) relationship of these Permian reefs. Because of its accessibility and unusually clean exposures, the Capitan reef has been studied in considerably more detail than other Permian reefs. The major canyons—McKittrick, Slaughter, Dark, Walnut, etc.—trend nearly at right angles to the reef axis. Detailed studies have revealed that the typical Permian reef consists of two basic fractions. The first is the framework builders—organic remains which afforded rigidity and resistance to wave action; the other is sediment which became trapped by the framework. The formation might be likened to tumbleweeds and other vegetation trapping wind-blown sand in the present West Texas environment. Reef-forming organisms consisted of such diverse forms as various algae, corals, bryozoans, brachiopods, and sponges. Algae and calcareous sponges were probably the greatest contributors to the reefs. The reefs, although elongate in overall form, were not continuous barrier-like ramparts. Their contours were interrupted by deep transverse channels which extended reefward from the deep water of the Delaware Basin through the reef and into the back-reef lagoon. These submarine canyons, believed to be essentially co-linear with the present transverse valleys, became avenues for transportation of clastic materials from the back-reef lagoons into the Delaware Basin. Units of the Delaware Mountain Group, the Brushy Canyon, Cherry Canyon, and Bell Canyon contain sands and shales transported by "turbidity currents" into water as deep as 2000 ft. The basin clastic units are in reality subsea fans (Fig. 8) which possess primary sedimentary structures identical to those observed in modern deep-sea fan accumulations that extend beyond continental slopes. Eustatic fluctuations of sea level are recorded in the Delaware Basin by alteration of thick clastic intervals (glacial maxima) and thin limestone layers (interglacials) which extend miles into the basin. The uppermost unit exposed in the walls of the large canyons, the Tansill limestone, records a progradation of back-reef limestone eastward across the top of the reef. This, again, is another indication of the general regressive tendency of Permian reefs.

At the end of the Guadalupian Epoch, one might visualize the Guadalupe Mountains National Park as follows. The shoreline was nearly coincident with the crest of the present Guadalupe escarpment. The back-reef lagoon to the west was mainly emergent. To the east, the Delaware Basin remained

unfilled by sediments, but contained water over 1000 ft deep. The basic "reef complex" physiography was still present.

At the beginning of the Ochoan Epoch, the Permian Basin appears to have tilted upward in the west and downward to the east, along an axis in the eastern part of the Delaware Basin. As a result, the Guadalupe Mountains National Park area became tilted upward and may have been emergent, whereas the eastern part including the Central Basin Platform became more deeply submerged. This "dead sea" received only periodic replenishment of water and the extremely arid climate of the time created a rate of evaporation considerably in excess of the rate of influx of water of normal sea-water salinity. With continued evaporation and eventual supersaturation of calcium sulfate came deposition of the Castile anhydrite and gypsum. Continued evaporation led to deposition of the Salado Salt and associated potash minerals. A final effort of transgression by the sea afforded deposition of the Rustler Formation. Concommitant with the withdrawal of the Rustler Sea occurred the deposition of the fluviatile sediments of the Dewey Lake Formation. If one might have viewed the Permian Basin at the end of the Ochoan Epoch, he would have seen no high Guadalupe Mountains. The Delaware Basin was filled, the Central Basin Platform was covered, the Midland Basin was filled, and the Capitan reef was buried. The Guadalupe Mountains were no more than low knobs which rose only slightly above a broad, flat depositional plain.

## MESOZOIC HISTORY

Triassic, Jurassic, and Cretaceous history adds little to the story of the Guadalupe Mountains National Park except a late Triassic subsidence of the Delaware Basin, which permitted the deposition of a rather thick sequence of the fluviatile deposits of the late Triassic Dockum Group. The area probably was completely emergent during the Jurassic Period. Cretaceous rocks were deposited over the area, but subsequent erosion has removed all save a few remnants in the Delaware Basin and across the Central Basin Platform. Thicker and more continuous sequences of Cretaceous rocks may be seen in areas south of the Guadalupe Mountains.

## CENOZOIC HISTORY

The Permian Basin along with the balance of Trans-Pecos Texas remained emergent following the close of the Cretaceous Period. In some places, notably the Guadalupe Mountains and the Llano Estacado, eastward flowing streams removed nearly all vestiges of Cretaceous rocks. To the south, volcanic activity produced the huge volcanic piles now seen in the Davis Mountains, the Sierra Vieja, and in the Big Bend region. During late Miocene and early Pliocene time, western Texas, along with most of western North America, was subjected to nearly vertical uplift and accompanying block mountain and graben basin faulting. The spectacular topography of the west side of the Guadalupe Mountains as well as that along the front of

the Diablo Plateau at the margin of Salt Basin were produced by this diastrophic episode. The eastern Guadalupes and the balance of the Permian Basin were not faulted, but uplift permitted groundwater to permeate and dissolve much of the Salado and Castile formations in the Delaware Basin. With removal, by solution, of the evaporite sequence, collapse of the overlying Permian, Triassic, and Cretaceous rocks produced a huge closed depression commonly called the "Pecos Depression." Debris eroded from the mountainous terrain to the west accumulated in and ultimately filled the "Pecos Depression" to overflowing and the blanket of fluviatile sand, gravel, and clay extended eastward to form the Ogallala Formation of the Llano Estacado. Preliminary evidence indicates that the surface of the High Plains was graded initially to the tops of the highest peaks in the Guadalupe Mountains. Again, as at the close of the Permian Period, the Guadalupe Mountains were buried, this time by Pliocene sands and gravels. Near the beginning of the Pleistocene Epoch, headward erosion by the Pecos River pirated the "Pecos Depression." With progressive deepening of the Pecos Valley and consequent removal of loosely consolidated sediment by stream erosion and transportation, the Guadalupe Mountains have been exhumed.

No references have been cited in this report as it is intended to present only a "thumb nail" sketch of salient features of the geological history of the Guadalupe Mountains National Park area. For more detailed discussions of the structure and stratigraphy of the region, the reader is referred to the following.

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# *Late Pleistocene Plant Communities in the Guadalupe Mountains, Culberson County, Texas*

THOMAS R. VAN DEVENDER, W. GEOFFREY SPAULDING, and ARTHUR M. PHILLIPS, III, University of Arizona, Tucson

For half a century the caves along the Guadalupe escarpment in New Mexico and Texas (Fig. 1) have provided exciting records of past biotas. Rich bone deposits in Burnet Cave (Howard 1932; Schultz and Howard 1935), Williams Cave (Ayer 1936), Dry Cave (Harris 1970), Pratt Cave (Gehlbach and Holman 1974), and the High Sloth Caves (Logan and Black, this volume) have documented dramatic changes in the mammalian fauna of the Guadalupe Mountains over the past 10,000 years. Large extinct animals including horse (*Equus* sp.), camels (*Camelops, Tanupolama*), and Shasta ground sloth (*Nothrotheriops shastense*) have been recovered. Bones of several small mammals, now restricted to high-elevation forests to the north, including the yellow-bellied marmot (*Marmota flaviventris*, Stearns 1942), bushy-tailed packrat (*Neotoma cinerea*, Harris 1970; Logan and Black, this volume; Schultz and Howard 1935), and the masked shrew (*Sorex cinereus*, Logan and Black, this volume), also have been recovered from these caves. However, most of these vertebrate fossils were collected in moist limestone caves where plant macrofossils and pollen are not commonly preserved. Because of this lack, most of the present theories on the Ice Age environments and paleoecology of the Guadalupe Mountains were based solely on the vertebrate record.

In this paper, we present a chronological sequence of late Pleistocene and Holocene plant communities spanning the last 13,000 years. The chronology is based upon plant macrofossils and pollen taken from the Upper Sloth Caves (C-05, C-08, and C-09, designations given by the National Park Service) and from Williams Cave (Fig. 1). These materials have been studied with the permission and support of the National Park Service and Guadalupe Mountains National Park. Most of the fossils from the Upper Sloth Caves were collected in conjunction with the recent excavation for verte-

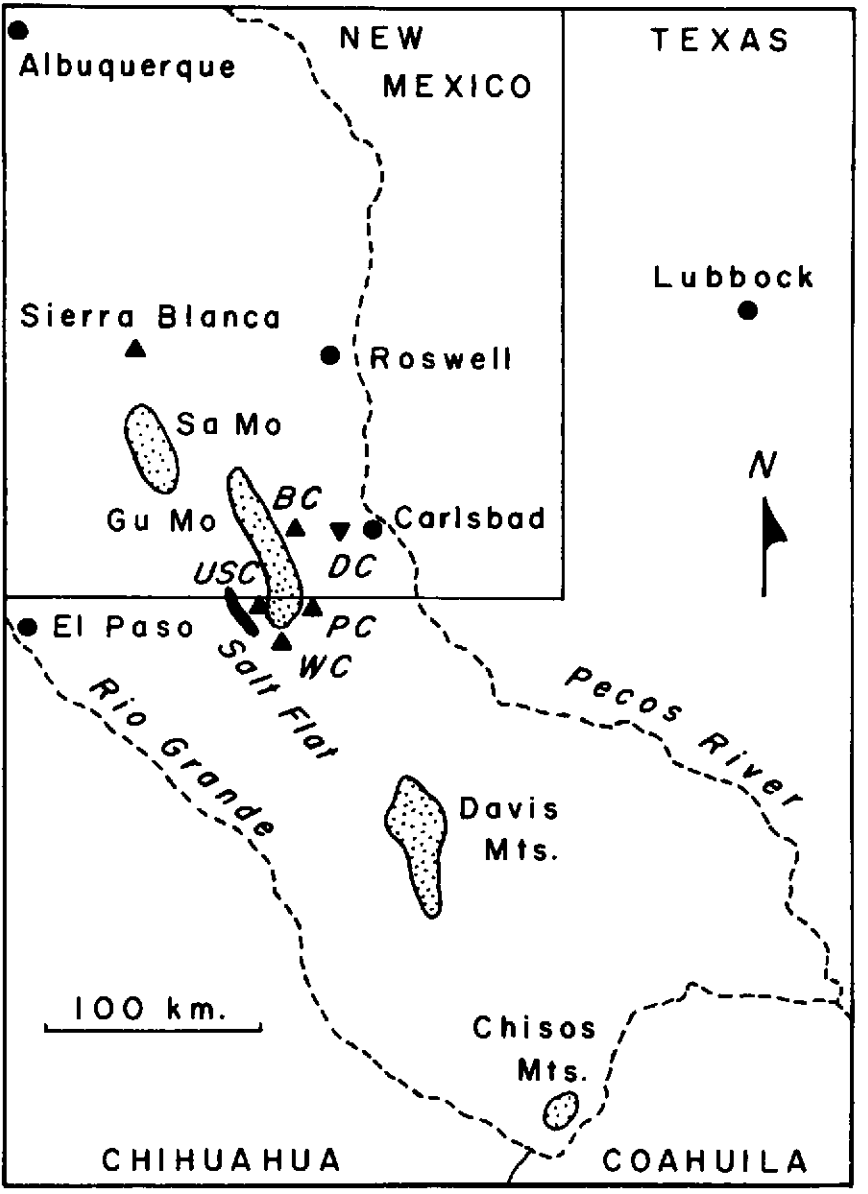


Fig. 1. Map of important localities mentioned in text. GuMo = Guadalupe Mountains, SaMo = Sacramento Mountains, BC = Burnet Cave, DC = Dry Cave, PC = Pratt Cave, WC = Williams Cave, USC = Upper Sloth Caves, N = north.

brate fossils by Lloyd E. Logan of Texas Tech University. The plant macrofossils will be deposited in the collections of the National Park Service,

Carlsbad, New Mexico. Plant nomenclature used in this paper follows Correll and Johnston (1970); tree distributions follow Little (1971).

## BIOCHRONOLOGICAL ZONES

The plant communities in the Guadalupe Mountains have gradually changed from relatively mesic woodland and forest associations during pluvioglacial climates in the late Wisconsin Glacial Epoch to the present xeric Chihuahuan desertscrub. This transition can be segregated into two late Pleistocene (Wisconsin 1 and 2) and at least two Holocene (Holocene 1 and 2) biochronological zones characterized by particular plant macrofossils (Tables 1, 2) and pollen assemblages (Fig. 2, Tables 3, 4). The macrofossil and pollen data are placed into a time perspective by stratigraphy and by radiocarbon dating of carefully selected material from known stratigraphic contexts. A summary of the characteristic plant species, pollen assemblages, and radiocarbon dates is presented in Table 2.

**Wisconsin 1A.**—The oldest samples of plant macrofossils and pollen were collected from an indurated fossil packrat (genus *Neotoma*) midden and from cave fill in two of the Upper Sloth Caves (C-08, C-09). These caves are located at 2000 m elevation below Shumard Peak on the steep west face of the Guadalupe Mountains. The macrofossils record a subalpine forest with *Picea* sp. (spruce), *Juniperus* sp. (juniper), *J. communis* (dwarf juniper), *Pseudotsuga menziesii* (Douglas fir), *Pinus strobiformis* (southwestern white pine, including *P. flexilis* of other authors), *P. edulis* (Colorado pinyon), *Ostrya knowltonii* (hop-hornbeam), *Quercus gambelii* (Gambel oak), *Arctostaphylos* sp. (manzanita), *Robinia neomexicana* (New Mexican locust), and *Rubus strigosus* (raspberry). Two radiocarbon dates on *Picea* sp. needles were 13,000 ± 730 (A-1539) and 13,060 ±280 (A-1549) radiocarbon years before present (BP). The present vegetation is a complex, high-elevation Chihuahuan desertscrub mixed with chaparral and grassland species. The only trees presently near the Upper Sloth caves are two relict *Pinus edulis* in protected, shady spots. The pollen assemblages (relative percentages) associated with the Zone W1A macrofossils are characterized by moderate *Picea*, moderate to high *Ostrya*, high Gramineae, and low Cheno-ams and short-spine Compositae (Fig. 2). *Rubus*-type Rosaceae and *Ribes* pollen are present.

*Picea* sp., *Juniperus communis*, and *Rubus strigosus* are no longer present in the flora of Texas. *Picea* sp. (*P. engelmannii* and *P. pungens*) and *Rubus strigosus* presently reach their southern limit in the Sacramento Mountains, New Mexico, 110 km to the north (Fig. 3; Little 1971). *Picea chihuahuana* (Chihuahuan spruce) presently occurs near Creel, Chihuahua, Mexico, 450 km to the southwest in the Sierra Madre Occidental at about 2215 m elevation. However, this species is distantly related to the Rocky Mountain species and certainly represents a much earlier distributional separation than the late Wisconsin (Gordon 1968). The distribution of *Rubus strigosus* differs somewhat in that it is present in pine forest and pine-oak woodland

TABLE 1. Late Pleistocene plant macrofossils recovered from cave fill and fossil packrat middens in the Guadalupe Mountains, Culberson County, Texas. WC = William's Cave; C-08 and C-09 = High Sloth Caves; (F) = cave fill; (M) = *Neotoma* midden.

| Species | Common names | W(F) | WC2 (M) | C–08 (F) | C–08 (M) | C–09 (F) |
|---|---|---|---|---|---|---|
| A. Modern local desert and scrubland species | | | | | | |
| *Agave* sp. | Century plant | | | X | | X |
| *Artemisia* cf. *ludoviciana* | Estafiata | | X | | | X |
| *Atriplex canescens* | Four-wing saltbush | X | X | X | | |
| *Brickellia* sp. | Brickell-bush | | | X | X | X |
| *Ceanothus* sp. | Buck-brush | | | | | X |
| *Cercocarpus montanus* | Mountain mahogany | | | X | | X |
| *Chenopodium* sp. | Goosefoot | | | X | | |
| *Chrysothamnus* sp. | Rabbit brush | | | | X | |
| *Cucurbita* sp. | Gourd | X | | | | |
| *Dasylirion leiophyllum* | Smooth-leaf sotol | | | X | | |
| *Echinocereus* sp. | Hedgehog cactus | | | X | | X |
| *Ephedra* sp. | Mormon tea | | | | X | |
| *Fallugia paradoxa* | Apache plume | | | X | | |
| *Fendlera* sp. | Fendler-bush | | | | | X |
| *Garrya ovata* | Silk-tassel | | | X | | |
| *Helianthus* sp. | Sunflower | X | X | | | |
| *Lappula* sp. | Stick-seed | X | | | | X |
| *Lesquerella* sp. | Bladder-pod | | | | X | |
| *Lithospermum* sp. | | | | | | X |
| *Mentzelia* sp. | Stick-leaf | | X | | | |
| *Mortonia scabrella* | Tick-weed | | | X | | X |
| *Nolina* sp. | Beargrass | | | X | | |
| *Oenothera* sp. | Evening primrose | | | X | | |
| *Opuntia imbricata* | Cane cholla | | X | X | | X |
| *O.* (*Platyopuntia*) sp. | Prickly pear cactus | | X | X | | X |
| *Panicum* cf. *arizonicum* | Panic grass | | | X | | X |
| *Phacelia* sp. | Wild heliotrope | | X | | | X |
| *Phoradendron* sp. | Mistletoe | | X | | | |
| *Physalis* sp. | Ground-cherry | | X | | | X |
| *Quercus pungens* or *undulata* | Scrub oak | | | X | | X |
| *Quercus* sp. | Oak | X | X | | | |
| *Rhus* sp. | Sumac | X | X | | | X |
| *Sphaeralcea* sp. | Globemallow | | X | X | | |
| *Yucca* sp. | Yucca | X | | X | | X |
| B. Relict species in the modern flora near sites | | | | | | |
| *Berberis haematocarpa* | Algerita | | | X | X | X |
| *B. trifoliolata* | Barberry | X | X | | | |
| *Pinus edulis* | Colorado pinyon | X | X | X | X | X |
| C. Woodland species present today at higher elevations in Guadalupe Mountains | | | | | | |
| *Celtis reticulata* | Net-leaf hackberry | | X | X | | |
| *Juniperus* sp. | Juniper | X | X | X | X | X |
| *Ostrya knowltonii* | Hop-hornbeam | | X | X | X | X |
| *Pinus strobiformis* | Southwestern white pine | | | X | X | X |

TABLE 1. (continued)

| Species | Common names | W(F) | WC2 (M) | C-08 (F) | C 08 (M) | C-09 (F) |
|---|---|---|---|---|---|---|
| *Prunus serotina* | Black cherry | | X | | | |
| *Pseudotsuga menziesii* | Douglas fir | | | X | X | X |
| *Quercus gambelii* | Gambel oak | | | X | | X |
| *Robinia neomexicana* | New Mexican locust | | X | X | X | X |
| D. Extralocal species not present in the modern flora of Guadalupe Mountains | | | | | | |
| *Arctostaphylos* sp. | Manzanita | | | X | | X |
| *Juniperus communis* L. | Dwarf juniper | | | | X | |
| *Picea* sp. | Spruce | | | | X | X |
| *Rubus strigosus* Michx. | Raspberry | | | | | X |

habitats of New Mexico, Arizona, the Rocky Mountain states, and extends southward into the Sierra Madre Occidental of Chihuahua and Sonora, Mexico. Its absence in the Guadalupe Mountains today is difficult to explain, but may indicate a hot, dry stress period during the Holocene. The nearest population of *Juniperus communis* is 325 km to the northwest in the southern end of the Rocky Mountains in north-central New Mexico (Fig. 3).

*Arctostraphylos* sp. could represent either *A. pungens* (point-leaf manzanita) or *A. uva-ursi* (bear-berry manzanita). *A. pungens* is a widespread southwestern species characteristic of chaparral communities. The only record of it in Trans-Pecos Texas is in the Davis Mountains, 110 km to the southeast (T. L. Burgess, pers. comm. 1975). *A. uva-ursi* is a low shrub in the understory of subalpine forests from the Rocky Mountains south into north-central New Mexico (Vines 1960). The remainder of the forest species in the W1A Zone presently occurs in the Guadalupe Mountains, but is restricted to mesic habitats such as McKittrick Canyon and The Bowl (upper Pine Springs Canyon) on the other side of the escarpment (Gehlbach 1967).

**Wisconsin 1B.**—Williams Cave is located at 1500 m elevation on the south-facing bajada below El Capitan Peak on the south end of the Guadalupe Mountains. An ancient packrat midden in Williams Cave contained a rich pinyon-juniper macrofossil assemblage including *Pinus edulis, Juniperus* sp., *Robinia neomexicana, Prunus serotina* (black cherry), *Celtis reticulata* (netleaf hackberry), and *Quercus* sp. (Table 1). A radiocarbon date on *Juniperus* sp. twigs and seeds was 12,010 ± 210 BP (A-1540). A pollen assemblage from a roughly contemporaneous cave fill sample from Williams Cave contained very high *Juniperus*, moderate *Pinus*, high total arboreal pollen ($\sum$AP; 82.5 to 90.5%), and moderate *Artemisia* pollen (Fig. 2, Table 2).

The fossil *Juniperus* material probably represents *J. monosperma* (one-seed juniper), but *J. pinchotii* (red-berry juniper) cannot be ruled out on the basis of leaf morphology. Both *J. deppeana* (alligator-bark juniper) and *J.*

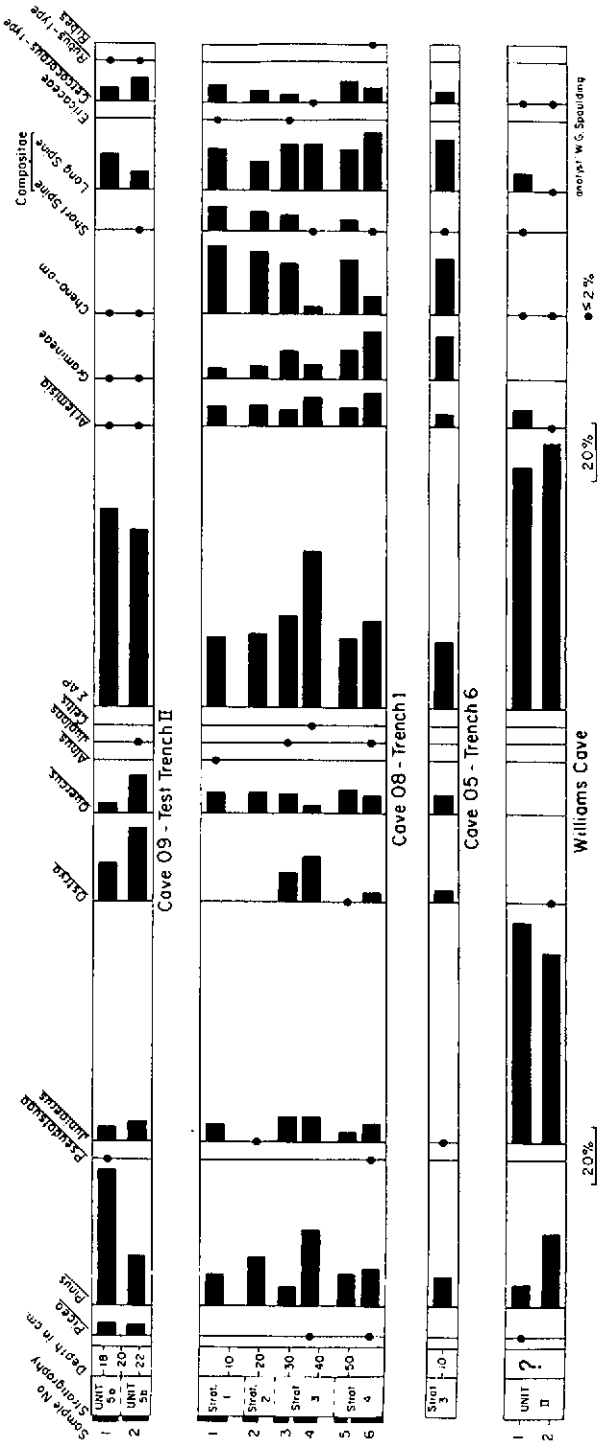


**Fig. 2.** A diagram of relative frequencies of selected pollen taxa. All percentages calculated from a sum of 200 grains. Pollen taxa not included in diagram are presented in Table 4.

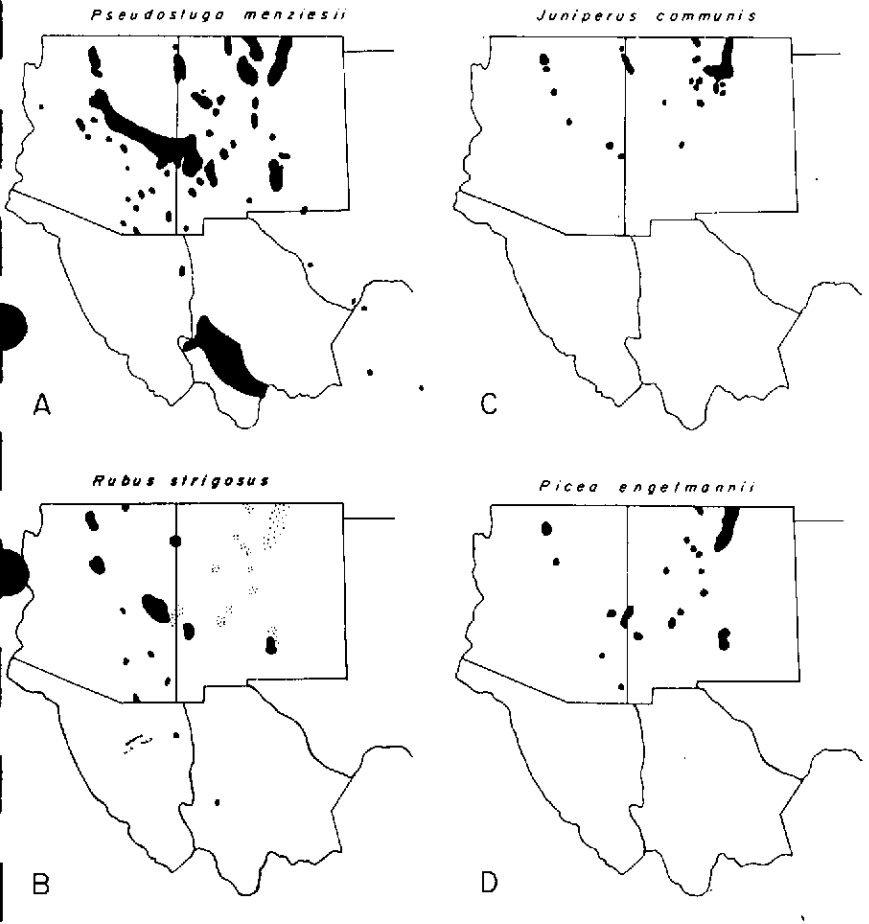


**Fig. 3.** Distribution maps of important species in the late Pleistocene plant macrofossil assemblages in the Upper Sloth Caves, Guadalupe Mountains, Culberson County, Texas. Maps A, C and D after Little (1971). Map B from University of Arizona Herbarium specimens; probable areas are stippled.

*copulorum* (Rocky Mountain juniper) can be identified, but were not in the Williams Cave deposits.

The present vegetation near Williams Cave is Chihuahuan desertscrub with shrub and succulent components. Important shrubs include *Larrea divaricata* (creosote-bush), *Acacia neovernicosa* (viscid acacia), *Mortonia scabrella* (sandpaper bush, tick-weed), *Fouquieria splendens* (ocotillo), *Prosopis glandulosa* (Torrey mesquite), and *Viguiera stenoloba* (skeleton-leaf goldeneye). Important succulents include *Agave lecheguilla* (lechuilla), *Dasylirion leiophyllum* (sotol), *Yucca baccata* (banana yucca), *Y. elata* (soapweed yucca), *Y. torreyi* (Torrey yucca), and many cacti in the

TABLE 2. Late Pleistocene and Holocene biochronological zonation in the Guadalupe Mountains, Culberson County, Texas. BP = years before present; m = meters; W = west; S = south; WC = Williams Cave; AP = aboreal pollen; W = Wisconsin; H = Holocene; A = Laboratory number University of Arizona.

| Zone | Elevation (m); slope | Cave | Radiocarbon dates (BP) | Characteristic plant species | Relative pollen percentages |
|---|---|---|---|---|---|
| W1A | 2000 W | C-08<br>C-09 | A-1549: 13,060 ± 280 (*Picea* needles)<br>A-1539: 13,000 ± 730 (*Picea* needles) | *Picea* sp., *Juniperus communis, Pseudostuga menziesii, Pinus strobiformis, P. edulis, Ostrya knowltonii, Quercus gambelii, Robinia neomexicana, Arctostaphylos* sp., *Rubus strigosus* | Samples: C-09: 1, 2; C-08: 6. *Picea* moderate; AP high. *Ostrya* high to moderate. Graminae high (C-08: 6). *Rubus*-type moderate (C-09: 1, 2). *Ribes* (C-08: 6) present. Cheno-ams and short-spine Compositae low. |
| W1B | 1500 S | WC | A-1540: 12, 040 ± 210 (*Juniperus* twigs) | *Pinus edulis, Juniperus* sp., *Quercus* sp., *Celtis reticulata, Robinia neomexicana, Prunus serotina* | Samples: WC: 1, 2. *Juniperus* very high; *Pinus* moderate; *Quercus* absent; AP high *Artemisia* low. Cheno-ams low. Graminae absent. |
| W2 | 2000 W | C-08 | A-1519: 11,590 ± 230 (Sloth dung)<br>A-1533: 11,760 ± 610 (Artiodactyl dung)<br>A-1583: 10,750 ± 140 (Sloth dung)<br>A-1584: 11,060 ± 180 (Sloth dung)<br>A-1534: 10,780 ± 140 (Sloth dung) | *Pseudostuga menziesii, Pinus strobiformis, P. edulis, Juniperus* sp., *Ostrya knowltonii, Quercus gambelii, Robinia neomexicana, Celtis reticulata* | Samples: C-08: 3, 4, 5. *Picea* moderate to absent; *Ostrya* high; *Pinus* and AP moderate to high. Cheno-ams low to moderate. Short-spine Compositae variable. Graminae moderate. |

TABLE 2. (continued)

| Zone | Elevation (m); slope | Cave | Radiocarbon dates (BP) | Characteristic plant species | Relative pollen percentages |
|---|---|---|---|---|---|
| H1 | 2000 W | C–05<br>C–08 | None | ?*Pinus edulis, Juniperus* sp., *Celtis reticulata, Opuntia* sp., *Dasylirion leiophyllum, Nolina* sp., *Rhus* sp. | Samples: C–05: 1, C–08: 1, 2. *Picea* absent. *Ostrya* low or absent; AP moderate. Chenoams and short-spine Compositae high. |
| H2 | 1500 S<br>2000 W | | None | Present flora | None |

*Coryphantha, Echinocereus, Mamillaria,* and *Opuntia* genera. A few relict *Juniperus monosperma* are in a sandy arroyo 1 km to the east at the same elevation as Williams Cave.

Presently, pinyon-juniper woodland probably analogous to the paleocommunity recorded in the Williams Cave packrat midden occurs as low as 1550 to 1700 m in the Pine Springs Canyon and Frijole Ranch areas. However, *Quercus* is more important in these areas than it was in the fossil community. Yet, the south face of El Capitan Peak above Williams Cave is so steep and rocky that a modern analogue to the paleocommunity might be over 2450 m elevation. The physiography of the Guadalupe Escarpment is so complex that we will not attempt to estimate the depression of vegetation zones due to Pleistocene climates.

Although the Williams Cave samples are intermediate in age between the two periods recorded in the Upper Sloth Caves, we feel that the ancient pinyon-juniper community probably corresponds to the more mesic of the two, Zone W1.

**Wisconsin 2.**—Trench 1 in Cave C-08 has a multilayered stratigraphy with both Holocene and late Pleistocene units. Stratum 3 (25 to 45 cm) contained an upper layer of dung of the extinct Shasta ground sloth and of wood (Lloyd E. Logan, pers. comm. 1975). Directly beneath this unit was a mat of leaf litter designated as Stratum 3a (40 to 45 cm). A large sample of the leaf litter was collected, sorted, and identified (Table 1). The macrofossils from Stratum 3a document a mixed conifer forest composed of *Pseudotsuga menziesii, Pinus strobiformis, P. edulis, Juniperus* sp., *Ostrya knowltonii, Quercus gambelii, Robinia neomexicana,* and *Celtis reticulata*. A similar stratigraphic section was seen in a nearby pit from a previous excavation. A radiocarbon date on large artiodactyl fecal pellets (possibly *Cervus elaphus merriami*, Merriam's elk) from the equivalent of Stratum 3a, Trench 1 in that pit (below the sloth dung layer) is 11,760 ± 610 BP (A-1533). A date on sloth dung from Cave C-05 is 11,590 ± 230 BP (A-1519), which demonstrates that the sloths inhabited the caves during Zone W2. The pollen samples from this zone are characterized by absent to moderate *Picea*, moderate to high *Pinus* and $\Sigma$ AP, high *Ostrya*, low to moderate Cheno-ams (Chenopodiaceae plus *Amaranthus*), and moderate Gramineae (Fig. 2, Table 2).

Zone W2 differs from Zone 1A (Caves C-08 and C-09) in the absence of the extralocal mesic forest species from the immediate vicinity of Cave C-08, i.e., *Picea* sp., *Juniperus communis, Rubus strigosus,* and *Arctostaphylos* sp. The difference in climate needed to account for this absence may not have been too dramatic. Spruce pollen is not transported as far, nor is spruce as prolific a pollen producer as pine (Potter and Rowley 1960). The presence of small, but significant amounts of *Picea* pollen suggest that spruce may have been restricted to mesic areas either in front of Caves C-05 and C-09 (north-facing) or in mesic habitats on the east side of the mountains rather than being completely extirpated from the area. Also, a skull of *Sorex cinereus* (masked shrew), a subalpine forest species presently living no closer

TABLE 3. Holocene and late Pleistocene plant macrofossils associated with pollen samples from Caves C-08 and C-09, Guadalupe National Park, Culberson County, Texas. Pollen data, depth of samples, and stratigraphy are presented in Fig. 2.

| | C-08; 1 | C-08; 2 | C-08; 3 | C-08; 4 | C-08; 5 | C-08; 6 | C-09; 1 | C-09; 2 |
|---|---|---|---|---|---|---|---|---|
| Species | | | | | | | | |
| A. Modern local desert and scrubland species | | | | | | | | |
| *Agave* sp. | | | X | | | | | |
| *Atriplex canescens* | | X | X | | | | | |
| *Cercocarpus montanus* | X | | X | | | | | |
| *Dasylirion leiophyllum* | | | | | | X | | |
| *Echinocereus* sp. | X | | | | | | | X |
| *Fallugia paradoxa* | X | X | | | X | | | |
| *Garrya ovata* | | | X | | | | | |
| *Kallstroemia parviflora* | | X | | | | | | |
| *Mortonia scabrella* | X | | | | | | | |
| *Oenothera* sp. | | | | | | X | | |
| *Opuntia* (*Platyopuntia*) sp. | X | X | | | | | | X |
| *Panicum* cf. *arizonicum* | | | | | X | | | |
| *Quercus pungens* or *undulata* | | | X | | | | | |
| *Sphaeralcea* sp. | | | | | | X | | |
| *Yucca* sp. | X | | X | X | | | X | X |
| B. Relict species in modern flora near sites | | | | | | | | |
| *Berberis haematocarpa* | | | X | X | X | X | | X |
| *Pinus edulis* | X | | X | | | X | | X |
| C. Woodland species present today at higher elevations in Guadalupe Mountains | | | | | | | | |
| *Celtis reticulata* | | | X | | | | | |
| *Juniperus* sp. | | | | | | X | | X |
| *Ostrya knowltonii* | | | | | | X | | |
| *Pinus strobiformis* | | | X | | X | X | | X |
| *Pseudotsuga menziesii* | | | X | X | | X | | X |
| *Quercus gambelii* | | | X | X | | | | X |
| *Robinia neomexicana* | | | | | X | X | | |
| D. Extralocal species not present in the modern flora of Guadalupe Mountains | | | | | | | | |
| *Arctostaphylos* sp. | | | X | | | | | |
| *Juniperus communis* | | | | | | | | X |
| *Picea* sp. | | | | | | | | X |
| *Rubus strigosus* | | | | | | | | X |

than northern New Mexico, was found in Stratum 3a with the Zone W2 assemblage (Lloyd E. Logan, pers. comm. 1975). Minor changes of this sort in the vegetational composition would be expected with a gradually warming climate. The most dramatic change in the vegetation was probably from

TABLE 4. Pollen counts of samples from Cave 09, Test Trench II (C-09), Cave 08, Trench I (C-08), Cave 05, Trench 6 (C-05) and Williams Cave (WC). Depth of samples and stratigraphy presented in Fig. 2.

| Pollen types | C-09; 1 | C-09; 2 | C-08; 1 | C-08; 2 | C-08; 3 | C-08; 4 | C-08; 5 | C-08; 6 | C-05 | WC 1 | WC 2 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Picea* | 8 | 7 | | | | 4 | | 3 | | 1 | |
| *Pseudotsuga* | 1 | | | | | | | 1 | | | |
| *Pinus* | 92 | 34 | 22 | 34 | 13 | 52 | 22 | 26 | 21 | 14 | 51 |
| *Juniperus* | 10 | 13 | 12 | 3 | 17 | 17 | 7 | 12 | 4 | 150 | 130 |
| *Ostrya* | 26 | 50 | | | 19 | 30 | 3 | 6 | 8 | | 1 |
| *Quercus* | 7 | 25 | 14 | 14 | 13 | 5 | 16 | 12 | 13 | | |
| *Alnus* | | | 1 | | | | | | | | |
| *Juglans* | | 1 | | | 1 | | | 1 | | | |
| *Celtis* | | | | | | 1 | | | | | |
| *Sarcobatus* | | | | | | | | 1 | | | |
| Cheno-ams | 1 | 2 | 46 | 42 | 34 | 5 | 37 | 12 | 38 | 1 | 3 |
| Gramineae | 4 | 4 | 7 | 9 | 19 | 10 | 19 | 32 | 29 | | |
| *Ephedra torreyana*-type | | 1 | 5 | 24 | 1 | | 5 | 3 | | | |
| *E. nevadensis*-type | | | | | | | 1 | | | | 1 |
| *Artemisia* | 4 | 4 | 13 | 14 | 11 | 19 | 13 | 22 | 8 | 12 | 3 |
| Short-spine Compositae | | 2 | 17 | 13 | 11 | 4 | 8 | 2 | 3 | 1 | |
| Long-spine Compositae | 24 | 12 | 28 | 20 | 31 | 31 | 28 | 39 | 35 | 12 | 3 |
| *Senecio*-type | | | | | | | | | 1 | | |
| *Cercocarpus*-type | 9 | 16 | 16 | 9 | 6 | 3 | 14 | 10 | 8 | 2 | 2 |
| *Rubus*-type | 1 | 3 | | | | | | | | | |
| *Eriogonum* | | | 3 | 2 | 3 | | | | | | |
| Ericaceae | | | 1 | | 1 | | | | | | |
| Cruciferae | | 1 | | | 1 | | | 2 | 1 | 1 | |
| Scrophulariaceae | 1 | 1 | | | 1 | 2 | | | | | |
| Onagraceae | | | | | 1 | | | | 1 | | |
| *Crossosoma*-type | | | | | 1 | | | | | | |
| Leguminosae | 1 | 1 | 1 | 1 | 2 | | 4 | | 3 | 1 | |
| *Ribes* | | | | | | | | 1 | | | |
| Saxifragaceae | 1 | 6 | | 1 | | 1 | | | | | |
| *Rhus* | | 1 | | | | | | 2 | | | 1 |
| *Cereus*-type | 1 | | | | | | | | | | |
| *Tidestromia* | | | | | | | 1 | | | | |
| Caryophyllaceae | | | | 1 | | 1 | | 2 | 2 | | |
| Nyctaginaceae | | | | | | | 1 | | 1 | 1 | |
| ?*Sambucus* | | | | | | | 1 | | | | |
| *Euphorbia* | | | | 1 | | | 1 | | | | |
| Malvaceae | | | | | | 1 | 2 | | | | |
| *Yucca* | | | | | | 1 | | | | | |
| Primulaceae | | | | 1 | | | | | | | |
| Undetermined | | 5 | 3 | 2 | 4 | | 2 | 2 | 7 | 2 | 1 |
| Unknown | 9 | 11 | 11 | 9 | 10 | 13 | 13 | 10 | 17 | 3 | 4 |
| N | 200 | 200 | 200 | 200 | 200 | 200 | 200 | 200 | 200 | 200 | 200 |
| ΣAP | 144 | 130 | 49 | 51 | 63 | 108 | 48 | 61 | 46 | 165 | 182 |
| Trilete, psilate spores | 2 | 6 | 19 | 20 | 9 | 3 | 12 | 14 | 2 | | |
| *Lycopodium*-type spores | | | | | 1 | | | | 17 | | |

Zones W2 to H1 (Holocene 1) accompanying the climatic change that marked the beginning of the Holocene.

**Holocene 1.**—Several undated stratigraphic units in Caves C-05 and C-08 appear to be early Holocene in age. The plant macrofossils are mostly xerophytic species that presently grow near the caves. *Juniperus* sp., *Celtis reticulata*, and perhaps *Pinus edulis* (some possibility of contamination because the sample contained but a single needle) are the only remnants of the former forests that grew near the caves. The climatic sequence during the Holocene is controversial for that portion of the Southwest where summer monsoonal rain is important (western Texas, southeastern Arizona, and New Mexico); r(Antevs 1962; Freeman 1972; Johnston 1963). The Antevs model of a warm, moist Anathermal period from 9000 to 7000 BP followed by a hot, dry Altithermal period was based on geological and palynological data from the Great Basin and a chronology extrapolated from the Swedish literature (Antevs 1952). That climatic sequence has been generally, and often uncritically, applied to the summer monsoon areas of the Southwest. However, Martin (1963a) and Mehringer et al. (1967) interpreted the pollen record for southeastern Arizona as indicating a warm, dry climate from 10,000 to 8000 BP and a warm, moist climate from 8000 to 3000 BP. Recently, Van Devender and Worthington (1977), using fossil reptile and amphibian data from Howell's Ridge Cave, Little Hatchet Mountains, southwestern New Mexico, suggested that both the Anathermal and the Altithermal periods were warm and moist and that the nearby playa did not dry up until about 4000 years ago. Perhaps *Juniperus* sp. and *Celtis reticulata* persisted near the Upper Sloth Caves in the Guadalupe Mountains during a warm but relatively moist period in the early Holocene. Such a climatic regime might explain the unusual occurrence of mesic reptiles such as *Phrynosoma douglassi* (short-horned horned lizard) and *Thamnophis* sp. (gartersnake) in Holocene deposits in Pratt Cave, McKittrick Canyon, on the east side of the Guadalupes (Gehlbach and Holman 1974).

**Holocene 2.**—This zone contains modern vegetation and suggests a modern climatic regime. It differs from H1 only in the absence of the xerophilous woodland species such as *Juniperus* sp., *Celtis reticulata*, and possibly *Pinus edulis*. The discussion above on the Altithermal controversy shows that the Holocene vegetation and climate are more complex than these two units would imply. Undoubtedly, a great many details remain to be learned.

## DISCUSSION

The late Wisconsin plant communities have been discussed in a surprising number of publications, considering the scarcity of plant fossils. Stearns (1942) and Murray (1957) suggested that the late Pleistocene life zones were lowered 1230 m and 1075 m, respectively, based on the present distributions of such subalpine mammals as *Marmota flaviventris* and *Neotoma cinerea*. Both authors believed that the Hudsonian or Canadian life zones (=

spruce–fir forest) formerly grew at 1400 m elevation in the vicinity of Burnet Cave, 50 km W of Carlsbad, Eddy County, New Mexico (Schultz and Howard 1935). Antevs (1955) suggested a 770-m depression of life zones at Burnet Cave, using estimates of snowline depression derived from cirque elevations of late Pleistocene montane glaciers in Colorado and New Mexico. The glacier nearest to the Guadalupe Mountains was on Cerro Blanco (= Sierra Blanca), 70 km W of Roswell, New Mexico. Antevs assumed that the subalpine mammals were transported to Burnet Cave from forest habitats on the nearby mountain crests which are at 2000 m elevation in this part of the Guadalupes. Recently, Galloway (1970) suggested a 1300 to 1400 m late Pleistocene lowering of timberlines in the entire Southwest, using periglacial solifluction deposits in the Sacramento Mountains just north of the Guadalupes. He assumed that the upper treeline was no higher than 2050 m and arrived at a paleoclimate of 10 to 11°C lower mean annual temperature than the present and 80 to 90% of the present precipitation. This scheme would place the lower edge of the Douglas fir–southwestern white pine forest, presently above 2400 m in the Guadalupe Mountains (Gehlbach 1967), along the Pecos River to the east at ca. 1075 m elevation. However, both Antevs (1955) and Leopold (1951) concluded that pluvial Lake Estancia, New Mexico, needed increased precipitation as well as reduced temperature to maintain it.

Taking Zone W1A in the biochronological sequence presented above, let us examine these ideas. *Picea* sp., *Pseudotsuga menziesii*, *Pinus strobiformis*, and other montane species existed at an elevation of 2000 m on the exposed, steep, relatively xeric west side of the escarpment 13,000 years ago. The present vegetation zones on the east side of the escarpment are lower, and probably the Zone W1A subalpine forest extended as low as 1700 m on that side where there is a gentler slope and a more mesic habitat. This forest probably occurred to at least 2475-m elevation above the Upper Sloth Caves. In the light of this evidence, as well as that of others (Wright et al. 1973), we reject the values for timberline depression given by Galloway (1970).

The Williams Cave record (Zone W1B) demonstrates that on the bajada at the southern end of the Guadalupes at 1500 m elevation the paleocommunity was a pinyon–juniper woodland (the *Juniperus–Pinus* dominance type of Gehlbach 1967). The pollen record from this zone has a very high $\Sigma$AP dominated by *Juniperus*. We interpret this as representing a woodland dominated by *Juniperus* (probably *J. monosperma*) with scattered *Pinus edulis*. The fossil pollen assemblages contained no record of the present Chihuahuan desertscrub vegetation. A xerophilous juniper woodland probably extended west to the Salt Flat playa at 1100 m and east to the Pecos River at 1075 m elevations. This reconstruction is supported by Wells' (1966) record of xerophilous woodland as low as 615 m in the Big Bend of Texas, 330 km to the southeast. We feel that a pinyon–juniper woodland extended northward along the eastern flanks of the Guadalupe Escarpment at similar

elevations at least to the Burnet and Dry Cave areas (1290 to 1420 m) west of Carlsbad. Today, the woodland extends lower on the east side of the Guadalupes, and the late Pleistocene community of this area was probably somewhat more mesic than that of the Williams Cave area. The distribution of *Pinus ponderosa* (ponderosa, or yellow pine) at that time is not known, as we have not found macrofossils of this species in our sites. It may not have expanded considerably beyond its present range. At any rate, the vegetation near Burnet Cave was not the Hudsonian or Canadian Zone forests suggested by Stearns (1942) and Murray (1957).

Based on the faunal record, Harris (1970) reconstructed the paleoenvironment of the Dry Cave area as Transition Zone big sagebrush (*Artemisia tridentata*) and grassland communities with scattered junipers and yellow pines. *Lagurus curtatus* (sagebrush vole) is a member of the Dry Cave fauna that is presently restricted to the big sagebrush communities farther north. *Artemisia tridentata* presently occurs no closer than north-central New Mexico. The Williams Cave and Upper Sloth Caves pollen samples did contain low to moderate amounts of *Artemisia* pollen, but *A. tridentata* is a prolific pollen producer (see discussion in Martin 1963b). *A. ludoviciana* (estafiata) is a widespread, common, herbaceous species that presently grows near both sites and was also a component of the Pleistocene macrofossil assemblages from the Upper Sloth Caves. The Williams Cave samples do not record a dense *A. tridentata* community and may only represent *A. ludoviciana*. If *A. tridentata* were present near Williams Cave, it must have been as widely scattered individual plants. The Williams Cave samples contained no grass pollen at all. Hence, the big sagebrush or grass reconstruction cannot be sustained for the Williams Cave area. Dry Cave is about 55 km NNE at 1290 m elevation and it is possible that *A. tridentata* was better represented there. At any rate, the paleocommunity in the Dry Cave area was probably an Upper Sonoran Zone pinyon-juniper woodland rather than a Transition Zone forest, grassland, or sagebrush community.

The Zone W1A forest on the top of the Guadalupe Mountains was a mixture of Hudsonian (*Picea* sp., *Juniperus communis*), Canadian (*Pseudostuga menziesii, Pinus strobiformis*), Transition (*Quercus gambelii, Ostrya knowltonii*), and Upper Sonoran (*Pinus edulis, Juniperus* sp.) Life Zone elements. *Abies concolor* (white fir) and *A. lasiocarpa* (cork-bark fir) are common subalpine forest, mixed-conifer, or pine forest species that were not found in any of the fossil samples, nor was *Abies* pollen found in any of our Guadalupe Mountains Pleistocene samples. *Abies* pollen cannot be transported great distances, but if *Abies* were at all common in the Pleistocene communities, some pollen grains would be expected. Stands of *Pinus ponderosa*, an important southwestern Transition Zone species, presently occur as low as 1700 m on the east side of the escarpment. It was not found in any of the Pleistocene macrofossil samples, although it was surely in the mountains at that time. The Zone W1A forest was a diverse mixed-conifer forest

that cannot be fitted easily into the Merriam Life Zone system. The responses of these species were individualistic in nature as was suggested by Gleason (1939).

If plant communities are considered as coincident, overlapping distributions of plant species along several environmental gradients (including a time gradient; McIntosh 1958, 1967; Whittaker 1967), the relationships of plant communities to climate must be general, i.e., the adaptations to climate are at the species level. Most animals have behavioral adaptations which help them to ameliorate extremes of temperature or moisture. Animals generally have a wider ecological amplitude than plants, and even the subalpine species in the Pleistocene faunas (*Marmota flaviventris* and *Neotoma cinerea*) are found occasionally in lower-elevation habitats (Harris 1970; Finley 1958). Perhaps the fauna and flora together should be viewed as a biotic continuum in which animal species occasionally lived in somewhat different habitats than at present. *Marmota flaviventris* and *Neotoma cinerea* may well have been more common in late Pleistocene pinyon–juniper woodlands than they are at present. An important consideration in the reconstruction of past environments using present biotic distributions is that the present climate is probably unusual. Most of the biota have endured a greater period of time under the Pleistocene glacio-pluvial climates than under the present interglacial conditions.

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# *Preliminary Report on the Ecology of Fire Study, Guadalupe Mountains and Carlsbad Caverns National Parks*

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The National Parks Act of 1916 states that the purpose of the national parks "is to conserve the scenery and the natural and historic objects and the wild life [*sic*] therein and to provide for the enjoyment of the same in such a manner and by such means as will leave them unimpaired for the enjoyment of future generations." Although the National Park Service has been largely successful in operating park lands for the enjoyment of the public, preservation attempts have oftentimes impaired these natural areas by bringing about unplanned and undesired changes in the ecosystems (Stone 1965). For example, by stressing the protection of objects rather than processes within ecosystems, suppression of all fires was justified easily in the parks (Agee 1974). Results of this action are well known in some instances, but little understood in others at present.

Leopold et al. (1963) drew major attention to management policies in the national parks and recommended as a primary goal "that the biotic associations within each park be maintained, or where necessary recreated, as nearly as possible in the condition that prevailed when the area was first visited by the white man."

The Leopold Committee (Leopold et al. 1963) urged that wildfire be restored to its role as an ecological factor where practical and suggested the use of controlled burns as a tool for restoring natural ecologic conditions to some national park areas. Based largely upon recommendations contained in the Leopold Committee Report, a new fire management philosophy has evolved in the past decade. The present administrative policies for natural areas (U.S. Department of the Interior, National Park Service 1970) state:

> The presence or absence of natural fires within a given habitat is recognized as one of the ecological factors contributing to the perpetuation of plants and animals native to the habitat.

Fires in vegetation resulting from natural causes are recognized as natural phenomena and may be allowed to run their course when such burning can be contained within predetermined fire management units and when such burning will contribute to the accomplishment of approved vegetation and/or wildlife management objectives.

Prescribed burning to achieve approved vegetation and/or wildlife management objectives may be employed as a substitute for natural fire.

In keeping with this policy, fire management plans for Guadalupe Mountains and Carlsbad Caverns National Parks designate natural burn units in portions of each park. The plans stipulate that the effects of fire on vegetation, including recovery rates, will be determined. Detailed investigations of the potential effects of wildfire on the interior mountain and canyon areas of Guadalupe Mountains National Park, especially in relation to its effect on relict taxa or plant communities, are called for before considering inclusion of these areas in a natural burn unit. In addition, a study to determine the feasibility of using controlled burns to restore or manipulate habitats that have been altered severely by human activities is required by the plan.

## HISTORICAL ASPECTS

There can be little doubt that the vegetation in the area has undergone change, especially during the last century. Photographs taken at Carlsbad Caverns National Park less than 40 years ago give evidence that dramatic vegetational changes have occurred since livestock grazing was eliminated from the park. Verbal accounts by lifelong residents of the area have told of lush grasslands once existing in areas presently dominated by *Larrea tridentata* and *Acacia constricta*. A report by Pope (1854) made no less than three references to the large pine forests covering the east slopes of the Guadalupe Mountains in the vicinity of the Pinery. Another reference in the Pope (1854) report told of the great abundance of grama grass surrounding a camp located between the salt flats and the west escarpment.

No one factor can account for all the observed and suspected vegetational changes. The effects of livestock grazing, past fire history, water table fluctuations, and possible climatic changes must be assessed. Attempts to determine the relative influence of each of these factors will be continued through searches for historical accounts and old photographs of the area, interviews with longtime residents of the area, tree-ring studies to detect past fire frequencies and possible climatic changes, and age–class determinations of trees in forested areas.

Overgrazing has shifted the competitive advantage in favor of lignophytes and allowed former grasslands to be invaded by shrubs (Humphrey 1953, 1974). Weakening of the grass cover also lowered the incidence of fires which were effective in checking the spread of woody species (Hastings and Turner 1965). Dog-hair thickets of *Pseudotsuga menziesii* and *Pinus ponderosa* found in portions of the relict coniferous forest may be due in part to the planting of seeds by the hooves of livestock.

Many of the pines reported by Pope (1854) to inhabit the east side of the Guadalupe Mountains were logged for construction and fuel purposes by the early settlers in the area. However, this activity alone does not seem to be a satisfactory explanation for the distribution or paucity of reproduction noted for *Pinus* in the area today.

The flow from Lower Pine Spring was reduced greatly following an earthquake in 1931. Whether the apparent lowering of the water table can be attributed entirely to tectonic movements, or if man's activities in the region also may have influenced ground-water levels in the area needs investigation. The 1931 earthquake also might account for the absence of young conifers in a meadow area at 2450 m elevation, located south of Pine Springs Canyon. At the same elevation, but to the north of the canyon, seedling establishment has led to the dog-hair thickets referred to previously.

The past role of fire in the area must be determined. Inner growth rings of sections from fire-scarred trees in the coniferous forest gave evidence that for one 150-year period, fires occurred on the average of every 25 years. The outer rings showed no evidence of fire for over 100 years. The sections were representative of but one location. To determine the past frequency of extensive burns, many more sections and cores must be examined. Accurate dating of the fires must await the completion of a master tree-ring chronology for the Guadalupe Mountains. Robinson (1969) reported that fires swept through the relict forest in Guadalupe Mountains National Park in about 1858 and again in 1908. There is evidence of the occurrence of smaller fires contained by natural barriers during the interim between extensive burns. Results from an analysis of the size-class distribution of conifers in The Bowl show that under the right set of environmental conditions the understory now could contribute to an extensive crown fire (Table 1). The same analysis indicated that *Pseudotsuga menziesii* has invaded more

TABLE 1. Density by size class of conifers in The Bowl. Based on data from thirty-six 5 by 25 m plots, mixed aspects.

| Species | Diameter at breast height | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 0–1 dm | | | | | | | |
| | <0.5 dm | | >0.5 dm | 1 to 2 dm | 2 to 3 dm | 3 to 4 dm | 4 to 5 dm | >5 dm |
| | <1 m Tall | >1 m Tall | | | | | | |
| *Pseudotsuga menziesii* | 3411 | 525 | 14 | 9 | 12 | 3 | 6 | 4 |
| *Pinus strobiformis* | 332 | 166 | 14 | 19 | 18 | 18 | 4 | 2 |
| *Pinus ponderosa* | 303 | 453 | 184 | 82 | 9 | 4 | 4 | 2 |
| *Juniperus deppeana* | 14 | 12 | 1 | 6 | 2 | 3 | 7 | – |
| Totals | 4060 | 1156 | 224 | 116 | 41 | 29 | 21 | 8 |

TABLE 2. Dominant species of the understory and reproductive stratum in relation to slope aspect in The Bowl. Understory trees (*Quercus spp.* and *Juniperus deppeana*) are not considered.

| Slope aspect (°) | Slope (%) | Series | Dominants | |
|---|---|---|---|---|
| | | | Overstory | Reproductive stratum |
| 160 | 16 | B-10 | *Pinus ponderosa* | *Pinus ponderosa* |
| 195 | 12 | B-11[a] | Mixed | Mixed |
| 225 | 16.5 | B-4 | *Pinus ponderosa* | *Pinus ponderosa* |
| 260 | 20.5 | B-7 | *Pinus strobiformis*<br>*Pinus ponderosa* | *Pseudotsuga menziesii*<br>*Pinus ponderosa* |
| 290 | 36.5 | B-12[b] | *Pseudotsuga menziesii*<br>*Pinus strobiformis* | *Pseudotsuga menziesii*<br>*Pinus ponderosa* |
| 320 | 13 | B-1 | *Pseudotsuga menziesii*<br>*Pinus strobiformis* | *Pseudotsuga menziesii* |
| 350 | 27.5 | B-8 | *Pseudotsuga menziesii*<br>*Pinus strobiformis* | *Pseudotsuga menziesii* |
| 40 | 21 | B-3 | *Pseudotsuga menziesii*<br>*Pinus strobiformis* | *Pseudotsuga menziesii* |
| 40 | 28 | B-5 | *Pseudotsuga menziesii*<br>*Pinus strobiformis* | *Pseudotsuga menziesii*<br>*Pinus strobiformis* |
| 80 | 18 | B-6 | *Pinus ponderosa* | *Pseudotsuga menziesii*<br>*Pinus ponderosa* |
| 105 | 16.5 | B-9[c] | *Pinus ponderosa*<br>*Pinus strobiformis* | *Pseudotsuga menziesii*<br>*Pinus strobiformis* |
| 110 | 15 | B-2 | *Pinus ponderosa*<br>*Pinus strobiformis* | *Pinus ponderosa* |

[a]A mesic habitat for this aspect. Relatively deep soil, gentle slope, and shaded.
[b]Plots actually spanned two different habitat types.
[c]Open canopy.

TABLE 3. Fire summary for Carlsbad Caverns National Park, 1940–74.

| Five-year period | Fire source | | | | | |
|---|---|---|---|---|---|---|
| | Lightning | | | Human | | |
| | Number | Total acres | Average acres/burn | Number | Total acres | Average acres/burn |
| 1940–44 | 6 | 164 | 27 | 6 | 45 | 7.5 |
| 1945–49 | 3 | 63 | 21 | 13 | 23 | 1.9 |
| 1950–54 | 6 | 190 | 32 | 9 | < 0.1 | < 0.1 |
| 1955–59 | 1 | 15 | 15 | 3 | < 0.1 | < 0.1 |
| 1960–64 | 3 | < 0.1 | < 0.1 | 1 | 3 | 3 |
| 1965–69 | 3 | 3 | 1 | 2 | 8 | 4 |
| 1970–74 | 9 | 9150 | 1017[a] | 2 | < 0.1 | < 0.1 |

[a]Excluding the 9100-acre Cottonwood Burn, the average becomes 6.6 acres.

southernly exposures (Table 2). Apparently, this can be attributed to the shade afforded by the overstory. Should the canopy become more open, *Pinus ponderosa* and *P. strobiformis* can be expected to increase in the reproductive stratum.

For centuries fires were set in southwestern pine forests by Indians for hunting and waging war (Cooper 1960; cited by Hanks and Dick-Peddie 1974). Pope (1854) wrote of the Indians setting fire to the prairie a few miles southeast of Guadalupe Peak. Seven days later he noted, "The young grass is springing up on the ground that was fired a few nights ago. The prairie still continues to burn; the light can be seen at a distance of 45 miles from camp. . . ."

The recorded fire histories for both parks are summarized in Tables 3–4. Since 1960, lightning-caused fires have outnumbered those caused by humans. Improved surveillance during periods of extreme fire danger and public assumption that "fires are bad" have contributed to the recorded reversal in trend. In general, human-caused fires have resulted in fewer acres burned per fire than those originating from lightning strikes. The former usually have been suppressed before they could spread because of easier access than most lightning-caused fires.

TABLE 4. Fire summary for Guadalupe Mountains National Park, 1960–74.

| | Fire source | | | | | |
|---|---|---|---|---|---|---|
| | Lightning | | | Human | | |
| Five-year period | Number | Total acres | Average acres/burn | Number | Total acres | Average acres/burn |
| 1960–64 | 1 | 3 | 3 | 0 | 0 | 0 |
| 1965–69 | 1 | <0.1 | <0.1 | 1 | <0.1 | <0.1 |
| 1970–74 | 12 | 725 | 60 | 2 | 30 | 15 |

Since the natural burn policy was initiated at Carlsbad Caverns National Park in 1972, less than one-tenth acre has burned due to nonsuppression. The Cottonwood Fire of 1974 burned approximately 9100 acres of park land and accounted for most of the total acreage burned during the 1970 to 1974 period. Although much of the fire burned in the natural burn zone, continuous suppression efforts were waged until the fire was declared out. Burned vegetation recovered rapidly in most areas following the fire (Figs. 1-2).

Usual late spring and early summer conditions of high temperatures, low relative humidites and fuel moisture values, high lightning probability, and moderate to strong winds contribute to potentially high fire danger situations when combined with adequate fuel supplies. Most of the recorded

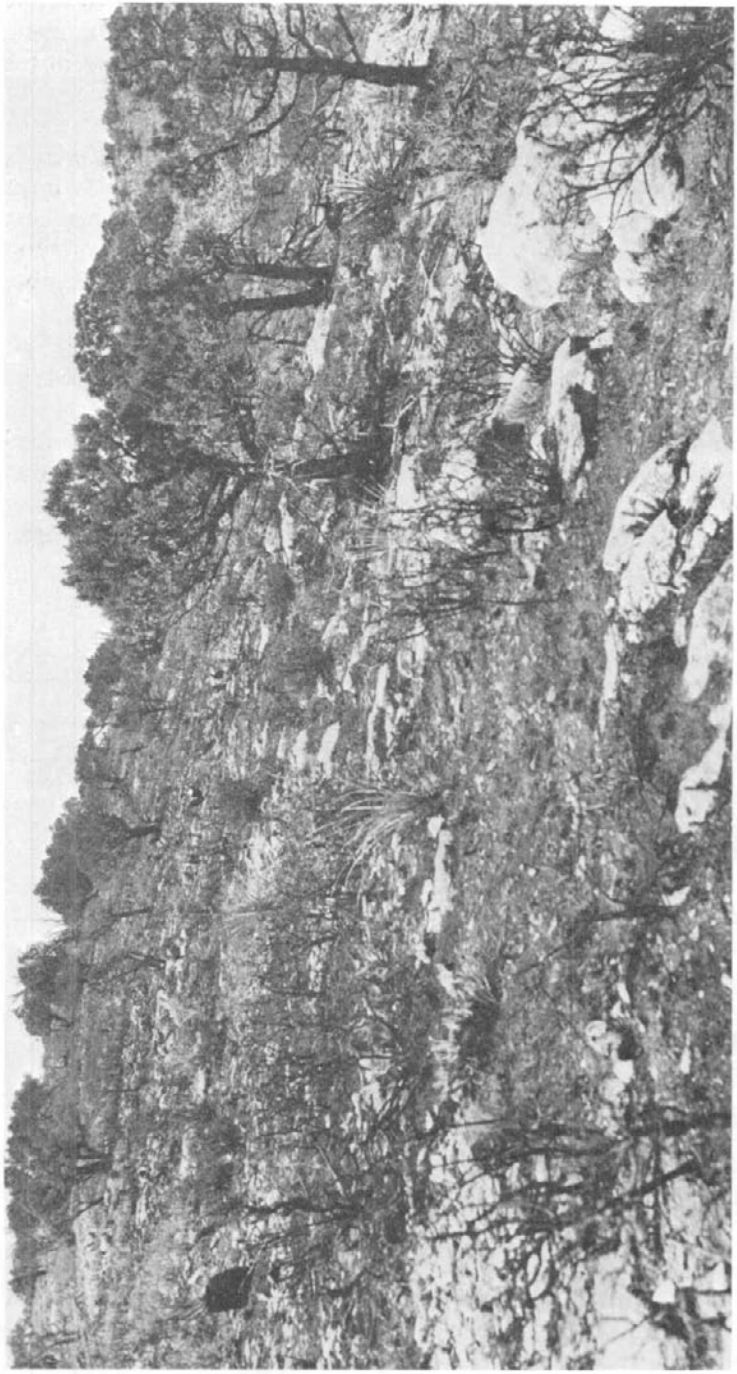

**FIG. 1.** View of the Cottonwood Burn near the west boundary of Carlsbad Caverns National Park as it appeared one month after the fire. Species of *Opuntia* and *Agave* were apparently heat-killed. Ground fuels consumed by the fire consisted mainly of grasses, the basal foliage of *Dasylirion leiophyllum* and *Nolina micrantha*, and *Quercus* leaves. Average scorch height on *Juniperus deppeana* was approximately 4

FIG. 2. Same view as Fig. 1, but 3 months after the fire. The dominant grass is *Muhlenbergia emersleyi*. New vegetative growth is evident for *Dasylirion lieophyllum, Nolina micrantha,* and *Quercus* sp. *Juniperus deppeana* show good recovery from scorch with little apparent damage. Above normal amounts of precipitation were received in the 3 months following the fire.

fires in the parks have been limited to relatively small areas, having been contained by natural barriers or suppressed by fire crews. Successful fire suppression efforts and the elimination of livestock grazing in both parks have resulted in a gradual accumulation of fuel over the years. With the present fuel loads in many portions of the parks, an increase in the number, size, and intensity of fires can be expected. Successive cat-face scars on trunks of *Juniperus deppeana* throughout the back country of Carlsbad Caverns National Park suggest that extensive fires have occurred periodically in the past.

## VEGETATION ANALYSIS

An attempt was made to examine all burns, one-tenth acre or larger in size, listed in the fire records of each park. It was not possible to identify the boundaries of burns that occurred prior to 1968. Of more than 35 burns located, eight were selected in the succulent desert formation for a comparative vegetation analysis. One of the eight selected for study was reburned during the summer of 1974 before sampling could be completed.

For each burn, a 25 by 50 m permanent plot was established on the burn and on a nearly identical adjacent unburned stand. Cover was determined for shrubs by species along ten 25-m line intercepts placed at 5-m intervals within each plot. Species within a 20 by 50 cm plot frame placed at 5-m intervals along each 25-m line were recorded by species according to one of six cover classes (fifty 0.1 $m^2$ subplots per 25 by 50 m plot). Intercept data were converted to coverage for individual species. Coverage and frequency values were calculated for species sampled in the subplots. Coverage values for species sampled in common by the two methods were in close agreement.

Species shared in common by pairs of stands for a given burn averaged less than 50% of the combined total species for the pairs, which suggested the presence of seral species on the burned plots. However, when species present in all control stands were compared with species present in all burn stands, no seral species were indicated. When the same comparison was made after eliminating from consideration those species with frequency values of 2% or coverage of 1% or less, species shared in common between control and burn pairs averaged nearly 100%. Species area curves indicated that the stands were oversampled by a factor of 2 in terms of taxa present. However, plots of cumulative mean coverage showed that between 40 and 50 subplots per stand were necessary to achieve coverage data.

Most of the fires have not been of an intensity to eliminate many species. The competitive balance among species was altered by burning, but not to the extent that invasion of the site by seral species was permitted. The most evident effect of fire was to change the relative cover values for species present. Coverage of grasses and forbs often increased after burning, whereas that of shrubs usually was reduced (Table 5). Similar results were

TABLE 5. Coverage values for burned (B) and control (C) stands.

| Growth form | Stone ?? | | Lefthook 68 | | Gunsight 68 | | Dark 71[a] | | Rattlesnake 71 | | Guadalupe Pass 71 | | Bean Burner 71 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | B | C | B | C | B | C | B | C | B | C | B | C | B | C |
| Graminoids | 48.1 | 23.2 | 63.0 | 42.3 | 49.2 | 41.4 | 34.1 | 35.3 | 52.2 | 31.1 | 83.0 | 91.2 | 52.2 | 59.2 |
| Forbs | 2.2 | 2.2 | 4.4 | 1.8 | 2.5 | 1.3 | 4.8 | 1.7 | 0.2 | 0.2 | 12.3 | 16.2 | 3.2 | 6.6 |
| Woody shrubs | 6.4 | 6.0 | 6.1 | 14.7 | 7.9 | 4.6 | 2.2 | 11.2 | 9.1 | 9.1 | 0.3 | 6.2 | 15.2 | 14.5 |
| Stem succulents and rosette shrubs | 4.1 | 25.6 | 6.0 | 13.8 | 10.1 | 21.1 | 4.0 | 20.2 | 15.2 | 42.4 | 1.6 | 6.0 | 0.9 | 1.7 |
| Total coverage | 60.8 | 57.0 | 79.5 | 72.6 | 69.7 | 68.4 | 45.1 | 68.4 | 76.7 | 82.8 | 97.2 | 119.6 | 79.6 | 82.0 |

[a]Not on park land and had experienced moderate grazing by cattle when sampled.

reported by Dwyer and Pieper (1967) for range land in south-central New Mexico.

Responses of individual taxa to fire were not consistent. Most of the variation observed probably is due to differences in fire intensities and in soil moisture availability following the burn. Factual data concerning the role of fire in the Chihuahuan Desert region are difficult to obtain because this has been a topic of little research (Humphrey 1974). Limited observations on the reaction of individual taxa to fire in the Chihuahuan Desert were reported by Kittams (1972) and Humphrey (1974). Information concerning shrub species whose distribution includes the Chihuahuan Desert region has been reported in studies conducted elsewhere (Reynolds and Bohning 1956; Pond and Cable 1960; Dwyer and Pieper 1967; White 1969; Pase and Lindenmuth 1971; Cable 1972; Wink and Wright 1973; Heirman and Wright 1973; Wright 1974a). Conflicting responses to fire reported for many taxa were attributed to varying seasonal and other environmental conditions that have seldom been well defined (Pieper et al. 1973). Wright (1974b) reported on the long-term effect of fire on several grasses common to this area and related the degree of response within individual taxa to annual precipitation.

## EXPERIMENTAL PRESCRIPTION BURNS

A series of experimental burns is planned in order to document the response of vegetation to fires under different burning conditions and fuel types. The behavior of both headfires and backfires will be documented in several habitat types for five ranges of fuel moisture—3 to 5%, 6 to 8%, 9 to 11%, 12 to 14%, and 15 to 17%. Attempts will be made to burn at the midpoint intervals. Tentative plans call for burning when winds do not exceed 25 kmph, air temperature is between 10 and 30°C, and relative humidity is between 20 and 60%.

The plot dimensions for each burn will be 10 by 10 m, with a 5-m buffer strip on each side to eliminate edge effects. Total area to be burned per fire, including the buffer strip, will be 400 $m^2$. A fire line at least 1 m wide will be cleared completely around the outside edge of each buffer strip. Individual plots for each of the 10 burns per habitat type will be picked randomly from a grid of 12 plots, leaving 2 plots per grid as controls.

A vegetation analysis of each plot will precede the actual burning and will be repeated periodically to follow recovery rates. Plant–water relations will be followed in selected taxa on burned and control plots. Fire intensity can be calculated as the product of the rate of fire spread and fuel energy consumed (van Wagtendonk 1974).

## SEED GERMINATION

Studies of temperature and water potential limits for germination, and the effect of fire on viability and germination are needed for selected species for which seeds serve as the primary means of propagation. Information from these studies, when considered with energy budget data from various habi-

tats, can be used to estimate the success of different taxa on fire-altered habitats.

Although no controlled environment studies of seed germination have commenced, a simple test was conducted twice in the laboratory with seeds harvested in November 1973. Seeds were placed in petri dishes on three layers of moistened filter paper. Tap water was added as needed. Light and temperature conditions were variable. Seeds were given no special pretreatments. Two replicates per trial were prepared and each replicate consisted of 50 to 150 seeds, depending on seed size. Germination counts were made daily and the results are summarized in Table 6.

TABLE 6. Results from two seed germination trials. Percent germination is on the fifteenth day of each trial.

| Species | Germination (%) | | Average number of days to reach 50% germination |
|---|---|---|---|
| | Feb–Mar trial | Aug–Sept trial | |
| *Agave lechuguilla* | 93 | 88 | 4 |
| *Arbutus xalapensis* | 80 | 90 | 10 |
| *Bouteloua curtipendula* | 3 | 23 | – |
| *Bouteloua gracilis* | 5 | 39 | – |
| *Bouteloua hirsuta* | 12 | 13 | – |
| *Dasylirion leiophyllum* | 9 | 0[a] | – |
| *Yucca torreyi* | 98 | 98 | 7 |

[a]Seeds infected with a fungus and failed to germinate.

Greater germination percentages were attained by *Bouteloua gracilis* and *B. curtipendula* during the second trial and most likely were due to after-ripening. Future studies should investigate the effect of stratification on seeds of species slow to germinate or with low germination percentages. Seed viability for some species will be tested with 2,3,5–triphenyl tetrazolium chloride.

*Agave lecheguilla* is a prolific seed producer and the seeds germinate readily in relation to other species tested. Apparently, this is an important factor in its success on sites where competition by other species has been substantially reduced, such as on overgrazed lands.

Although seed viability in *Arbutus xalapensis* was high, growth of seedlings progressed slowly in the laboratory. Field conditions necessary for germination of seeds and establishment of the species probably occur infrequently. Even in those years favorable for germination, seedlings may die because their roots cannot keep pace with the descending depth of available soil moisture.

## PLANT WATER STATUS

Important in the consideration of relict species, and especially those occupying tension zones, is their ability to survive in conditions imposed by

fire-altered habitats. Water availability is undoubtedly the greatest single limiting factor controlling the distribution of plants in this area. Information concerning the seasonal water status of these species under present conditions is important in predicting their future success in modified microenvironments.

Some plants are capable of regulating the magnitude of internal moisture stress, whereas others lack this ability and conform to the various stresses of their environment (Hickman 1970). The pressure chamber technique for measuring moisture relations in plants (Scholander et al. 1965; Waring and Cleary 1967) affords a convenient means for following the functional moisture stress in many plants under field conditions. Several taxa have been monitored periodically at Carlsbad Caverns National Park since October 1974. Representative species and the range of water potentials observed with the pressure chamber were as follows: *Pinus edulis*, −14 to −17 bars; *Juniperus pinchotii*, −17 to −20 bars; *Berberis trifoliolata*, −30 to −36 bars. These values represent baseline data, as none of the species was subjected to moisture stress during the monitoring period. As the drying season progresses, various adaptations of different taxa to decreasing moisture supplies will be sought by following their functional water stress patterns with diurnal measurements.

Additional studies concerning the moisture status of plants will include observations of stomatal diffusive resistances and cell osmotic potentials. Arid land plants possess numerous physiologic, morphologic, and anatomic adaptations for conserving moisture. Stomatal function is important to water economy. At finite transpiration rates, the lower limit of soil moisture availability is determined conceptually by the mesophyll osmotic potential, the resistance to water flow (controlled largely by the stomates), and the rate of transpiration. When the stomates are closed and the transpiration rate is zero, the cell osmotic potential determines the lower limit of soil moisture availability to the plant. Therefore, plants with low osmotic potentials have a definite advantage in moisture competition with plants possessing higher osmotic potentials, other factors being similar. Cell osmotic potentials and stomatal diffusive resistances will be observed for species during the intensive study of functional moisture stress.

## ENERGY BUDGETS

The degree of microenvironment modification of fire-altered habitats varies according to the intensity of the burn. Where fuel loads are light, burning will effect little change. Some areas presently have fuel loads, which, if burned under the right set of environmental conditions, would lead to significant changes. Information concerning the degree of change that can be expected under given burning conditions in specific habitats is important in predicting which taxa can survive in the fire-altered habitats, and what long-term effects on soil, soil microorganisms, and faunal populations can be expected. The degree of change can be estimated for each community type by

a consideration of the energy budget for a two-dimensional surface (Lowry 1969).

No studies are planned on this phase of the investigation until more information from other parts of the study are available.

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# *The Guadalupe Mountains—A Chink in the Mosaic of the Chihuahuan Desert?*

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My purpose is to place the Guadalupe Mountains, botanically, into a broad regional framework, on the basis of floristic and vegetational evidence. This has relevance in the current trend toward studying the floras of biotically coherent geographic units instead of the traditional (and probably still more practical) political-geographic units. One of the first of the biotic units delineated as an area for special floristic study was the so-called Sonoran Desert, which Shreve (1942) courageously delineated and which Wiggins wrote up floristically (Shreve and Wiggins 1964). Shreve (1942) also attempted to delineate the Chihuahuan Desert, with which he was less well acquainted.

*In 1971, in proposing to write a Chihuahuan Desert Flora*, I found it necessary and desirable to draw a line on the map to delineate the Chihuahuan Desert Region. Anybody who has tried to draw a line on a map purporting to separate biotically distinct regions knows how hazardous this can be to the integrity of communication. For the line has an unwarranted narrowness and inflexibility that contradicts everything we as field observers know about biotic, climatic, and substrate continuity, about the usual gradualness of transitions, and about the mosaic nature of the substrate and of the climate in those areas of much topographic relief. All these conditions conspire to give us in nature both tightly chinked biotic mosaics and broad biotic transitions that defy our line-drawing attempts. As a poet once said, "Nature mocks at human categories."

Nevertheless, lines *are* drawn on maps and in some cases they more or less successfully delineate biotic areas; in my case the line-drawing was a practical necessity. Lines thus drawn always represent compromises, and mine was no exception.

The line (Fig. 1) excludes the uppermost parts of the Guadalupe Mountains, which in fact constitute part of the northern boundary of the Chihuahuan Desert Region. Some confidence in this placement of the boundary may be inspired by the general consensus expressed in a recent symposium on the Chihuahuan Desert at Alpine, Texas. Many of the participants who

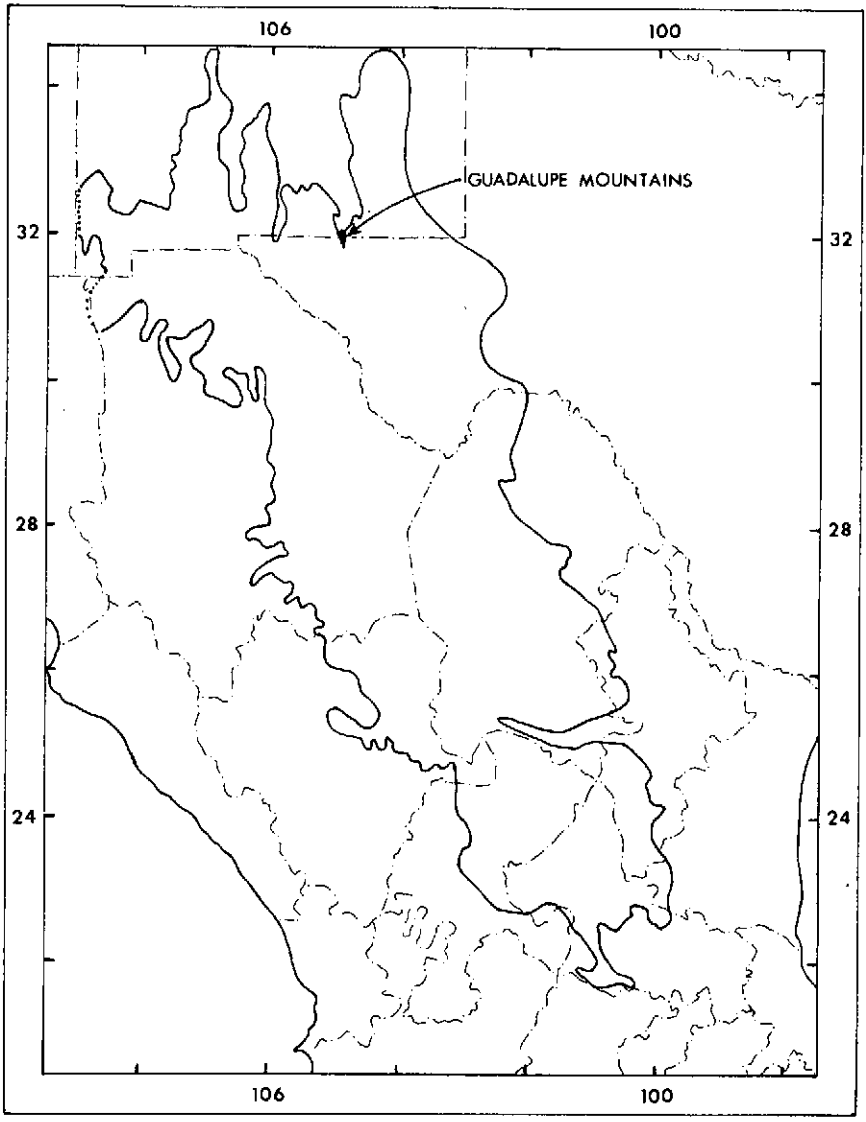


FIG. 1. Sketch-map showing the extent of the Chihuahuan Desert Region and the placement of the Guadalupe Mountains.

delineated the northern part of the chihuahuan Desert Region drew it in this area to exclude the higher part of the Guadalupe Mountains.

Those of us who have worked a long time with the flora of western Texas and northern Mexico are impressed by the botanical features of the Guada-

lupe Mountains, which seem to us to reflect strong influence of the southern Rocky Mountains and the mounainous parts of the Colorado Plateau, particularly those massifs which are largely calcareous. As examples, on the upper slopes we find the common ground cover of *Berberis repens* Lindley with *Fragaria bracteata* Heller and *Carexe burnea* Boott here and there, and the poisonous *Hymenoxys richardsonii* (Hooker) Cockerell var. *floribunda* (Gray) K. Parker on the overgrazed exposures, and much *Pinus edulis* Engelm. mixed with the other gymnospermous plants. In the better-watered canyons we find such plants as *Amelanchier utahensis Köehne, Aster hesperius* Gray, *Lonicera arizonica* Rehder, *Physocarpus monogynus* (Torrey) Coulter, *Polygonatum cobrense* (Wooton & Standley) Gates, *Robinia neomexicana* Gray, *Valeriana arizonica* Gray, and *Zigadenus elegans* Pursh, all of which are very special to us, reminiscent of the Rocky Mountains, and found nowhere else in Texas and nowhere in the Chihuahuan Desert Region.

As the only one of our Texas "front ranges" over 2000 m in altitude which is of calcareous rock (the Davis Mountains at 2500 m and the Chisos Mountains at 2400 m are of igneous rocks), the Guadalupe Mountains may be expected to show some other interesting, and, for Texas, unique floristic elements. Figure 2, in fact, shows what a truly massive and abrupt topographic, climatic, and biotic barrier these mountains are. Thus it may not be too surprising to find here such widespread north-temperate species as *Cystopteris bulbifera* (Linnaeus) Bernhardi, *Glyceria striata* (Lamarck) Hitchcock, *Lactuca graminifolia* Michaux, and *Lilium philadelphicum* Linnaeus var. *andinum* (Nuttall) Ker-Gawler, all of which are rather strongly mesophytic or even aquatic in their preferences, and all of which are rare or unknown elsewhere in Texas.

Neither is it too surprising that a few species which are found in the limestone Edwards Plateau 200 km to the southeast have small disjunct populations in the Guadalupe Mountains, which provide a relatively mesic island for their survival. These species include *Lithospermum parksii* I. M. Johnston var. *rugulosum* I. M. Johnston and *Liatris punctata* Hooker.

All these botanical components have led us to emphasize the relationships of the Guadalupe Mountains to biotic regions other than the Chihuahuan Desert Region, and I think it is wise and expedient to adhere to this exclusion. Thus I answer the question posed by my title in the negative, at least as it pertains to the uppermost parts of the Guadalupe Mountains.

Before we become too settled in our convictions, however, I think it is desirable briefly to look at the Guadalupe Mountains from a more northerly vantage point, let us say from the point of view of a botanist working in the northern half of New Mexico. Such a botanist visiting the Guadalupe Mountains would be struck primarily by the extent that the truly montane vegetation is areally restricted and depauperate. A suggestion of affinity to the southern Rockies would strike him as a trifle far-fetched and strained, and he would be more inclined to emphasize the numerous species which

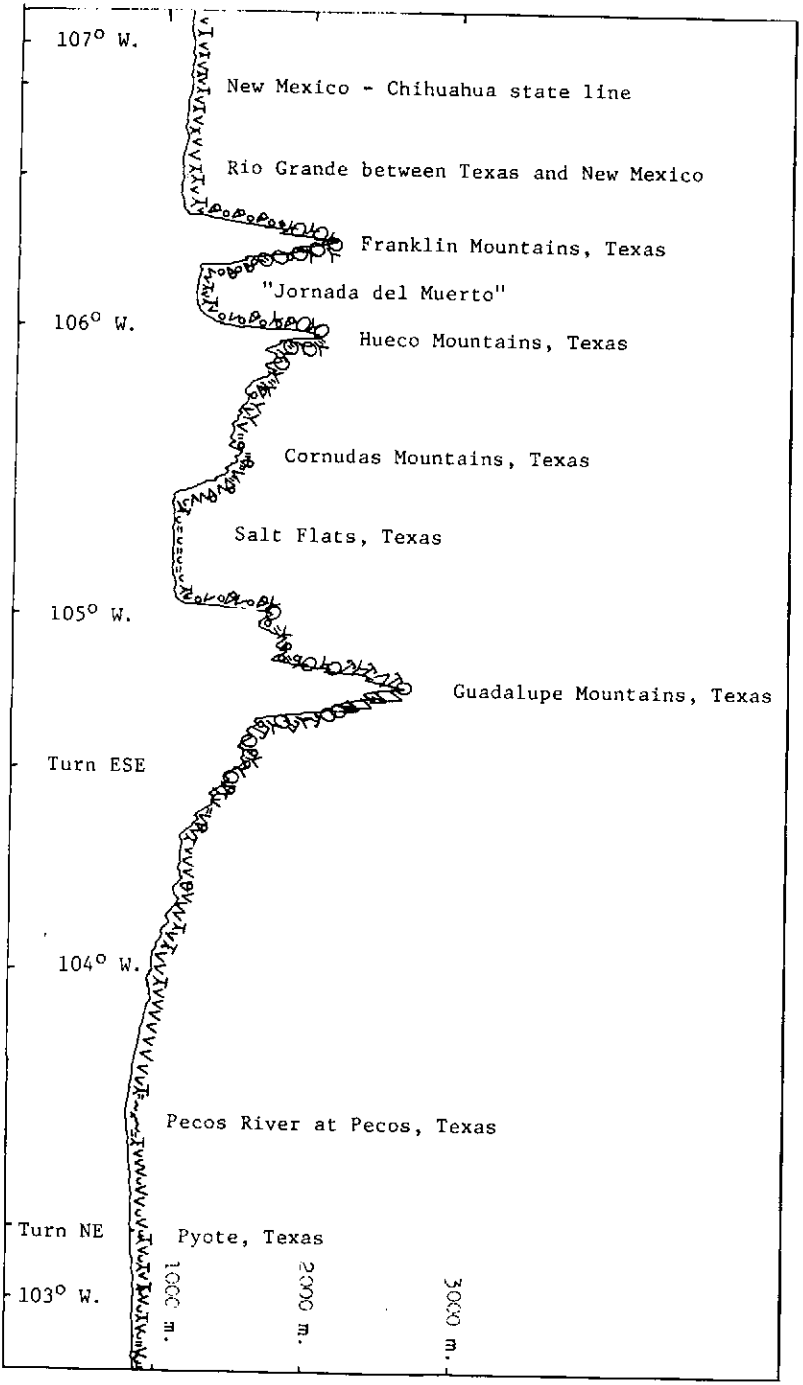


**FIG. 2.** Roughly east–west topographic profile through the Guadalupe Mountains just south of the 32nd parallel.

find their northern, northeastern, or northwestern limits in or near these mountains, indicating more southern affinities. The floristic elements at moderate elevations which are at or near their northernmost distributional limits in the Guadalupe Mountains include *Arbutus xalapensis* Kunth, *Chrysactinia mexicana* Gray, *Sophora secundiflora* (Ortega) DeCandolle and its relatives, *Juglans microcarpa* Berlandier, *Dichondra brachypoda* Wooton & Standley, *Quercus pungens* Liebman, *Rhamnus serrata* Schultes, *Selaginella lepidophylla* (Hooker & Greville) Spring, *Selaginella pilifera* A. Brown, and *Menodora longiflora* Gray. At lower elevations more and more strongly xerophytic elements are found at or very near their northernmost or northwesternmost limits; these include *Phyllanthus polygonoides* Sprengel, *Jatropha dioica* Cavanilles, *Bernardia obovata* I. M. Johnston, *Condalia warnockii* M. C. Johnston, *Leucophyllum minus* Gray, *Stenandrium barbatum* Torrey & Gray, *Ibervillea tenuisecta* (Gray) Small, *Ruellia parryi* Gray, *Mammillaria lasiacantha* Engelmann, and a number of other Cactaceae, *Viguiera stenolaba* Blake, *Boerhavia linearifolia* Gray, *Mimosa biuncifera* Bentham, *Cassia lindheimeriana* Scheele, and *Acleisanthes longiflora* Gray.

In summary, it appears that a balanced view of the Guadalupe Mountains will include a recognition of a dilute, weak, fragile, marginal, and areally restricted vegetational island reminiscent of the Southern Rockies and the mountains of the Colorado Plateau, as well as a vast area surrounding on three sides which is clearly part of the Chihuahuan Desert Region. In fact, there are mountain ranges wholly within the Chihuahuan Desert Region that strongly resemble the Guadalupe Mountains and that support more extensive gymnospermous forests, e.g., the Sierra de la Madera, Coahuila. The reason they are included within the Chihuahuan Desert Region is that they are more centrally located and completely surrounded by desert vegetation. The Guadalupe Mountains, at least the upper 500 m, are excluded because they are surrounded on only three sides by desert, and they are at the northern limit of that desert vegetation.

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# *Summary of the Vegetative Zones of the Guadalupe Mountains National Park, Texas*

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As even the nonbiologist could readily notice, the vegetation of the Guadalupe Mountains National Park is extremely varied and often of unique composition. Topographic, climatic, and edaphic factors interact to produce this vegetational mosaic in which the delimitation of general zones is often difficult if not impossible. Our purpose is to summarize the various vegetative regions of the Guadalupe Mountains National Park, with special attention given to those transitional and unique associations that defy such classification.

Warnock (undated) and Gehlbach (1967) have treated the vegetative communities of the Guadalupe Mountains region, thus some of our observations represent duplication. Gehlbach, however, described only the eastern escarpment, primarily McKittrick Canyon, and neither author commented adequately on certain portions of the park's higher elevations. Table 1 summarizes briefly the vegetative zones and specific plant associations of Warnock and Gehlbach. Potter and Robinson (1968) did describe a considerable portion of the coniferous forest areas in the park; again, however, some areas of interest were not included in their study area. In addition to these references, Glass and Reisch (1974) conducted an Interagency Browse Survey for the Guadalupe Mountains National Park and included therein is a detailed vegetation map for the entire park. The plant names used in this paper correspond to those in Correll and Johnston (1970).

## VEGETATIVE ZONES

For sake of simplicity, and in many cases for accuracy, we will categorize the park into three general biotic communities—desert, woodland, and forest. Specific plant associations within each of these zones can then be treated individually, whether a specific descriptive tag can be applied or not.

TABLE 1. Two schemes of vegetation classification for the Guadalupe Mountains. B. H. Warnock's (undated) formations and associations are in the left column. F. R. Gehlbach's (1967) system for the east escarpment only is listed by formations and dominance types in the right column. Nomenclature changes have been made to conform species names to Correll and Johnston (1970).

| WARNOCK | GEHLBACH |
|---|---|
| Desertscrub<br>*Prosopis glandulosa*<br>*Larrea tridentata–Prosopis glandulosa* | Shrub desert<br>*Larrea tridentata–Flourensia cernua*<br>*Acacia neovernicosa–Larrea tridentata* |
| Grassland<br>*Agave lecheguilla–Dasylirion leiophyllum*<br>*Bouteloua eriopoda–Aristida pansa*<br>*Dasylirion leiophyllum–Forsellesia spinescens*<br>*Dasylirion leiophyllum–Cercocarpus montanus* | Succulent desert<br>*Dasylirion leiophyllum–Agave lecheguilla*<br>*Juniperus monosperma–Agave lecheguilla* |
| Woodland<br>Chaparral: *Cercocarpus montanus–Ceanothus greggii–Quercus undulata–Q. pungens*<br>Evergreen/deciduous complex: *Quercus* sp.–*Juniperus* sp.–*Pinus edulis–Mimosa borealis–Acacia neovernicosa*<br>Canyon: *Arbutus xalapensis–Acer grandidentatum–Prunus serotina–Quercus muhlenbergii–Q. grisea–Juniperus monosperma–J. deppeana–Pinus edulis* | Evergreen woodland<br>*Quercus grisea–Juniperus (monosperma?)*[a]<br>*Quercus grisea–Juniperus deppeana*[b]<br>*Juniperus deppeana–Pinus edulis* |
| Riparian: *Populus* sp.–*Salix* sp.–*Juglans microcarpa–Celtis reticulata* | Deciduous woodland<br>*Juglans microcarpa–Dasylirion leiophyllum*<br>*Fraxinus velutina–Ostrya knowltonii* |
| Coniferous forest<br>*Pinus ponderosa*<br>*Pseudotsuga menziesii–Pinus strobiformis–P. ponderosa* | Coniferous forest<br>*Pinus ponderosa*<br>*Pseudotsuga menziesii–Pinus strobiformis* |

## Desert

Considerable portions of the region below the west and east escarpments would qualify as desert. Because of the dominance of microphyllous shrubs such as *Larrea tridentata, Prosopis glandulosa, Acacia neovernicosa, Flourensia cernua,* and *Atriplex canescens,* this vegetation is often referred to as desertscrub. On most of the west bajada below 5000 ft there is "typical"

desertscrub in which *Larrea* dominates either totally or in association with *Bouteloua eriopoda, Sporobolus airoides,* and *Erioneuron pulchellum.* Some of the more unique plant associations in the park occur in particular edaphic situations on the lower west side. A more thorough review of the desert vegetation of this region is available (Burgess and Northington 1975); however, a brief overview of some of the more salient features is presented herein.

Near the edges of the Salt Flat, *Sporobolus airoides* dominates, with *Atriplex canescens, Frankenia jamesii,* and *Allenrolfea occidentalis* constituting an open shrub stratum. Heavy clay soils, for example, in the vicinity of Homsley's Dugout, support extensive stands of *Atriplex canescens.* Adjacent to this area, near the west boundary of the park, are gypsum dunes and ridges in various stages of stabilization. A mosaic of associations covers these sites dominated variously by *Coldenia hispidissima, Bouteloua breviseta, Sporobolus nealleyi, Poliomintha incana, Ephedra torreyana, Yucca elata,* and *Opuntia polyacantha.*

To the northeast of this gypsum complex a large area of quartz sand occurs. These "red dunes" have *Prosopis glandulosa, Atriplex canescens, Croton dioicus,* and *Yucca elata* sharing dominance with a *Sporobolus* complex including *S. giganteus, contractus,* and *flexuosus.* In portions of these quartz sands, the grass species so dominate that the recognition of a grassland biotic community could be defended. In fact, Warnock would contend that most of the lower elevations (and often up to 7500 ft) of the park should be classified as grassland from which overgrazing has produced the current desertscrub communities. Such a view could well be supported in light of the geographic proximity of the plains grasslands immediately to the north and east. As Lowe (1964) pointed out, although the Chihuahuan Desert has more grasses than the Sonoran Desert and even in light of some investigators' contentions that the entire Chihuahuan Desert should be considered a grassland climax, the current status of the region is that of a natural desert dominated by numerous climax shrubs.

As previously pointed out, however, the position of the Guadalupe Mountains National Park is transitional between the Chihuahuan Desert and the plains grasslands. There are certainly clear-cut examples of both communities within the park boundaries, but equally as prevalent are transitions in which a plethora of plant taxa are found variously in association.

Whether the lower elevations of this region are disclimax grasslands invaded by succulents and microphyllous shrubs due to overgrazing, or a true desert climax with increased coverage of grass species due to the proximity of the plains grassland biome is certainly an interesting question. The fact that grassland associations of varying complexities do exist within the park cannot be ignored. Due to the great variability exhibited in relation to grass coverage, associated species presence, and edaphic influences, we feel it best to examine several major grassland communities within the park and treat exercises in classification as a futile game of semantics.

Some of the nicest examples of grassland associations occur just above the alluvial fans among the limestone slopes on the west escarpment. Such a community on the rocky slopes above Williams Ranch is dominated by *Bouteloua eriopoda* with significant numbers of *Agave lecheguilla, Viguiera stenoloba,* and *Fouquieria splendens*. This area certainly would be called grassland by Warnock, whereas Gehlbach would consider this as succulent desert. An alluvial fan in the northwest corner of the park reveals an open grass cover of *Bouteloua eriopoda, Aristida glauca,* and *A. pansa,* punctuated with scattered *Yucca torreyi* and *Krameria glandulosa*.

Between 5500 and 6000 ft on the west escarpment, there exist areas of less slope and deeper soils derived from eroded sandstone which are almost totally grass dominated. The major grass taxa in these areas include *Bouteloua hirsuta, B. warnockii, B. gracilis, B. eriopoda, Lycurus phleoides, Eragrostis lugens, Muhlenbergia setifolia, Stipa neomexicana,* and *Aristida glauca*. In rockier areas these grass species become "invaded" by several shrub species, especially *Dasylirion leiophyllum, Parthenium incanum, Viguiera stenoloba, Mortonia scabrella, Leucophyllum minus,* and *Dalea formosa*. At higher elevations (above 6500 ft) on the west escarpment, dominance shifts from grass species such as *Muhlenbergia pauciflora,* to *Cercocarpus montanus, Choisya dumosa, Forsellesia spinosa, Nolina micrantha, Yucca baccata,* and *Dasylirion leiophyllum*.

On the more gradual slopes of the east escarpment are found grass-dominated areas which often have *Dasylirion* and *Opuntia* species mixed with *Juniperus pinchotii*, or in more riparian sites *J. deppeana, Quercus grisea,* and *Arbutus xalapensis*. The most common grass species in these grassland-succulent desert-woodland communities are *Bouteloua curtipendula, B. gracilis, Lycurus phleoides, Muhlenbergia setifolia, Aristida glauca*, and *Stipa neomexicana*. Areas near Pine Spring Canyon and Nipple Hill show plant associations ranging from short-grass grassland to succulent desert-grassland to succulent desert-open woodland-grassland. Such complex mosaics render useless general classification schemes that would effectively delineate biome formations on a local basis.

Possibly, the creation of intermediate terminology to describe the considerable acreage within the park that, depending on the author, could be classified as either grassland or succulent desert would be effective. To that end we will refer to these vegetative assemblages as "succulent grassland." Another possible term to describe this complex is "Ensotal" (M. C. Johnston, pers. comm.).

## Woodland

As we have already pointed out, especially on the east escarpment, open woodland-grassland transitions occur, leading to many of the true woodland associations. These transitions occur as one goes from the desert floor up into the more mesic and cooler arroyos and canyons. Warnock would

refer to this association as canyon woodland. The more xeric of these riparian communities contain *Juglans microcarpa* and *Dasylirion leiophyllum*. On a xeric to mesic gradient, *Quercus grisea* (and some *Juniperus monosperma*) replace *Juglans*. These taxa are then replaced by *Quercus undulata* and *Juniperus deppeana* which grade into *Quercus muhlenbergii, Ostrya knowltonii*, and *Acer grandidentatum*. An accurate delimitation of deciduous as opposed to evergreen woodlands in these canyons is sometimes difficult although deciduous taxa usually predominate.

Another factor that further complicates canyon vegetation structure is slope effect. As these riparian associations move out onto rocky slopes which are especially common in the McKittrick Canyon complex and on the west side, the nature of the vegetative structure changes yet again. The presence of low growing oaks, *Dasylirion leiophyllum, Fouquieria splendens, Ceanothus greggii, Cercocarpus montanus, Mimosa biuncifera,* and scattered *Agave neomexicana* present a chaparral-like association. Such associations also occur in similar habitats of Dog Canyon with the regular addition of *Nolina micrantha*.

In addition to these riparian (deciduous), chaparral, and evergreen woodland associations, one of the most unique vegetative zones in the entire park occurs in several localities of the McKittrick Canyon system. These areas represent a seral stage in the development of a deciduous woodland and are characterized by *Adiantum capillis-veneris* and later, *Cladium jamacense*. These mats or "hanging terraces" are potentially threatened by human visitation because relatively little trampling is sufficient to disturb them significantly. As these present a favorable habitat for distributional limits of several taxa (such as *Cladium*) in the region, concern for their preservation is well warranted.

The lower slopes of both Upper Dog and West Dog Canyons are characterized by deeper and less rocky soils. These slopes have rather extensive stands of *Pinus edulis* and *Juniperus monosperma* sharing dominance (a Pinyon-Juniper evergreen woodland). In the alluvial bottoms are found grassy meadows of *Stipa tenuissima* or in some of the more xeric areas of West Dog Canyon, *Bouteloua gracilis*.

Between Cox Tank and Coyote Peak occurs a unique region previously undescribed as a significant plant association in the Guadalupes. In scattered stands throughout this area *Juniperus monosperma* and *Sophora gypsophila* var. *guadalupensis* share co-dominance. *Yucca baccata* and *Cercocarpus montanus* are commonly associated species in these areas as are *Bouteloua curtipendula* and *Aristida glauca* in rockier regions. Also common to the more xeric, steep, rocky slopes in this northwest canyon complex are *Nolina micrantha, Dasylirion leiophyllum*, and *Agave neomexicana*. As one moves along a xeric to mesic gradient, *Juniperus monosperma* is replaced by *Pinus edulis* and finally merges into the edges of coniferous forest forms.

### Forest

As would be expected by now, there exist numerous transitional areas between evergreen and/or deciduous woodland zones and the easily recognizable coniferous forest regions. In the more xeric forest associations, *Pinus ponderosa* dominates with significant amounts of *Muhlenbergia pauciflora* (and *Quercus gambelii*) on open slopes. The more mesic forest associations have *Pseudotsuga menziesii* and *Pinus strobiformis* sharing dominance with *Pinus ponderosa* as an associated subdominant in some areas. The most typical coniferous forest associations occur in The Bowl, but notable stands occur throughout the higher elevations near Bush Mountain, Blue Ridge, and the McKittrick Canyon drainage. One small stand of *Populus tremuloides* still occurs west of The Bowl where it is locally still a subdominant.

### Rock Outcrops

A plant association that warrants attention in this overview but does not fit naturally in any of the preceding three general vegetation zones is the complex of taxa that inhabits the steep limestone rock faces throughout the park. Although many of these habitats do occur in association with the riparian woodlands of the McKittrick drainage system, they also occur on the east and west escarpment faces and in portions of the Dog Canyon drainage in association with everything from almost desert to montane formations. In these habitats are found a large number of the unique taxa from the park including *Chaetopappa hersheyi, Cystopteris bulbifera*, and *C. fragilis, Epithelantha micromeris, Hedeoma apiculatum, Nama xylopodum, Perityle quinqueflora, Phanerophlebia auriculata, Pinaropappus parvus*, and *Salvia summa*. In addition to these "rock endemics," *Fendlerella utahensis, Fendlera rupicola, Petrophytum caespitosum, Hedyotis nigricans*, and *Philadelphus hitchcockianus* are also found in these habitats. Thus each of these areas is a separate and fairly distinct group of associations that is of particular interest due to the numbers of taxa restricted to such habitats which are in some way unique distributionally.

## SUMMARY

Our purpose was to present a brief summary of the major vegetative zones in the Guadalupe Mountains National Park region with special emphasis given to selected plant associations that exhibit "typical" plant class formations and to those that represent transitions between them. A thorough (quantitative) analysis of the vegetational associations in the Guadalupes is certainly needed as can be seen by the categorization difficulties encountered in this short overview. The critical message here is an awareness of the uniquely complex vegetational mosaics of this region produced by sudden and extreme topographic and edaphic interfaces in an essentially arid climate. These various floristic elements occur at a crossroads of major biotic assemblages: Rocky Mountain Forest; Chihuahuan Desert Scrub;

Great Plains Grassland; and some elements of the Sierra Madrean Woodland (Southwestern Mountains). This geographical position is in a zone of climatic interface which results in temporally unstable habitats containing unique plant associations. Such complexity is what makes this area so striking and interesting to both the scientist and to the general public. Because most of the area in question is part of the Guadalupe Mountains National Park, preservation of these features is more assured as is the opportunity of exposing the public to nature at its heterogeneous best.

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# *Status of Rare and Endangered Plant Species of the Guadalupe Mountains National Park, Texas*

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The flora of the Guadalupe Mountains National Park has been described accurately in general terms by almost every scientist who has visited the region. A summation of these observations would include comments about vegetational mosaics; community diversity with sudden transitions; and certainly there would be reports of rare, endemic, or unique taxa occurring in the delicate habitats produced by such topographic and edaphic diversity. There is good cause for such profuse descriptive phraseology and equally good cause for the more recently escalating number of warnings and expressed fears for the future of this area. We certainly concur with all such descriptions and unfortunately we must join the growing numbers of people who feel a real and immediate concern for the future of this beautiful and unique region. This concern is based on our recent survey work in the park for the National Park Service. Although this study is still active and not complete, we feel that sufficient data are already available for inclusion in this symposium volume.

This report will emphasize the unique taxa within the park and, based on these data, recommendations will be presented for management of the critical areas of the park. Appendix I summarizes most of the plant taxa that we consider unique, along with the criteria used to establish their degree of uniqueness. This list also includes distributional, ecological, and interpretative comments where applicable. At a later date this list will be expanded and corrected where necessary as a result of continuing, but as yet unfinished, identification efforts by both our own and outside personnel. For the most part our taxonomy follows that of Correll and Johnston (1970).

## UNIQUE FLORISTIC FEATURES: AREA BREAKDOWN

A brief presentation of notable floristic elements in discrete areas within the park follows. More information on each species is presented in Appendix I.

### McKittrick Drainage Complex

The integrity of the McKittrick drainage is central to preservation of the unique flora of the park. It is the most mesic and extensive system within the range, and supports representative populations of a majority of the rare and endemic taxa.

### General

For control of erosion and floods, maintenance of vegetative cover throughout the watershed is essential. This should not preclude the possibility of controlled burning to thin stands of young conifers at higher elevations; in fact, by reducing available fuel and thereby lessening the intensity of accidental burns, this practice could be beneficial to the drainage system. We expect that Dr. G. M. Ahlstrand's research will provide needed information for burn management.

Several endemic species can be found in crevices of limestone cliffs and ledges throughout this drainage. Among these are *Nama xylopodum, Chaetopappa hersheyi, Pinaropappus parvus, Salvia summa, Hedeoma apiculatum, Valeriana texana,* and *Polygala rimulicola*. Their preservation is aided by the inaccessible locations of some colonies.

Forested canyon bottoms above about 7000 ft shelter disjunct populations of several Rocky Mountain species, some found nowhere else in Texas. These include *Fragaria bracteata, Swertia radiata,* and *Physocarpus monogynus.*

Many unique taxa are concentrated along streams and adjacent boulders and gravel alluvium. The accessibility and relatively small area of this habitat make it one of the most vulnerable in the park to human impact. Species in this habitat include *Aquilegia chaplinei, Glyceria striata, Stephanomeria wrightii, Sisyrinchium demissum, Lactuca graminifolia, Rosa woodsii, Streptanthus sparsiflorus, Equisetum kansanum, Aster hesperius, Penstemon cardinalis, Asclepias tuberosa,* and *Viola missouriensis.*

### Special Considerations

**South McKittrick.**—A small canyon draining northeast from the earth tank in The Bowl appears more mesic than most canyons in the drainage, and it contains a well-developed forest flora including *Smilacina racemosa, Corallorhiza striata,* and *Rosa woodsii.* This canyon merits attention as a preservation area.

The mats of vegetation which have developed on seeps in limestone ledges support several rare or endemic species (*Aquilegia chaplinei, Zigadenus elegans,* and *Physocarpus monogynus*). Often dominated by *Cladium jamaicense* or *Adiantum capillus-veneris*, these are among the most unique plant associations in the Guadalupes. Within the park the best-developed mats or "hanging terraces" are located between Turtle Rock and The Narrows. The wet limestone base makes these mats unstable and vulnerable to foot traffic.

The Narrows is an area of steep limestone cliffs and pools which obstruct passage up the narrow canyon bottom. Its location is approximately 2.6 km S, 2.0 km W Pratt Lodge. The ferns *Cystopteris bulbifera* and *Phanerophlebia auriculata* grow in shaded crevices, and *Viola missouriensis* is common on more sunlit sites. Protection of this area is aided by its remoteness from existing trails.

**North McKittrick.**—Devil's Den contains most of the *Celastrus scandens* found in the park. A small colony of this species occurs on a slope and adjacent streambed a short distance below a dry waterfall in the lower part of the canyon (about 0.5 km N, 1.1 km W Pratt Lodge). This area also supported the greatest density of *Streptanthus sparsiflorus* observed in 1974.

The New Mexico segment of the south fork of North McKittrick contains an area of pools, seeps, and well-developed "hanging terraces." Most species of the unique canyon flora can be found here, including the only *Lilium philadelphicum* we could find in the Guadalupes. A few small *Celastrus scandens* occur near the junction of Devil's Den with main North McKittrick and a small trail into the area has become more evident during the past 2 years, indicating increased usage.

**Lower McKittrick.**—Widely scattered plants of *Yucca faxoniana* occur on slopes and small side canyons, and *Sophora secundiflora* also can be found in similar habitats. Unusual forms of *Agave* are scattered on alluvial terraces and slopes along with *Agave neomexicana* and *A. lecheguilla*. *Grindelia havardii* grows along the streambed.

**East Escarpment—General**

Lower elevations are a mixture of desert and grassland species, with corridors of riparian woodland along the streambeds. There is a gradual transition to coniferous forest at the top. Protection from overgrazing undoubtedly has favored growth of grasses and associated species. As in the McKittrick drainage, limestone cliffs of the escarpment support a flora with a high percentage of endemic species.

**Special Considerations**

Smith Spring supports small populations of *Glyceria striata* and *Viola missouriensis*, typical of McKittrick Canyon. In addition, Smith Canyon contains a pocket of forest where *Heterotheca viscida*, *Asclepias tuberosa*, *Streptanthus sparsiflorus*, and *Penstemon cardinalis* subsp. *regalis* have been collected. The area is easily visited by a relatively short walk.

Both Choza Spring and Upper Pine Spring have communities of stream-side plants including *Lobelia cardinalis*. Manzanita Spring, though somewhat trampled along the edges, also has a few stream-side species and contains the only *Potamogeton* found in the park. All three areas are of easy access.

*Yucca faxoniana* is rare over most of the area; however, an aggregation of about 30 plants is located on the ridgetop south of Smith Spring, and a smaller group occurs on the north side of the mouth of Pine Spring Canyon.

**Upper Dog Canyon**

Riparian woodland along the streambed and a more xeric vegetation of sotol, grasses, and low shrubs on the slopes produce a diverse flora. Several trees of the undescribed drooping form of *Juniperus scopulorum* are found along the streambed about 300 m south of the ranger station. *Lesquerella valida* has been collected from several slopes in this area.

**Humphrey Canyon—PX Flat**

This area contains the most extensive Pinyon–Juniper woodland in the park. The only *Sophora gypsophila* found in the United States occur here (Fig. 1).

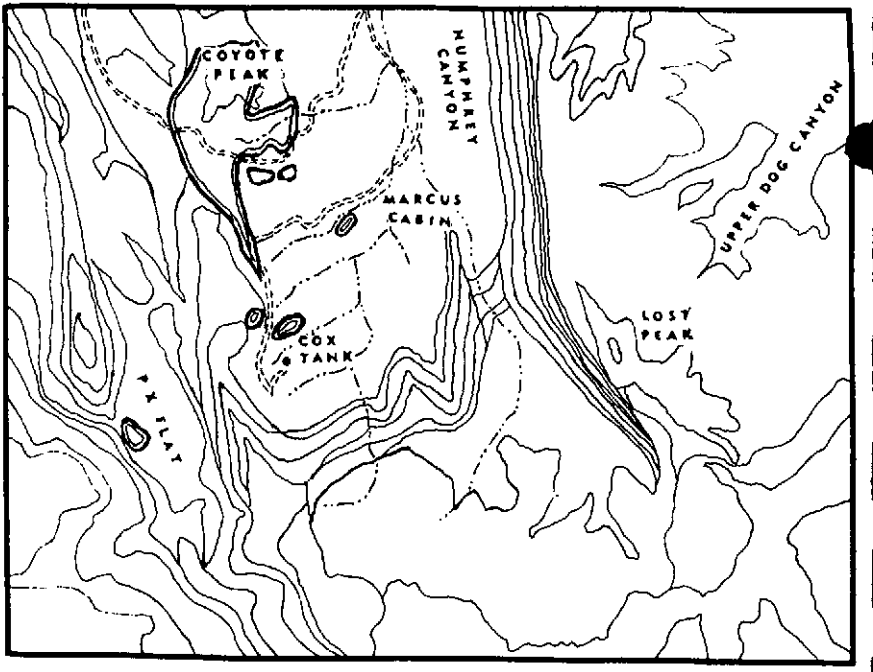


**Fig. 1.** Heavy solid lines outline the distribution of *Sophora gypsophila* var. *guadalupensis* in the Guadalupe Mountains National Park, Texas, as provided by Roger Reisch and field-checked by the authors; light, solid lines indicate contour; dot–dash lines represent intermittent streambeds; parallel dashed lines indicate a jeep road.

**West Side—General**

The West Side contains associations representative of most types of northern Chihuahuan Desert vegetation. Most of the bajada is covered by *Larrea tridentata* or a desert grassland dominated by *Bouteloua eriopoda*.

*Coryphantha dasyacantha, Penstemon dasyphyllus,* and *Bouteloua warnockii* have been collected on the slopes of the west escarpment, and most of the endemic limestone cliff plants have been recorded from the canyons.

**Special Considerations**

A small colony of *Jatropha dioica* occurs on the south slope of the south Stagecoach Hill (0.8 km N, 3.5 km E Lewis Well).

Bone Spring is the only known location for *Astragalus humistratus* in the park, and supports a few plants of *Lobelia cardinalis* and *Forestiera pubescens.* A small group of *Yucca faxoniana* grows on the south rim of Bone Canyon.

The lower elevations of the northwest corner of the park contain desert grassland where *Opuntia schottii* was collected. Lower canyons in this area have *Sophora secundiflora* along the streambeds.

Areas of wind-deposited sand contain species not found elsewhere in the park, among them *Penstemon ambiguus, Caesalpinia jamesii, Dalea scoparia, Oryzopsis hymenoides, Panicum ramisetum,* and *Sporobolus giganteus.* Gypsum outcrops and the few gypsum dunes included within the park support a flora with several species of restricted distribution, including *Senecio warnockii, Gaillardia multiceps, Dicranocarpus parviflorus, Coryphantha scheeri, Nama carnosum,* and *Mentzelia humilis.* The best example of a gypsum outcrop association is located about 1.2 km S, 5.5 km W summit Bush Mountain. The largest gypsum dune seen within the park is about 400 m southwest of Lewis Well; the most extensive gypsum dunes are immediately west of the park.

## PROPOSED MANAGEMENT FOR FLORISTIC PRESERVATION

Ideally, there should be no compromises in the preservation of rare or endemic species. Unfortunately, limited resources and manpower necessitate alternatives. Policymakers should bear in mind that biological communities are not static, especially in the variable climate of the Trans-Pecos. Continued monitoring of resources and a certain amount of managerial flexibility permitting more stringent protection measures in dry years or during peak visitation periods are essential to adequate floristic preservation. Managers are always faced with compromising recreational or preservational usage, and the acceptable level of community degredation appears to be largely a result of local policy. The staff of Guadalupe Mountains National Park is to be commended for its close monitoring of the area and its concern for preservation as reflected by management policies. To a large extent, these policies appear to have been successful in minimizing damage in critical areas, and many of our recommendations coincide with current management practices.

A hierarchy of the relative status of locations and species requiring preservational action follows. Criteria for ranking include: (1) degree of unique-

ness (the number and kinds of species present); (2) size of the habitat; and (3) vulnerability to human impact—including substrate stability and current accessibility. We know of no objective function to integrate the above factors, and the order is based largely on our personal judgment. The status of each area will require re-evaluation as new or improved roads and trails change visitor use patterns.

**Most Critical Areas**

South McKittrick Canyon between Turtle Rock and The Narrows.
South fork of North McKittrick Canyon (including New Mexico segment).

**Critical Areas**

Remainder of South McKittrick drainage, including higher areas between Bush Mountain and The Bowl.
North McKittrick Canyon.
Devil's Den.
Forest and meadows on Blue Ridge.
The Bowl.
Smith Spring.
*Sophora gypsophila* in West Dog Canyon.

**Require Periodic Monitoring for Possible Action**

Limestone cliff associations at higher elevations throughout the park.
*Jatropha dioica* colony on south Stagecoach Hill.
Upper Pine Spring.
Choza Spring.
Drooping form of *Juniperus scopulorum* in Upper Dog Canyon.
*Lesquerella valida* in Upper Dog Canyon.
*Yucca faxoniana* (Lower McKittrick Canyon, ridgetop south of Smith Spring, north side of mouth of Pine Spring Canyon, south rim of Bone Canyon).
*Populus tremuloides* west of The Bowl.
Bone Spring.
Gypsum outcrop, 1.2 km S, 5.5 km W summit Bush Mountain.
Gypsum sand and beach ridges west of Lewis Well.
Quartz sandhills ("red sands") west of Bush Mountain.

**Recommendations**

The following management recommendations are arranged by area. Within each area they are ordered from (A) most desirable (minimal degradation from human impact) to (B) or (C) minimum required for resource preservation. Unless contradictory, assume measures in (B) or (C) are included in (A). The requirements and ecology of most unique species are largely unknown, and in some cases these alternatives are little more than

educated guesses. For proper management there is no substitute for continued monitoring and informed revision of policy as necessary.

**Entire Park**

**Grazing and Browsing.**—(A) Monitor browsing and grazing impact continuously and take appropriate measures to prevent extensive degradation; to include thinning elk and deer populations. (B) Maintain fences to prevent trespass grazing by stock.

**Burning.**—Policy should be based on the results of Dr. G. M. Ahlstrand's current research. Consideration should be given to protecting the drooping *Juniperus scopulorum* in Dog Canyon, the *Yucca faxoniana* aggregations, and *Sophora gypsophila* from intense fires.

**Human traffic.**—Specific recommendations are made for each area. In this report, we recognize the following categories of access: Controlled access—visitor entry monitored and if necessary limited; Limited access—daily visitor quota to distribute impact; and Restricted access—no entry except to interested investigators or small groups accompanied by a ranger interpreter. To maintain the integrity of the range no vehicular traffic should be allowed above 6000 ft elevation. The resulting increased impact on higher parts of the watershed would result in an unacceptable level of habitat degradation.

**McKittrick Drainage**

**Lower Canyons.**—(A) Permanent ranger stationed at Pratt Lodge; daily patrols. (B) Low visitor quota; irregular patrolling. (C) Limited access; day use only; moderate visitor quota; intensive patrolling.

**South McKittrick.**—(A) Restricted access to area northeast of The Bowl and Guadalupe Trail and southwest of McKittrick Trail; canyons draining Blue Ridge—Bush Mountain area. (B) Restricted access to canyon bottom including The Narrows to south of Turtle Rock. Day use only for remainder of areas in (A). Visitor quota for high elevation camps. No overnight horse or mule use. Monitoring and periodic "resting" of camping areas. No new trails.

**North McKittrick.**—(A) Restricted access to Devil's Den; south fork of North McKittrick, including New Mexico segment. (B) Day use only. Management authority and regular patrols of New Mexico segment of south fork of North McKittrick. Restricted access to Devil's Den.

**East Escarpment**

(A) Restricted access to Smith Canyon above Smith Spring. Boardwalk to protect Smith Spring from soil compaction and channel visitor traffic. Restricted access to Choza and Upper Pine springs. (B) Frequent patrol of Smith Spring to prevent foot traffic beyond fence. Regular patrol of Upper Pine and Choza springs to prevent camping. No camping areas near springs or smaller canyons.

**Dog Canyon**

(A) and (B) Limit number and location of campers to aid recovery of meadows. No vehicular traffic beyond ranger station.

**Humphrey Canyon—PX Flat**

(A) and (B) Limited access. Day use only in vicinity of *Sophora gypsophila.*

**West Side**

(A) Route improved roads away from *Jatropha dioica* colony, gypsum dunes, and quartz sandhills. Boardwalk at Bone Spring to prevent trampling of *Astragalus* and *Lobelia.* (B) No vehicular traffic off existing roads. Regular patrol and maintenance of fences to prevent trespass grazing. Limited access to Bone Spring.

## SUMMARY

The thrust of this report is the enumeration of all known plant taxa considered unique within the park boundaries and management recommendations designed to insure preservation of the communities. Although additions, corrections, and revisions are anticipated with continuing field and laboratory work, the distribution, ecology, and significance of each of these taxa are as thorough and complete as presently possible.

The management recommendations are based on our understanding of the plant communities in the park and are made in light of our observations of present visitor frequency and environmental variation. It must be reiterated that successful preservation of the park's unusual biota depends on continued monitoring and flexibility in management design. Unexpected environmental fluctuations and/or vastly escalated public interest in the park could well render these recommendations inadequate, especially in certain regions of the park. Continued survey and transect activity will result in our expected changes in the unique plant list found in this report.

## APPENDIX I

Two codes are used in the appendix to permit more rapid assessment. Relative degree of uniqueness is given by Roman numerals as follows:

I. Endemic to a relatively limited area in and/or around the Guadalupe Mountains;
II. Widespread in other states, but known in Texas from very few localities, usually known only from the Guadalupes;
III. Of distributional interest; includes species with relatively small ranges and those near the limits of their known occurrence in the park;
IV. Rare within the park, but may be common elsewhere in Texas;
V. Not seen by the authors, but previously recorded from the park.

The Arabic numerals give areas within the park in which the species has been found. The following zones have been defined primarily by watershed and elevation (Fig. 2).

1. Lower McKittrick Canyon below Pratt Lodge;
2. South McKittrick drainage below 7000 ft and including peak west of Turtle Rock;
3. North McKittrick drainage including the New Mexico segment of the south fork of North McKittrick;

4. South McKittrick drainage above 7000 ft excluding The Bowl;
5. The Bowl drainage above the earth tank;
6. Pine Spring Canyon drainage including Guadalupe Peak and El Capitan above 8000 ft and the wash southwest of Houser House;
7. The East Escarpment except McKittrick drainage;
8. Upper Dog Canyon drainage;
9. Humphrey Canyon drainage and PX Flat;
10. Salt Basin drainage.

**Omissions from Appendix I**

Several taxa are not included in this list because of a present lack of information. There are at least two species of *Philadelphus* in the park, including the endemic *P. hitchcockianus*; however, more study is needed to clarify distribution in the park. Four species of *Symphoricarpos* are recorded from the park. *S. guadalupensis* is endemic, but we have not yet obtained the flowering material critical for identification. Our understanding of sedges at this time is insufficient to properly analyze our collections for *Carex eburnea*, a species found in the northeastern United States, known in Texas only from the Guadalupe Mountains. Similarly, other notable species have not been reported here, but more information will be provided to the park service as it becomes available.

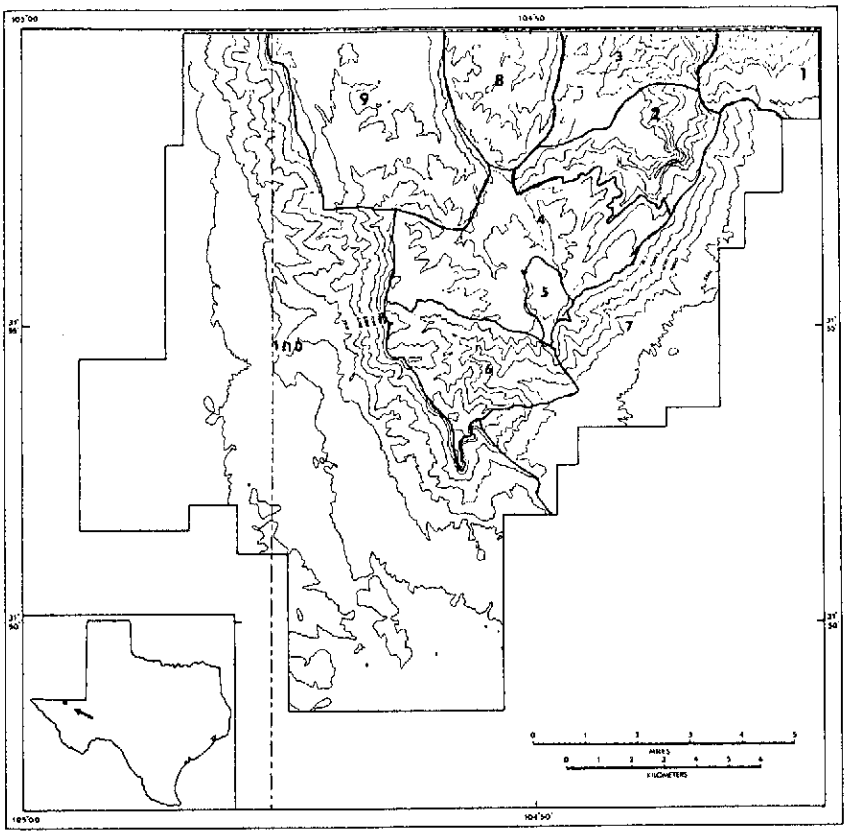


**Fig. 2.** Distributional zones of plants in the Guadalupe Mountains National Park as referred to in Appendix I.

| Name | Category | Zones |
|---|---|---|
| *Amelanchier utahensis* Koehne<br>Scattered, high, forested slopes and riparian woodland. | II | 2,3,4,6 |
| *Andropogon hallii* Hackel<br>Appears restricted to gypsum dunes. Found immediately west of park boundary, probably rare in zone 10. | IV | 10 |
| *Anthericum torreyi* Baker<br>Scarce; open slopes above 6000 ft. | III,(IV?) | 4,8 |
| *Aquilegia chaplinei* Standl.<br>Common, wet limestone crevices and gravel alluvium. Known only from Guadalupe Mountains. | I | 2,3 |
| *Asclepias tuberosa* L.<br>Scattered in North and South McKittrick, Smith Canyon, and Pine Spring Canyon. Usually in sunlit pockets of soil on limestone ledges. Disjunct population of primarily eastern species. | III | 2,3,6,7 |
| *Aster hesperius* Gray<br>Scattered among *Cladium jamaicense* along streams in McKittrick; scarce in meadows in The Bowl. | II | 2,3,5 |
| *Arbutus xalapensis* H.B.K.<br>Common in lower canyons throughout the park. A Mexican species near its northern limit. Does not appear to be reproducing well. | III | 1,2,3, 6,7,10 |
| *Astragalus albulus* Woot. & Standl.<br>Abundant at Bone Spring, not seen elsewhere. Only known occurrence in Texas. | II | 10 |
| *Astragalus pictiformis* Barneby<br>Scattered on open slopes and meadows in Humphrey Canyon. A desert grassland species of southern New Mexico and northern Trans-Pecos Texas. | III | 7,9 |
| *Berberis repens* Lindl.<br>Widespread in forested areas. | II | 2,3,4, 5,6,8 |
| *Bouteloua warnockii* Gould & Kapadia<br>Common on dry limestone slopes. Considered rare over most of range (southern New Mexico to Coahuila). | III | 7,9,10 |
| *Caesalpinia jamesii* (T. & G.) Fisher<br>Uncommon; only on quartz sandhills. | IV | 10 |
| *Campanula rotundifolia* L.<br>Scattered on slopes and mesic limestone ledges. | II | 2,4,5 |
| *Castilleja latebracteata* Penn.<br>Widespread but scarce at higher elevations. Generally on woodland slopes. | IV | 2,3, 7,10 |
| *Celastrus scandens* L.<br>Small colony on slope and dry streambed of Devil's Den (0.5 km N, 1.1 km W Pratt Lodge); also a few plants near mouth of Devil's Den and south fork of North McKittrick, and South McKittrick. | II | 2,3 |
| *Centaurea americana* Nutt.<br>Only seen on meadow north of Upper Dog Canyon Ranger Station. | IV | 8 |

| Name | Category | Zones |
|---|---|---|
| *Cevallia sinuata* Lag. | IV | 10 |
| Uncommon; limestone cliffs and dry washes in lower northwest corner of park. | | |
| *Chaetopappa hersheyi* Blake | I | 2,3,6,7 |
| Scattered populations in crevices of limestone cliffs. Usually above 6000 ft but extending lower in North and South McKittrick. | | |
| *Choisya dumosa* (Torr.) Gray | III | 1,2,3, 6,7,10 |
| Common in lower canyons throughout park. Considered infrequent over most of Trans-Pecos (Correll and Johnston 1970). | | |
| *Chrysothamnus nauseosus* subsp. *bigelovii* (Gary) Hall & Clem. | V | 2,6, 7,10 |
| Scattered on limestone ledges. | | |
| *Chrysothamnus pulchellus* (Gray) Greene | IV | 7,10 |
| Previously collected in Smith Canyon (B. L. Turner 112, Sul Ross Herbarium). Uncommon on quartz sandhills on west side. Analysis incomplete. | | |
| *Chrysothamnus spathulatus* L. C. Anderson | II | 2,6, 7,10 |
| Open slopes. Analysis incomplete. | | |
| *Corallorhiza striata* Lindl. | III,IV | 4 |
| Scarce; humus in forested canyon bottom approximately 2.9 km N, 1.5 km E summit of Hunter Peak. | | |
| *Coreopsis lanceolata* L. | II,III | 2,3 |
| Identification tentative. A species of the eastern United States previously unreported from west Texas. Single specimen collected by B. H. Warnock (22804) in South McKittrick, labeled "infrequent." Collected in North McKittrick. | | |
| *Coryphantha dasyacantha* (Engelm.) Orcutt. | III | 4,10 |
| Limestone ledges. Difficult to distinguish from more widespread *C. strobiliformis*. Specimens keying to this taxon collected on Blue Ridge and southwest of Cutoff Mountain. Probably occurs over most of west escarpment. Termed "endemic" in Correll and Johnston (1970). | | |
| *Coryphantha macromeris* (Engelm.) Britt. & Rose | IV | 10 |
| Apparently uncommon. Open bajada and arroyos below 4500 ft. | | |
| *Coryphantha scheeri* (O.Ktze.) L. Benson | IV | 10 |
| Very scarce. Gypseous soil near Lewis Well. | | |
| *Cystopteris bulbifera* (L.) Bernh. | II,IV | 2 |
| Previously collected at ". . . upper part of canyon near pools and rope swing" in 1964 (D. S. Correll 29803, SMU, UT Austin Herbaria). Material from The Narrows (approximately 2.6 km S, 2.0 km W Pratt Lodge) has been tentatively identified to this species. Locally common in shaded limestone crevices. | | |
| *Cystopteris fragilis* (L.) Bernh. | III | 3,4,6 |
| Described as "local and rare" (Correll and Johnston 1970). Uncommon, usually in shaded moist limestone crevices. | | |

| Name | Category | Zones |
|---|---|---|
| *Dalea frutescens* Gray<br>Apparently uncommon in park. Previously collected in Lower McKittrick (B. H. Warnock 9445, Sul Ross Herbarium). Locally occasional on slopes at Upper Pine Spring and in South McKittrick. | IV | 1,2,7 |
| *Dalea scoparia* Gray<br>Scattered on open areas of quartz and gypsum sand. More common on gypsum dunes immediately west of park. Probably at the eastern limits of its range here. | III | 10 |
| *Delphinium virescens* Nutt.<br>Previously collected a short distance east of the park, and to be expected in zone 7. A plains species probably near its western limit in Texas. | IV | 9,10 |
| *Dicranocarpus parviflorus* Gray<br>Restricted to gypseous soils. Can become abundant in years with good summer rains. Most common in Lewis Well–Holmsley's Dugout area near west boundary. | III | 10 |
| *Epipactis gigantea* Hook.<br>Previously collected in South McKittrick (B. H. Warnock 22811, 1968, Sul Ross Herbarium), labeled "infrequent." Seen by us at limestone seeps in New Mexico segment of south fork of North McKittrick, South McKittrick, and Lower McKittrick. | IV | 1,2,3 |
| *Epithelantha micromeris* (Engelm.) Weber<br>Widespread in park, limestone ledges up to 7500 ft. Common in parts of North McKittrick. Reported to be heavily collected for sale in some parts of the state. | III | 2,3, 7,10 |
| *Equisetum kansanum* J. H. Schaffn.<br>Common along stream in parts of South McKittrick and at Bone Spring. | III | 2,10 |
| *Forestiera pubescens* Nutt.<br>Previously referred to as *F. neomexicana*; Correll and Johnston (1970) consider Texas material to be a complex of intergrades between both taxa, and a more careful analysis is needed. Scattered and infrequent, often along streambeds. On west side a small colony occurs at Bone Spring. | III | 2,4,8, 9,10 |
| *Fragaria bracteata* Heller<br>Generally uncommon; forested slopes and canyons above 7500 ft. | II | 4,5 |
| *Gaillardia multiceps* Greene<br>Considered rare in Texas (Correll and Johnston 1970). Restricted to sandy gypsum soil on dunes and beach ridges along west boundary near Lewis Well. Occasional to uncommon. | III | 10 |
| *Glyceria striata* (Lam.) Hitchc.<br>Uncommon. Scattered locations along streams in South McKittrick and Devil's Den. Small colony at Smith Spring. Rare in Texas. | II | 2,3,7 |
| *Grindelia havardii* Steyerm.<br>Uncommon; open sites near streambeds. Type locality ". . . dry gravelly wash near mouth of McKittrick Canyon" | III | 7 |

| Name | Category | Zones |
|---|---|---|
| (J. A. Moore, J. A. Steyermark 283, 1931, UT Austin Herbarium). Limited distribution including Chisos Mountains; Crockett County, Texas; and New Mexico. | | |
| *Hackelia grisea* (Woot. & Standl.) I. M. Johnst. Apparently scarce; dry streambed in Devil's Den. Analysis of material incomplete, probably also in zones 2 and 4. Occurs in mountains of Texas and New Mexico. | III,IV | 3 |
| *Hedeoma apiculatum* W. S. Stewart Generally scarce, small colonies or isolated individuals in crevices of limestone cliffs. Bottom and slopes of South McKittrick, Devil's Den, south fork of North McKittrick, Hunter Peak, and higher parts of Pine Spring Canyon. Endemic to Guadalupe Mountains. | I | 2,3,6 |
| *Heterotheca viscida* (Gray) Harms Considered rare in Texas (Correll and Johnston 1970). Previously collected in Smith and Bear canyons (B. H. Warnock and M. C. Johnston 16583, Sul Ross Herbarium; B. L. Turner 1253, C. L. Lundell 14390, SMU). Analysis of our material incomplete. | V | 7 |
| *Hymenopappus biennis* B. L. Turner Previously collected in South McKittrick, The Bowl, and Pine Spring Canyon (L. C. Hinckley 4472, B. H. Warnock 10997, M. C. Johnston 3168, Sul Ross; D. S. Correll 13920, C. H. Muller 8287 SMU; M. S. Young s.n., UT Austin). Analysis of our material incomplete. In Texas known only from Guadalupe Mountains. | V | 2,4, 5,6 |
| *Hymenopappus flavescens* Gray Apparently rare in park. Collected just outside of west boundary on quartz sandhills. Previously collected near east boundary, and to be expected in zone 7. | IV | 10 |
| *Hymenoxys richardsonii* (Hook) Cockll. Common in open areas throughout high parts of park. Southern limit of range. | II | 4,5,6 |
| *Ipomoea lindheimeri* Gray Widespread but scarce. Usually twining among low trees and shrubs. Endemic to west Texas. | III | 1,3,7 |
| *Ipomopsis arizonica* (Greene) Wherry Scarce; meadows and open slopes above 6200 ft. May be more abundant after favorable rainfall distribution. | III,IV | 4,5 6,8 |
| *Jatropha dioica* Cerv. Restricted to small colony on south slope of south Stagecoach Hill (0.8 km N, 3.5 km E Lewis Well). A species characteristic of the southern Chihuahuan Desert occurring here as the most northerly known disjunct. | III,IV | 10 |
| *Juniperus scopulorum* Sarg. (undescribed drooping form) This species is scattered in mesic sites throughout higher parts of the park. Several individuals with a distinct drooping habit grow along streambed about 0.3 km S Upper Dog Ranger Station, and single individual observed at Upper Pine Spring. As a species, it is near southern limit of range here. | (I?),III | (7?),8 |

| Name | Category | Zones |
|---|---|---|
| *Lactuca graminifolia* Michx. Scarce, usually on open gravel alluvium. In summer 1974 best growth observed in South McKittrick about 2.8 km S, 1.7 km W Pratt Lodge. | II | 2,3 |
| *Lesquerella valida* Greene Apparently uncommon, but easily overlooked. Usually on open slopes. A poorly known species occurring in southern New Mexico, Guadalupe Mountains, and Sierra Diablo (Texas). | I | 1,2, 4,8 |
| *Lilium philadelphicum* L. Only observed in mats of vegetation on limestone seeps, south fork of North McKittrick (New Mexico segment) and South McKittrick. Previously collected from South McKittrick (B. H. Warnock 22801, Sul Ross), labeled "rare." | II | 2 ,3 |
| *Lithospermum multiflorum* Gray Widespread but often infrequent. Canyon bottoms; open slopes at higher elevations. In Texas known only from forested mountains in the Trans-Pecos. | III | 2,3,4, 6,7 |
| *Lithospermum parksii* I. M. Johnst. Generally scarce. Open or partially wooded slopes. May be confused with *L. multiflorum*. Species of limestone soils in West Texas. The variety *rugulosum* I. M. Johnst. is known from four localities; we have collected it near the top of Bear Canyon. | II-III,IV | 1,2, 6,7 |
| *Lithospermum viride* Greene Widespread and common. Usually in mesic, partially shaded sites. Probably also occurs in zones 2,4,5,8. Known from limestone soils in mountains of west Texas; ranges from New Mexico to Nuevo Leon. | III | 3,6,7 |
| *Lobelia cardinalis* L. Common on sunny margins of permanent streams. On the east slope occurs at Smith, Choza, and Upper Pine springs. On west side seen only at Bone Spring. The varieties *pseudosplendens* McVaugh and *multiflora* (Paxt.) McVaugh appear to intergrade in the park, and in Texas both are known only from the Trans-Pecos. | III | 2,3, 7,10 |
| *Lonicera arizonica* Rehd. Collected on forested limestone ledges about 0.5 km E summit of Guadalupe Peak and from South McKittrick. Analysis incomplete. Not known elsewhere in Texas. | II | 4,6 |
| *Machaeranthera blephariphylla* (Gray) Shinners Common, open or partially wooded limestone slopes between 5000 and 7500 ft. In Texas known only from limestone mountains in the Trans-Pecos. | III | 7,8,9 |
| *Mammillaria lasiacantha* Engelm. Apparently uncommon, but easily overlooked. Limestone ledges and alluvial fans below 6000 ft. A species occurring on limestone in the northeastern Chihuahuan Desert. | III | 10 |
| *Mentzelia humilis* (Urban & Gilg.) Darl. Scattered; restricted to gypsum soils and outcrops. Known only from gypsum in west Texas and New Mexico. | III | 10 |

| Name | Category | Zones |
|---|---|---|
| *Monotropa latisquama* (Rydb.) Hult. Generally uncommon, coniferous forest. In Texas known only from forested mountains of Trans-Pecos. | III | 4,5,7 |
| *Nama carnosum* (Woot.) C. L. Hitchc. Within park collected on gypsum outcrop 1.3 km S, 5.5 km W summit of Bush Mountain. Also seen immediately west of park boundary. A species restricted to gypsum soils of the northeastern Chihuahuan Desert. | III | 10 |
| *Nama xylopodum* (Woot. & Standl.) C. L. Hitchc. Widespread, limestone cliffs generally above 6000 ft. Endemic to limestone mountains of Trans-Pecos. | I | 1,2,3,4, 5,6,7,10 |
| *Oenothera caespitosa* Nutt. Scarce, collected on limestone ledges on west side of Bush Mountain summit. Previously collected in similar habitat on Pine Top (B. H. Warnock and B. L. Turner 181, Sul Ross). Probably at southern limit of its range here. | II | 4,5 |
| *Opuntia schottii* Engelm. Found only in the lower northwest corner of the park, where it is locally common on alluvial fans. | IV | 10 |
| *Oryzopsis hymenoides* (R. & S.) Ricker Infrequent, quartz and gypsum sand on the west side. Considered rare in Texas (Correll and Johnston 1970) which is eastern limit of range. | III | 10 |
| *Ostrya knowltonii* Cov. Common in riparian woodland above 6000 ft, extending lower in McKittrick. Only known occurrence in Texas. | II | 2,3,4, 6,7 |
| *Panicum ramisetum* Scribn. Uncommon on quartz sandhills. Probably near the western limit of its range here. | IV | 10 |
| *Penstemon ambiguus* Torr. Scarce on quartz sand. Characteristic of sandhills to the east of the park. | IV | 10 |
| *Penstemon brevibarbatus* Crosswhite Scarce; open grassy slopes. Collected in Pitchfork Canyon and north of Frijole. Previously found in South McKittrick (B. H. Warnock and M. C. Johnston 16523, Sul Ross). Endemic to western Edwards Plateau and Trans-Pecos. | III,IV | 2,7,8 |
| *Penstemon cardinalis* Woot. & Standl. subsp. *regalis* (A. Nels.) Nisbet & Jackson Generally uncommon; most abundant on limestone ledges and gravel alluvium in South McKittrick. Less frequent on limestone ledges in higher parts of Bear and Smith canyons. The subspecies *regalis* (A. Nels.) Nisbet & Jackson is considered endemic to the Guadalupe Mountains. | I | 2,3,4,7 |
| *Penstemon dasyphyllus* Gray Scattered on rocky slopes above 5500 ft W. of Guadalupe Peak. Previously thought to occur in Texas only in southern Trans-Pecos. | III | 10 |

| Name | Category | Zones |
|---|---|---|
| *Penstemon fendleri* T. & G. | IV | 1, 7 |
| Apparently scarce in park. Alluvial terraces in Lower McKittrick. Previously collected "1 mile west of Pine Spring along highway" (B. H. Warnock and M. C. Johnston 16302, Sul Ross). | | |
| *Perityle quinqueflora* (Steyerm.) Shinners | I | 2,3, 6,10 |
| Scattered populations on limestone cliffs; reaches greatest density in canyon bottoms between 5000 and 7500 ft. Endemic to limestone areas of Trans-Pecos and adjacent New Mexico. | | |
| *Peteria scoparia* Gray | V(IV?) | 7 |
| Previously collected in lower Pine Canyon (B. H. Warnock 20837, Sul Ross), labeled "rare." Only two plants seen by us on the 9K Ranch about 20 mi. E of the park. Not seen in the park to date. | | |
| *Phanerophlebia auriculata* Underw. | III,IV | 2 |
| Only collected at The Narrows (about 2.6 km S, 2.0 km W Pratt Lodge) where it is uncommon in limestone crevices. Considered rare in the Trans-Pecos (Correll and Johnston 1970). | | |
| *Physocarpus monogynus* (Torr.) Coult. | II | 2,4,5 |
| Generally scarce; seeps in South McKittrick and mesic slopes and canyons at higher elevations. Sole locality for Texas. | | |
| *Pinaropappus parvus* Blake | I | 2,3,6, 7,10 |
| Scattered populations on limestone cliffs throughout higher elevations and extending lower along canyon bottoms. Endemic to northern Trans-Pecos and adjacent New Mexico. | | |
| *Polygala rimulicola* Steyerm. | I | 2,3,6, 7,10 |
| Scattered populations on limestone cliffs; generally above 6000 ft but occurs lower in McKittrick. Common in some areas. Endemic to Guadalupe Mountains and Sierra Diablo. | | |
| *Populus tremuloides* Michx. | II,IV | 4 |
| Small population at streambed junction about 2.5 km E of summit of Bush Mountain; consists of scattered trees in riparian forest of *Pinus strobiformis, Pseudotsuga menziesii, Acer grandidentatum*, and *Ostrya knowltonii*. Does not appear to be reproducing well, and probably will die out unless there is a local burn followed by protection from browsing. Another group reported for the park by C. Peterson (1973) about 4 km S, 1½ km W Pratt Lodge. Not yet seen by us. | | |
| *Prosopis pubescens* Benth. | IV | 10 |
| In the park known from three small trees on embankment of abandoned highway in Guadalupe Canyon, about 2.9 km S, 2.5 km E summit of Guadalupe Peak. Probably introduced. | | |
| *Rhamnus smithii* Greene | (IV?),V | 5 |
| Previously collected "near West bowl" (B. H. Warnock, 22844, Sul Ross), labeled "infrequent." Not seen by us. | | |
| *Rhus toxicodendron* L. | IV | 2,4 |
| Apparently scarce. Mesic sites in canyon bottoms. | | |

| Name | Category | Zones |
|---|---|---|
| *Robinia neomexicana* Gray<br>Generally scarce; mesic, forested slopes and canyon bottoms, usually above 7000 ft. In Texas known only from Guadalupe and Franklin mountains (Correll and Johnston 1970). | II | 2,4,5,7 |
| *Rosa stellata* Woot.<br>Widespread; often locally common. Open slopes above 7000 ft, and on limestone ledges in North McKittrick and Devil's Den. Both the variety *stellata* and the variety *earlansoniae* W. H. Lewis have been collected within the park. More analysis is needed. | III | 3,4,8, 9,10 |
| *Rosa woodsii* Lindl.<br>Scarce; collected among boulders near Turtle Rock and in forested canyon bottom northeast of The Bowl. | III,IV | 2,4 |
| *Salvia farinacea* Benth.<br>Occasional; mostly in open meadows and dry, gravelly streambeds. Probably near western limit of its range here. | III | 1,2,3 |
| *Salvia summa* A. Nels.<br>Generally scarce; more mesic sites on limestone cliffs; usually above 6500 ft. On west side found in a narrow canyon about 0.5 km N, 0.9 km W summit of Bush Mountain. Also collected in Bear and Smith canyons. | I | 2,6, 7,10 |
| *Selinocarpus lanceolatus* Woot.<br>Uncommon; restricted to gypsum soils. Limited distribution in Trans-Pecos Texas and New Mexico. | III | 10 |
| *Senecio neomexicanus* Gray<br>Generally scarce; mesic slopes and limestone ledges. Only known occurrence in Texas. May intergrade with another species in the park. Currently being studied by a specialist. | II | 2,4,8 |
| *Senecio warnockii* Shinners<br>Scarce within park; restricted to gypsum. Only collected on gypsum outcrop about 1.2 km S, 5.5 km W summit of Bush Mountain; also seen near gypsum dunes just west of park boundary. Known only from Culberson and Hudspeth counties, Texas, and adjacent New Mexico. | I | 10 |
| *Sisyrhinchium demissum* Greene<br>Uncommon; streamsides in South McKittrick. Previously collected at Smith Spring (B. H. Warnock 5405, Sul Ross). Sole occurrence in Texas. May be confused with *S. ensigerum* Bickn. which is more abundant in park. | II | 2,7 |
| *Smilacina racemosa* (L.) Desf.<br>Scarce; mesic forests. Previously collected in South McKittrick and The Bowl. Found by us in small canyon 2.8 km N, 1.3 km E summit of Hunter Peak. In Texas known only from forested mountains of the Trans-Pecos. | III,IV | 2,4,5 |
| *Solanum leptosepalum* Correll<br>Uncommon, mesic canyon bottoms and slopes above 6500 ft. Probably near northern limit of range. | III | 4,8 |
| *Sophora gypsophila* var. *guadalupensis* Turner & Powell<br>Common over a limited area south of Coyote Peak and in adjacent New Mexico. Otherwise known only from a small population on gypsum outcrop 20 mi. southwest of Coyame, Chihuahua, Mexico, and referred to there as var. | I | 9 |

| Name | Category | Zones |
|---|---|---|
| *gypsophila*. Currently being studied intensively to determine relationship between populations. | | |
| *Sophora secundiflora* (Ort.) DC. Scattered over south-facing slope of Lower McKittrick, and in lower portions of canyons in the low-northwestern corner of park. Probably near the northern and western limit of range here. | III | 1,10 |
| *Stephanomeria wrightii* Gray Uncommon; usually on gravel alluvium in streambeds. Considered infrequent in the Trans-Pecos (Correll and Johnston 1970). | III | 2,3,6 |
| *Streptanthus sparsiflorus* Roll. Scarce; gravel alluvium and limestone ledges in canyon bottoms. In summer 1974, largest population seen in Devil's Den about 0.4 km N, 1.2 km W Pratt Lodge. Very scarce in upper Smith Canyon. Previously collected near summit of Pine Top (G. L. Webster 4595, Sul Ross). Endemic to Guadalupe Mountains. Two other species (*S. platycarpus* Gray and *S. carinatus* Wright) have been reported from park, and may be confused. Abundance highly variable; dependent on seasonal rainfall. | I | 2,3,7 |
| *Swertia radiata* (Kell.) O. Ktze. Scattered throughout high elevations; best growth observed in mesic canyon bottoms. In Texas known only from Guadalupe Mountains. | II | 3,4, 5,7 |
| *Valeriana arizonica* Gray Scattered populations on limestone outcrops in mesic canyons. | II | 4 |
| *Valeriana texana* Steyerm. Widespread but generally uncommon; more mesic crevices in limestone cliffs and ledges above 6000 ft. Endemic to Guadalupe Mountains. | I | 2,3,4 6,7 |
| *Viguiera multiflora* (Nutt.) Blake Single specimen collected on ridgetop about 2.3 km S, 0.6 km E summit of Lost Peak. Identification tentative, but if confirmed, represents first record from Texas. | II | 4 |
| *Viola missouriensis* Greene Uncommon; greatest density observed on limestone ledges of South McKittrick below The Narrows. Scarce in crevices of boulders at Smith Spring. Occurs here as a marginal disjunct population. | II | 2,3,7 |
| *Yucca faxoniana* Sarg. Scarce; limestone ledges and alluvial fans between 5000 and 6700 ft. Greatest density observed on ridge south of Smith Spring. Small colonies on north side of mouth of Pine Spring Canyon and south rim of Bone Canyon. Probably near northern limit of range here. Large individuals in Lower McKittrick referred to *Y. carnerosana* (Trel.) McKelvey in Correll and Johnston 1970. | III,IV | 6,7,10 |
| *Zigadenus elegans* Pursh. Uncommon; in mats of vegetation at seeps. Sole known occurrence in Texas. | II | 2,3 |

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# Agave—*Complex of the Guadalupe Mountains National Park; Putative Hybridization Between Members of Different Subgenera*

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When I began surveying the flora of Guadalupe Mountains National Park, my observations of the diversity of *Agave* in McKittrick Canyon prompted me to investigate the variation within this group. Two distinct taxa appeared to be present along with a third group which appeared morphologically intermediate. I naturally formed the hypothesis that the third group was of hybrid origin.

Field collections began in early summer of 1973 and are continuing through the present. Due to the paucity of material found in 1974 caused by drought early in the year, I have limited the analysis presented here to the first year's collection which is comprised of flowers and leaves of 46 plants from Guadalupe Mountains National Park, Texas.

## TAXONOMY

Specimens collected during the first year were identified with the key prepared by Dr. Howard Scott Gentry for the *Manual of the Vascular Plants of Texas* (Correll and Johnston 1970). According to the key, five species were collected within the park—*Agave lecheguilla, A. chisosensis, A. gracilipes, A. neomexicana*, and *A. parryi.*

*Agave lecheguilla*, in the subgenus Littaea, is easily recognized by its smaller size and spike-like inflorescence (Fig. 1). It is often a dominant on xeric rocky slopes below 5500 ft elevation throughout the park. As a species, it occurs from arid north-central portions of Mexico north through New Mexico, and is often considered a characteristic plant of the Chihuahuan Desert. Particularly robust specimens, including a form with yellow flowers, can be found in Lower McKittrick Canyon.

Populations of a larger *Agave* in the subgenus Euagave, section Parrayanae occur primarily on open sites from about 5500 ft elevation to the highest parts of the range above 8000 ft. Plants which key to *A. parryi* on the

**Fig. 1.** *Agave lecheguilla* in Lower McKittrick Canyon, Guadalupe Mountains.

basis of their relatively larger leaves were found in open woodland on the slopes of McKittrick Canyon; however, most plants collected from higher parts of the park were identified as *A. neomexicana*. *A. parryi* was described by Englemann (1875) who considered it to range from northern Arizona through western New Mexico, ". . . and perhaps eastward to the mountains below El Paso." *A. neomexicana* was described from the Organ Mountains in south-central New Mexico by Wooten and Standley (1913). Dr. Gentry has provided much needed help in the classification of this complex. After his trip to the Guadalupes in 1974, Dr. Gentry kindly wrote to explain that, based on his observations, *A. parryi* does not occur east of

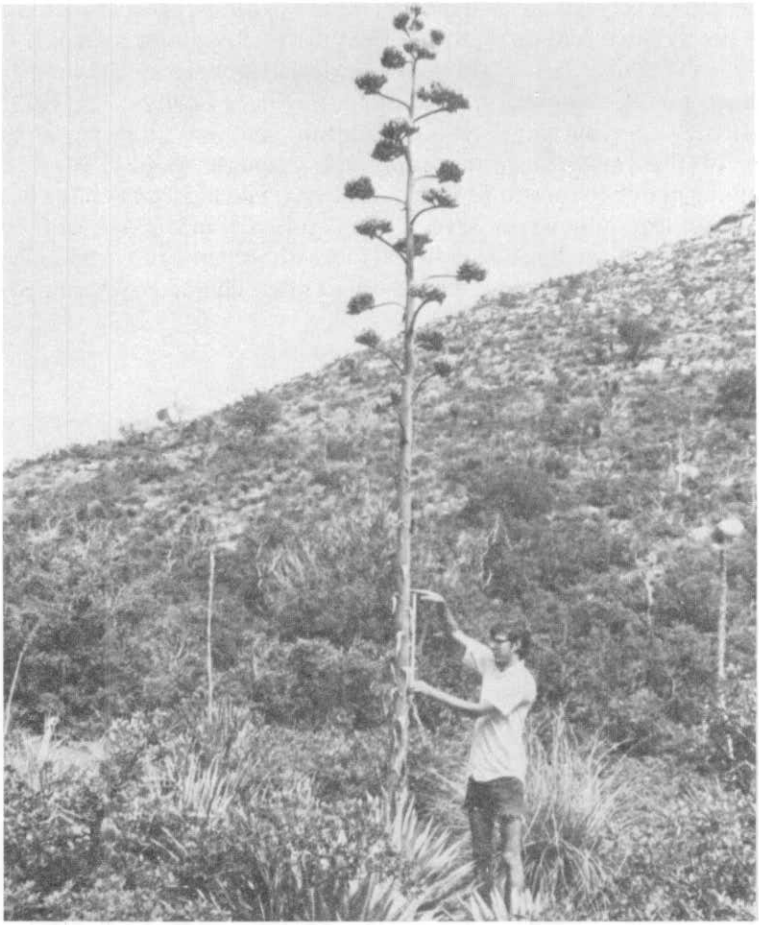

**Fig. 2.** *Agave neomexicana* in Lower McKittrick Canyon, Guadalupe Mountains.

the Rio Grande. However, he has pointed out that the type of *A. havardiana*, another species in the section Parrayanae, was cited by Trelease (1911) as "Guadaloupe Mountains" from a collection by Harvard in 1881. Although I have seen no plants large enough to fit with this species inside the park, Dr. Gentry has found a single *A. havardiana* on the bajada east of the Guadalupe Mountains, and its presence in the park is possible. Based on these considerations, the larger form of *Agave* in the Guadalupe Mountains (Fig. 2) will be called *A. neomexicana* throughout this report. Caution is advisable in applying this name indiscriminately, for *A. gracilipes* is also present in the park, and is indistinguishable from *A. neomexicana* on the basis of leaves

alone. Dr. Gentry has advised me that the major differences between the two taxa are relative length of the floral tube (1/3 as long as tepals in *A. gracilipes*, 1/2 to 2/3 as long in *A. neomexicana*), and season of bloom (early summer for *A. neomexicana*, autumn for *A. gracilipes*). In 1973, the McKittrick Canyon plants bloomed in June and July, whereas in higher parts of the range flowering continued through August. Most later-blooming plants could still be included with *A. neomexicana* on the basis of floral tube length; however, several plants collected in late August from the area north of Lost Peak had floral tubes short enough to be called *A. gracilipes*, even though with respect to all other characters examined they were closer to *A. neomexicana*.

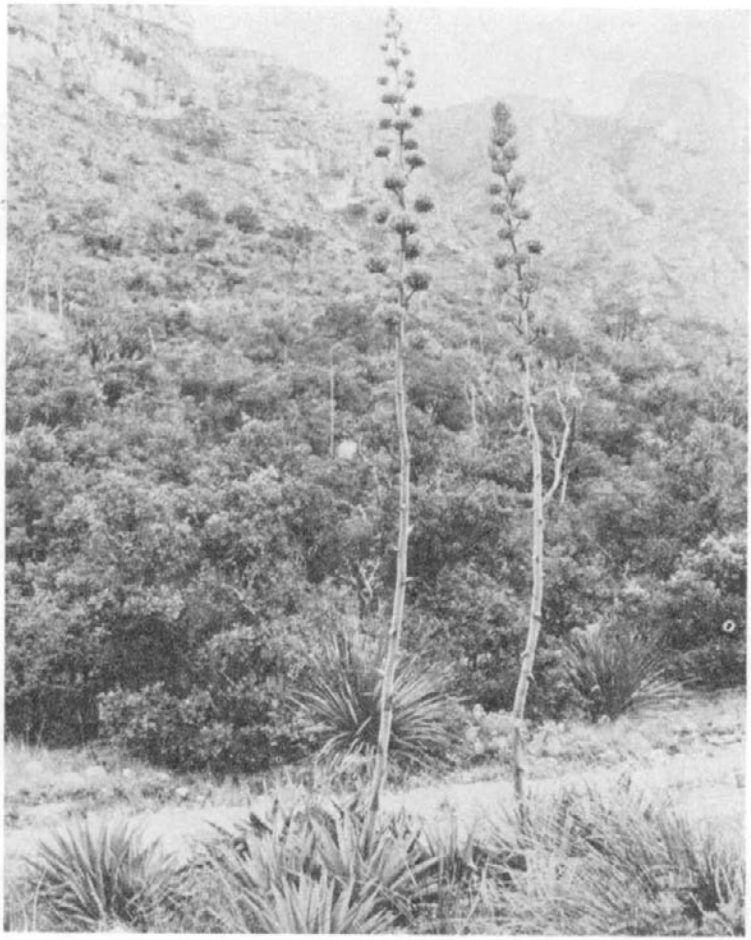

**Fig. 3.** Putative hybrid *Agave* (*A. gracilipes*) in Lower McKittrick Canyon, Guadalupe Mountains.

Some confusion may exist in delimiting *A. gracilipes* and *A. chisosensis*. The former species was described from Sierra Blanca in Hudspeth County, Texas (Trelease 1911), and the latter was first collected in the Chisos Mountains of Brewster County, Texas (Muller 1939). Gentry, in Correll and Johnston (1970), differentiates between the two taxa on the basis of panicle structure. In *A. gracilipes* it is ". . . usually narrow and closely branched with 20 to 30 lateral branches in upper half to third of shaft . . . ," whereas in *A. chisosensis* the panicle is described as ". . . racemose, 5-6 m. tall; flowers short-pedicillate, borne in compact clusters of 10 to 12 . . . ." C. H. Muller's original description (1939) of *A. chisosensis* reads as follows: "Panicle very strict and spike-like, its branches 4-5 cm. long, densely flowered. . . ." Floral characters as described for both species are generally similar; however, there are differences in dimensions. *A. chisosensis* is larger with respect to all dimensions given except the length of the ovary. The only other difference of note appears to be the ratio of tepal width to tepal length, being 1:3 to 1:5 in *A. gracilipes*, and about 1:3 in *A. chisosensis*. There appear to be two main differences in leaf morphology between the species as described. In *A. chisosensis* the leaves are over 50 cm long, and the corneous margin is continuous from the base to the terminal spine. Leaves of *A. gracilipes* are under

TABLE 1. Mean and standard deviation of variables measured for each *Agave* taxon.

| Variable | *A. lecheguilla* | *A. neomexicana* | *A. "gracilipes"* |
|---|---|---|---|
| Inflorescence | | | |
| Total height (dm) | 28.2, 7.5 | 34.9, 5.8 | 37.4, 5.7 |
| Mid-panicle branch length (cm) | 3.0, 1.5 | 27.8, 9.4 | 10.6, 8.1 |
| Number of panicle branches | 72, 24.2 | 14, 4.2 | 39, 22.5 |
| Leaf | | | |
| Length (cm) | 28.4, 6.8 | 26.5, 6.2 | 32.1, 6.4 |
| Maximum width (cm) | 3.2, 0.7 | 8.6, 1.2 | 6.2, 1.3 |
| Maximum marginal tooth (mm) | 5.4, 1.5 | 5.0, 1.1 | 5.3, 2.0 |
| Marginal tooth at widest part of blade (mm) | 3.7, 1.7 | 1.7, 1.1 | 2.9, 1.9 |
| Corneous margin length (mm) | 254, 66 | 72, 22 | 164, 95 |
| Terminal spine length (mm) | 25.9, 3.2 | 34.2, 9.4 | 29.4, 9.2 |
| Flowers (all in mm) | | | |
| Ovary body | 14.2, 2.1 | 26.2, 5.3 | 19.1, 3.6 |
| Ovary neck | 4.6, 1.1 | 5.2, 1.5 | 5.6, 2.0 |
| Tube length | 3.5, 1.0 | 12.7, 2.4 | 7.0, 1.8 |
| Filament insertion | 3.2, 1.1 | 8.9, 2.0 | 5.1, 1.1 |
| Maximum tepal length | 14.9, 2.0 | 15.8, 1.9 | 16.1, 2.0 |
| Minimum tepal length | 13.6, 2.0 | 13.7, 1.7 | 14.3, 1.9 |
| Outer tepal width | 4.0, 0.7 | 5.7, 1.0 | 4.9, 0.7 |
| Filament length | 34.7, 6.0 | 42.1, 7.1 | 38.5, 6.7 |
| Anther length | 14.1, 1.9 | 19.6, 2.5 | 16.9, 2.1 |

30 cm in length, and the terminal spine is decurrent at most to about the middle of the blade.

The putative hybrid form (Fig. 3) appears close to the above two species. Plants were found blooming from July through October, and several panicles were killed by frost prior to capsule maturation. The greatest concentration of this taxon was observed in McKittrick Canyon on alluvial terraces and open slopes mostly between 5000 and 6000 ft elevation. Other plants which could be included in this group were seen on the bajada east of the park, on a small hill southwest of El Capitan, and at Juniper Well in Lincoln National Forest north of the park. Mean leaf length of the putative hybrid specimens was 32 cm, closer to *A. gracilipes*; furthermore, the mean length of the corneous margin from the terminal spine was half the mean total leaf length, another *A. gracilipes* character. All mean floral dimensions were close to those described for *A. gracilipes*, but the tepal width:length ratio was an inconclusive 1:3. Panicle structure was variable as to number and length of branches (Table 1), but the mean branch length was longer than that described for *A. chisosensis*. Based on this analysis, I have concluded that the putative hybrid can probably be grouped with *A. gracilipes* if a name must be given.

## METHODS AND RESULTS

Several approaches are desirable for investigating patterns of variation because each different avenue increases the perspective. The most obvious, and probably most important, is the analysis of morphology. Other possibilities for clarifying relationships include data on phytochemistry, karyotypes, and ecological parameters. At this time only morphology has been studied enough to warrant presentation, although data are being gathered on all the above aspects for later summarization.

Measurements of the following characters were taken from two leaves per plant: total length, maximum width, number of marginal teeth on each side, maximum marginal tooth length, length of marginal teeth on each side of the widest part of the leaf, length of corneous margin decurrent from the base of the terminal spine, and length of terminal spine. The floral measurements used by Dr. Gentry (1972) were adopted for this study. Ten flowers per plant, when available, were evaulated with respect to the following variables: length of ovary body, length of ovary neck, length of floral tube, length from bottom of the floral tube to point of filament insertion, maximum tepal length, minimum tepal length, width of outer tepal, filament length, and anther length.

Leaf and flower data were analyzed separately by computer. Overall statistics, analysis of variance, and a principal components analysis were done using the program SIMPLE developed by Dr. Charles Gaskins at Texas Tech University. A discriminant analysis was done with the program BMD 07M, part of a package of biomedical computer programs from the University of California (Dixon 1971). Statistical analysis by computer generally

confirmed the conclusion intuitively reached in the field; that the putative hybrid form bridged a morphological gap between *A. neomexicana* and *A. lecheguilla*. Principal components analysis of overall variation showed no clear trends in the relative contributions of the variables. An analysis of variance indicated that the variation of floral dimensions within a plant was much less than between plants, as expected. Two strategies were used in the BMD 07M stepwise discriminant analysis. In one strategy a classification scheme was derived to distinguish between *A. lecheguilla* and *A. neomexicana* specimens, then data from the putative hybrid were classified by the same scheme. The other strategy considered each group a separate entity, and a scheme was derived to discriminate among all three groups.

Discriminant analysis of leaf data showed that width, total length, and length of corneous margin were the best characters to distinguish among the three groups. Group means for all variables are presented in Table 1. When treated as a separate group, the putative hybrid was in an intermediate position morphologically and appeared to be contiguous or overlap slightly with *A. neomexicana* and *A. lecheguilla*. In the two-group strategy, the putative hybrid was somewhat closer to *A. lecheguilla*.

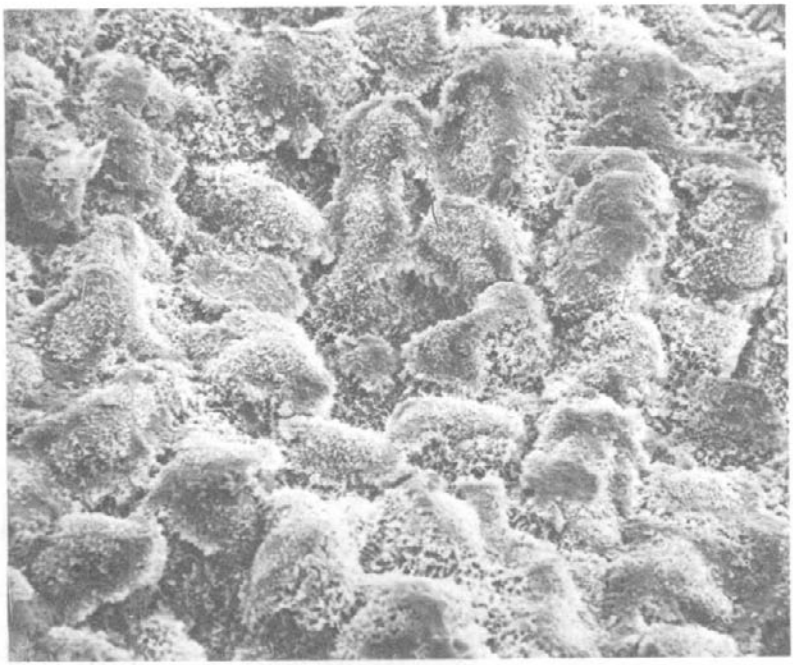

**Fig. 4.** Scanning electron micrograph of cuticle surface from *Agave neomexicana*. 500 ×.

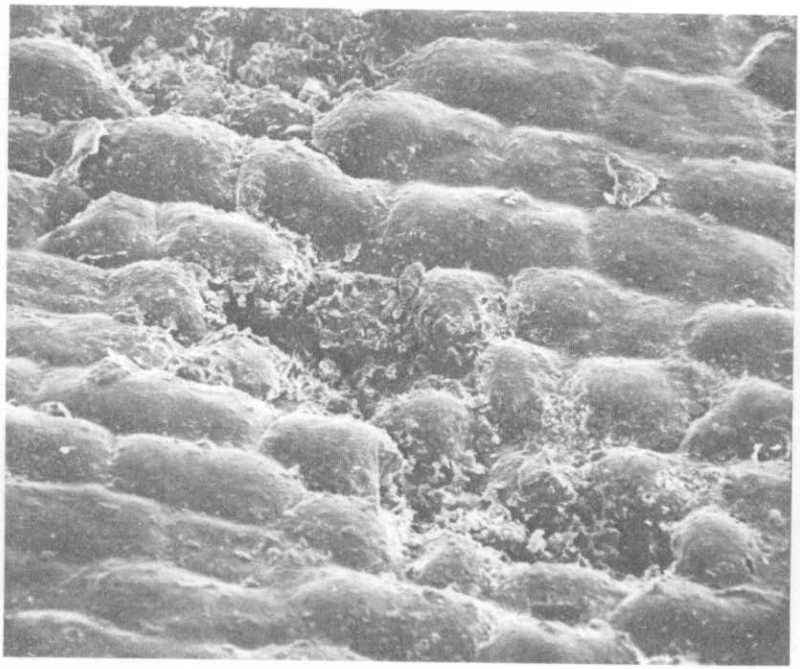

**Fig. 5.** Scanning electron micrograph of cuticle surface from *Agave lecheguilla*, 500×.

Based on data from floral characters, discriminant analysis using the three-group strategy again showed the putative hybrid in an intermediate position, somewhat closer to *A. lecheguilla* but merging into the other two species. Results from the two-group strategy had the same pattern. Characters which could best distinguish among the three groups were, in order of decreasing importance, floral tube length, length from bottom of tube to filament insertion, and width of outer tepal.

Flavonoid analysis of leaf extracts was done by two-dimensional paper chromatography as described by Mabry et al. (1970). Initial results were promising, but the pattern of variation rapidly became confusing. Experimentation has indicated differences in flavonoid patterns between flowering and immature rosettes of the same clone. In addition, changes in compound patterns resulting from slow drying of intact leaves seem probable. Investigation of seasonal variation in flavonoid pattern is currently underway. Thus much work remains before an analysis of flavonoids in *Agave* can be interpreted properly.

Blunden and Jewers (1973) have proposed that cuticle and stomate anatomy could be used to differentiate species of *Agave*. Comparison of photographs taken by scanning electron microscope (Figs. 4–6) shows dis-

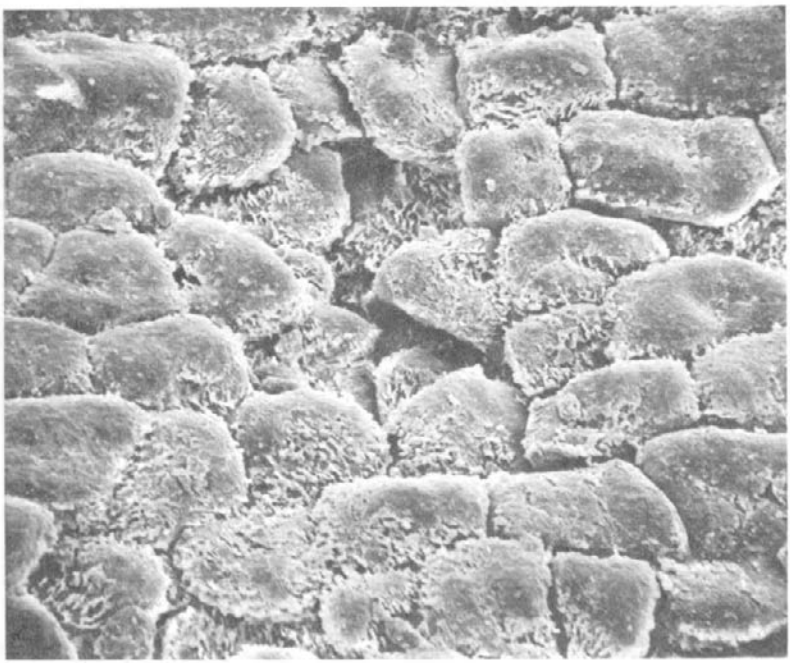

**Fig. 6.** Scanning electron micrograph of cuticle surface from putative hybrid *Agave* shown in Fig. 3, 500 ×.

tinct differences in surface texture and shape of cuticular cells from *A. neomexicana* and *A. lecheguilla*. Notice also that the cuticle of a putative hybrid appears intermediate between the two species. Conclusions should not be made from these single specimens, but they indicate a promising source of information for *Agave* systematics.

## DISCUSSION

Calling the intermediate form *Agave gracilipes* does not negate the possibility of hybrid status. Morphological patterns for the three groups indicate that locally *A. gracilipes* occupies a position morphologically if not genetically between *A. lecheguilla* and *A. neomexicana*. Furthermore, the lack of sharp morphological discontinuity between the three taxa probably reflects a similar genetic situation, so that even if *A. gracilipes* is not itself a hybrid, there are hybrids between that taxon and the other two species. Studies of karyotypes in the genus show a relatively stable base number of $n = 30$ and indicate a strong possibility of alloploidy and autoploidy (Granick 1944). The only chromosome counts reported for species occurring in the Guadalupe Mountains are $2n = 55$, 60, and 120 for *A. lecheguilla* (Granick 1944; Cave 1964). The only apparent barrier to cross pollination is time of

bloom, and there is considerable overlap among the three taxa. The large amount of nectar attracts a variety of hummingbirds, wasps, bees, butterflies, and beetles; and it seems reasonable to postulate a nonspecific pollination strategy. The late bloom of the putative hybrid is perplexing because it gives these plants a decided disadvantage in sexual reproduction under the current regional climate. This could help account for the relatively limited distribution of this form in the region. This characteristic is clearly different from both proposed parental species, and could signify genes not currently present in other local taxa. However, until the mechanism of bloom induction is known, it is difficult to evaluate the genetic significance of this factor. In any case, asexual cloning appears to be an effective propagating strategy on a local basis.

To conclude, morphological data from 1973 collections of *Agave* in Guadalupe Mountains National Park show a good possibility of hybrid origin for some populations tentatively included with *A. gracilipes*. There appears to be backcrossing with the two proposed parental species—*A. neomexicana* and *A. lecheguilla*. However, I can make no firm conclusions without more data, which I am continuing to gather for future analysis.

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# *The Land and Freshwater Mollusca of the Guadalupe Mountains National Park, Texas*

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On 1 November 1922, H. A. Pilsbry (often considered the father of southwestern malacology) and James H. Ferriss hiked from the west along the old PX trail into the Texas Guadalupe Mountains, thus making the first recorded attempt to collect mollusks in the Permian Reef. They had started their hike in Orange, New Mexico (which no longer exists), and during their entire 11-day trip, Pilsbry believed that they were collecting in New Mexico. Their search carried them to areas across the west side, up to the area of Bush Mountain and up Pine Springs Canyon twice. Pilsbry (1939, 1946) later recorded only the larger species collected and none of the smaller species that they surely gathered. Perhaps more strangely, though, is that after this beginning, no other major molluscan collecting efforts were made in the Guadalupe Mountains until 1974.

Pilsbry did return for one day on 18 July 1935 with Cyril Harvey; they climbed to about 6500 ft on the southern flank of "Signal" (Guadalupe) Peak. Metcalf (1970) published Pilsbry's field notes of these trips. In 1934 and 1935, H. C. Fountain, who aided P. B. King during his geological survey of the Guadalupes of Texas, collected four species of living snails from Pine Springs Canyon and a series of fossil snails from alluvial deposits in Bell Canyon and in Pine Springs Canyon. The material was identified by Dr. J. P. E. Morrison of the U.S. National Museum, and the list was published in King's (1948) Geology of the southern Guadalupe Mountains.

In July 1950, Dr. E. P. Cheatum with his wife Edith and their two small sons visited the Texas Guadalupes to collect Mollusca. Shortly after arriving at the small motel at Pine Springs, Texas, Dr. Cheatum became ill and was confined to the room for most of their stay which, historically, was unfortunate as will be explained in the discussion of *Ashmunella edithae*. He did make one excursion into McKittrick Canyon but the treks up the mountains were made by his wife and eldest son who were accompanied by a group

of geologists. The results of this trip were published by Pilsbry and Cheatum (1951).

Mr. Munroe L. Walton of Glendale, California, collected in Pine Springs Canyon on 19 March 1952 and 23 October 1952, and published (1963) on one of the two collected species and sent the other to Dr. J. C. Bequaert.

In April 1958 and April 1961, Dr. Joseph C. Bequaert collected a series of small mollusks from washed up debris in Bell Canyon at the Highway 180 crossing and live *Physa* in the bed of the canyon. He visited McKittrick Canyon on 4 and 5 April 1966, where he collected another series of small gastropods. Soon after, he presented the National Park Service an unpublished checklist of all known mollusks collected in the Park. The manuscript (Bequaert 1966) was made available to me for incorporation into this report.

Other investigators periodically have collected mollusks in the Park, including Dr. Fred Gehlbach, Baylor University, who informed Dr. Bequaert that over a 10-year period while doing ecological work in the Park, he had collected gastropods. These were deposited in the University of Michigan, Museum of Zoology, but no publications have resulted.

Dr. Artie L. Metcalf, University of Texas at El Paso, has worked periodically on the Guadalupe Mollusca. He graciously has made much of his data available to me and has a manuscript in preparation listing species he collected in Pine Springs Canyon, with a description of a new fossil *Ashmunella*.

Mr. Lloyd E. Logan, Texas Tech University, while investigating Quaternary vertebrate remains from Sloth and Dust caves, sifted fossil gastropods from floor sediments. The material was sent to me for identification, and Mr. Logan kindly permitted me to incorporate the species list into this report.

My first trip to the Texas Guadalupes was made with Dr. E. P. Cheatum and Mr. Hal P. Kirby in November 1969. We collected at Smith Spring and McKittrick Canyon. In November 1970, the three of us returned accompanied by William E. Wilson. Wilson and I worked up Pine Springs Canyon, Pipeline Canyon, The Bowl, and up the south walls of McKittrick Canyon where we collected *Ashmunella carlsbadensis* for the first time in Texas. Cheatum and Kirby worked the lower levels. Dr. Cheatum, Wilson, and I made a brief stop in McKittrick Canyon in November 1971. All of the material collected thus far was published with the molluscan data that Mr. Lloyd Pratt, Fort Worth Museum of Science and History, had gathered from the Chisos Mountains and west Texas in general (Cheatum et al. 1972).

Fourteen members of the museum staff spent 2 weeks in July 1974 collecting mainly at the upper elevations. Main camp was established at the ranger's headquarters in Upper Dog Canyon and we backpacked into the mountains from there. The "rainy season" had begun which greatly aided collecting as most of the gastropods were above ground. I returned in December 1974 with staff members Walt Davis, Bill Wilson, and Steven Runnels, at which time we collected in Pine Springs Canyon, Bone Canyon, along the summit of the eastern escarpment, and near most of the springs

along the east side of the mountains. Also, during this last trip, we collected to the head of Pine Springs Canyon.

The bulk of this report is the data gathered from these two intensive trips in 1974. The collecting sites are listed below, grouped by altitude intervals. Lesser known sites are indicated by degrees, minutes, and seconds from the U.S. Geological Survey Guadalupe Peak, Texas, Quadrangle map, 1933 edition.

## COLLECTING SITES 1974

5000 to 5500 ft (1500 to 1650 m)
- floor of McKittrick and South McKittrick canyons
- Choza Spring
- Manzanita Spring
- Juniper Spring
- Bone Canyon

5500 to 6000 ft (1650 to 1800 m)
- Lower Pine Springs Canyon (to first big bend)
- Smith Spring
- Spring at base of Pipeline Canyon

6000 to 6500 ft (1800 to 1950 m)
- 104° 50′ W, 31° 59′ 30″ S (ravine just west of Ranger Station in Upper Dog Canyon)
- 104° 51′ W, 31° 59′ 30″ S (trail to Coyote Peak)
- 104° 50′ E, 31° 59′ N (canyon heading on east ridge of Upper Dog Canyon by Devil's Den Canyon)
- 104° 50′ W, 31° 59′ 30″ S
- 104° 50′ 30″ E, 31° 58′ 30″ N
- Pine Springs Canyon

6500 to 7000 ft (1950 to 2100 m)
- 104° 50′ 30″ E, 31° 58′ S ("Spring" Canyon off Lost Peak Trail)
- 104° 50′ 20″ W, 31° 57′ 17″ N
- Upper Portion of Pine Springs Canyon
- Lower Pipeline Canyon

7000 to 7500 ft (2100 to 2500 m)
- 104° 49′ 31″ W, 31° 59′ N
- 104° 50′ E, 31° 57′ 30″ N
- 104° 51′ W, 31° 56′ 30″ N
- 104° 50′ 35″ W, 31° 56′ 20″ N
- 104° 51′ W, 31° 55′ 30″ N
- Pine Springs Canyon

7500 to 8000 ft (2250 to 2400 m)
- Pipeline Canyon
- Pine Springs Canyon
- 104° 51′ 20″ W, 31° 55′ 45″ N (Aspen Grove)
- 104° 51′ 30″ W, 31° 56′ 35″ N
- 104° 50′ 20″ W, 31° 57′ 17″ N
- Lost Peak

8000 to 8300 ft (2400 to 2490 m)
- 104° 52′ W, 31° 56′ 40″ N (Blue Ridge Trail area)
- 104° 52′ 20″ W, 31° 56′ 55″ N (Blue Ridge Trail area)
- 104° 52′ 40″ W, 31° 56′ 55″ N (Blue Ridge Trail area)
- 104° 51′ 35″ W, 31° 56′ 35″ S
- East escarpment to just beyond Smith Spring Canyon
- The Bowl (southern area only)

## Checklist of Land and Freshwater Mollusca of the Guadalupe Mountains National Park, Texas

This list represents all published and unpublished species for the Texas Guadalupe Mountains. Strictly indigenous species are noted as are species that are known currently only as fossils. All current taxonomic changes are also incorporated and are explained in the systematic discussion section. Numbers in parentheses indicate species included in each group.

Pelecypoda (1)
- Family Sphaeriidae
  - *Pisidium casertanum* (Poli)

Gastropoda (aquatic) (5)
- Family Hydrobiidae
  - *Hydrobia* sp.
- Family Lymnaeidae
  - *Lymnaea humilus* (Say)
- Family Physidae
  - *Physa virgata* (Gould)
- Family Planorbidae
  - *Helisoma trivolvis trivolvis* (Say)
  - *Gyraulus parvus* (Say)

Gastropoda (terrestrial) (55)
- Family Helminthoglyptidae
  - *Humboldtiana ultima* Pilsbry
- Family Urocoptidae
  - *Metastoma roemeri roemeri* (Pfeiffer)
  - *Holospira montivaga montivaga* Pilsbry (indigenous)
  - *Holospira montivaga* form *brevaria* Pilsbry (indigenous)
  - *Holospira pityis* Pilsbry and Cheatum (indigenous)
  - *Holospira oritis* Pilsbry and Cheatum (indigenous)
  - *Holospira danielsi* Pilsbry and Ferriss
- Family Bulimulidae
  - *Rabdotus dealbatus dealbatus* (Say)
  - *Rabdotus dealbatus durangoanus* (Martens)
- Family Thysanophoridae (Sagdidae)
  - *Thysanophora hornii* (Gabb)
- Family Endodontidae
  - *Helicodiscus nummus* (Vanatta)
  - *Helicodiscus singleyanus singleyanus* (Pilsbry)
  - *Helicodiscus eigenmanni* Pilsbry
  - *Discus cronkhitei* (Newcomb)
  - *Punctum minutissimum* (Lea)
  - *Punctum vitreum* H. B. Baker
- Family Zonitidae
  - *Zonitoides arboreus* (Say)
  - *Glyphyalinia indentata paucilirata* (Morelet)
  - *Nesovitrea electrina* (Gould)
  - *Nesovitrea* sp.
  - *Euconulus fulvus* (Müller)
  - *Striatura meridionalis* (Pilsbry and Ferriss)
  - *Vitrina pellucida alaskana* Dall
  - *Hawaiia minuscula minuscula* (Binney)
  - *Hawaiia minuscula neomexicana* (Cockerell and Pilsbry)

Family Limacidae
*Deroceras laeve* (Müller)
Family Polygyridae
*Ashmunella kochi amblya* Pilsbry
*Ashmunella rhyssa rhyssa* (Dall) (fossil only)
*Ashmunella carlsbadensis* Pilsbry
*Ashmunella edithae* Pilsbry and Cheatum (indigenous)
*Ashmunella* sp. nov.
Family Succineidae
*Succinea luteola* Gould
*Succinea* sp.
Family Cionellidae
*Cionella lubricella* (Porro)
Family Pupillidae
*Gastrocopta armifera* (Say)
*Gastrocopta procera procera* (Gould)
*Gastrocopta pentodon* (Say)
*Gastrocopta pilsbryana* (Sterki)
*Gastrocopta ashmuni* (Sterki)
*Gastrocopta contracta* (Say)
*Gastrocopta pellucida* (Pfeiffer)
*Pupilla muscorum muscorum* (Linné) (fossil only)
*Pupilla blandi* Morse
*Pupilla sonorana* (Sterki)
*Pupoides albilabris* (C. B. Adams)
*Pupoides hordaceus* (Gabb) (fossil only)
*Vertigo milium* (Gould)
*Vertigo gouldii arizonensis* Pilsbry & Vanatta
*Vertigo ovata* (Say)
Family Valloniidae
*Vallonia perspectiva* Sterki
*Vallonia gracilicosta* Reinhardt
*Vallonia parvula* Sterki (fossil only)
*Vallonia cyclophorella* Sterki (fossil only)
Family Strobilopsidae
*Strobilops labyrinthica* (Say)
Family Oreohelicidae
*Oreohelix soccorensis soccorensis* Pilsbry (fossil only)

## SYSTEMATIC DISCUSSION

Pelecypoda
Family Sphaeriidae

*Pisidium casertanum* (Poli)

**General Distribution.**—Worldwide; this is by far the most common *Pisidium*.
**Guadalupe Park Distribution.**—Springs at base of Pipeline Canyon (Cheatum et al. 1972).
**Comments.**—King (1948:145) reported a fossil *Pisidium* sp. from Bell Canyon, 1 mi. N of the Hegler Ranch. This, in addition to those in Cheatum et al. (1972), constitutes the only pelecypod reports for the Guadalupe Mountains.

Gastropoda (freshwater)
Family Hydrobiidae

*Hydrobia* sp.

**Comments.**—A single fragmented shell was obtained from under a rock, in a pine stand, on the ridge (7400 ft) that forms the east side of Upper Dog Canyon. The location of this gill-breathing aquatic genus remains the greatest mystery of the Guadalupean snail fauna.

Family Lymnaeidae

*Lymnaea humilis* (Say)

*Fossoria obrussa* (Say), in King (1948:145) as a fossil from Bell Canyon.

*Lymnaea* (*Galba*) *obrussa* (Say), in Bequaert (1966) citing King (1948:145).

**General Distribution.**—Canada, United States, and northern Mexico.

**Guadalupe Park Distribution.**—Manzanita Spring (Cheatum et al. 1972) Choza Spring.

**Comments.**—This is a relatively common lymnaeid in the Southwest and should be found in more aquatic localities in the Guadalupes.

Family Physidae

*Physa virgata* (Gould)

*Physa anatina* Lea, in King (1948:145) Bell Canyon as a fossil.

*Physa forsheyi* Lea, in Bequaert (1966), "living in pools and slowly running water of Bell Canyon, near the crossing of Hwy 180."

**General Distribution.**—Common over most of south-central and southwestern North America. In California at least as far north as Sacramento and San Francisco Bay, northernmost Baja California, and eastward, southernmost Nevada, Utah, and Colorado; northward it is replaced by *P. gyrina*; southern Kansas (Taylor 1966:211).

**Guadalupe Park Distribution.**—McKittrick Canyon, spring at base of Pipeline Canyon, drift in Delaware Creek.

**Comments.**—This is probably the most common freshwater snail in the Southwest.

Family Planorbidae

*Helisoma trivolvis trivolvis* (Say)

*Helisoma trivolvis lentum* (Say), in Cheatum et al. (1972) in Manzanita Spring.

**General Distribution.**—"Atlantic coast and Mississippi River drainages, northward to Arctic British America and Alaska and southward to Tennessee and Missouri. The southern distribution is not clear owing to the mixing with related species" (Baker 1928:332).

**Guadalupe Park Distribution.**—Manzanita Spring, Choza Spring.

**Comments.**—A conservative taxonomic approach is taken here in the relationship of *H. t. trivolvis* and *H. t. lentum* until the distribution and validity of *lentum* is established. In Texas, the shell characters are quite variable within populations and unreliable for taxonomic purposes.

*Gyraulus parvus* (Say)

**General Distribution.**—"Eastern North America, east of the Rocky Mountains from Florida to Alaska" (Baker 1928:377).

**Guadalupe Park Distribution.**—Manzanita Spring (Cheatum et al. 1972).

**Comments.**—The flat, open pond constructed at Manzanita Spring would appear to be a preferred stopping place for migrating aquatic birds as indicated by the presence of *H. t. trivolvis* and *G. parvus*. Both are known to be easily transported in mud on the feet of such birds.

Gastropoda (land)

Family Helminthoglyptidae

*Humboldtiana ultima* (Pilsbry)

**General Distribution.**—Guadalupe Mountains: Pine Springs Canyon (Pilsbry 1939:408–409). Pilsbry and Ferriss during their trip in 1922 to the mountains on 2 November, went up the PX trail, apparently, to the area just north of Bush Mountain (Sta. 237). There they collected the first "Lysinoe." However, on 9 to 11 November, they collected living specimens "just above the box above the Gateway" (Sta. 240) (Devils' Hall). Apparently, Pilsbry described the holotype from this site. Also occurs in the Sierra Diablo Mountains (Cheatum and Fullington, unpubl.).

**Guadalupe Park Distribution.**—General throughout the mountains above 6500 ft elevation. Usual habitat, forested ravines and rocky outcrops.

**Comments.**—The shell in the northern portion of the mountains is larger (average height, 27.9 mm), darker, and the bands are wider and much darker than the shell of the southern area (south of Lost Peak), where it becomes smaller (average height, 25.3 mm) and lighter. In the Bush Mountain area, the banding is highly variable. In the Aspen Grove area, most of the sampled population had only two bands rather than the usual three.

King (1948:145) reported *H. ultima* as a fossil from alluvial deposits on the north side of Pine Springs Canyon, 1 mi. W of Pine Springs. The thin shell does not lend itself well to fossilization although I do have fossil specimens from Sloth Cave. These specimens were sent to me by Lloyd Logan who is investigating the caves on the west side.

The Guadalupe Mountains are the northernmost localities for this Mexican genus although other species occur on mountaintops in West Texas. It is also the largest snail indigenous to North America.

Family Urocoptidae

*Metastoma* (*Holospira*) *roemeri roemeri* (Pfeiffer)

**General Distribution.**—Westward in Texas from the type locality at New Braunfels, Texas, to the Franklin Mountains at El Paso, Texas. It also occurs in the Sacramento and San Andreas mountains of southeastern New Mexico (Bequaert 1966).

**Guadalupe Park Distribution.**—At elevations from 5000 to 6500 ft Pilsbry (1946:115) reported it from the Guadalupe Mountains east of Orange, in Lincoln and Eddy counties, New Mexico, collected during the Pilsbry and Ferriss trip in 1922. It is almost certain that these localities are from the northwestern side of the Guadalupes, Culberson County, Texas. Pilsbry and Cheatum (1951:88) reported that a Mrs. Fischer collected it from Bone Canyon. The Dallas Museum of Natural History has collected it from the following localities: Bone Canyon, Pine Springs Canyon, Smith Spring Canyon, McKittrick Canyon, and Pipeline Canyon, 8100 ft.

**Comments.**—*M. r. roemeri* apparently occurs only along the low-level, xeric rocky exposures that flank the mountains. It has not been collected within the mountains. Fossil specimens were taken from Sloth Cave.

*Holospira montivaga montivaga* Pilsbry, 1946

**General Distribution.**—Guadalupe Mountains: Type Locality, "New Mexico, Guadalupe Mountains east of Orange, the types from a terraced butte in a deep, dry canyon (our station 240), about 2 miles south of the PX trail over the Mountains" (Pilsbry 1946:124). Again, Pilsbry was in error thinking that he and Ferriss, during their 1922 trip, were in New Mexico. My estimate is that the site is near the north end of Blue Ridge as stated by Metcalf (1970:35).

**Guadalupe Park Distribution.**—General over the mountains at elevations over 5000 ft.

**Comments.**—As with *Humboldtiana ultima*, the shells of *H. m. montivaga* are larger (average height, 18.0 mm) in the northern section of the mountains and become smaller southward. The *H. m. montivaga, H. m.* form *brevaria, H. pityis*, and *H. oritis* complex have become extremely problematic with respect to the data compiled during this survey. For the present time, all species are being retained, but evidence strongly leans toward a synonomization. The problem will be discussed later.

*Holospira montivaga* form *brevaria* Pilsbry, 1946

**General Distribution.**—Guadalupe Mountains: Type Locality, New Mexico, "eastern slope of Guadalupe Mountains near south end, above Walter Glover's ranch house in Pine Springs Canyon, below the rock Gateway (Devil's Hall), (Pilsbry and Ferriss)" (Pilsbry 1946:125).

**Guadalupe Park Distribution.**—General over the mountains at elevations over 6300 ft except in McKittrick Canyon. This distribution is based upon the strict definition of this form as having coarser ribbing than *H. m. montivaga*. Spire height differences (*H. m. brevaria* = 8–12 mm, *H. m. montivaga* = 15 mm; Pilsbry 1946) had no meaning when reasonably large populations were examined.

**Comments.**—The only area where at least 85% of the population (46 specimens) sampled conformed to this form was in the vicinity of the type locality.

*Holospira pityis* Pilsbry and Cheatum, 1951

**General Distribution.**—Guadalupe Mountains: Type Locality, "Guadalupe Range: Pine Springs Camp, Texas" (Pilsbry and Cheatum 1951).

**Guadalupe Park Distribution.**—Pine Springs Canyon, The Bowl near Pipeline Canyon, and the vicinity of Guadalupe Peak.

**Comments.**—By description, *H. pityis* is distinguished by its very fine, close-set ribbing and height (8.5 mm) from *H. m. brevaria*. In The Bowl area near the eastern escarpment and Pipeline Canyon, and in lower Pine Springs Canyon, the populations conform 90% to the description. However, in the Guadalupe Peak area and upper (above 7000 ft) Pine Springs Canyon, the height and ribbing characters merge with the characters for *H. m.* form *brevaria*. Fossil specimens from Sloth Cave conform more closely to *H. pityis*, but the point could well be argued.

*Holospira oritis* Pilsbry and Cheatum, 1951

**General Distribution.**—Guadalupe Mountains: Type Locality, "this species was collected near Pratt's lodge in McKittrick Canyon in the Guadalupe Range approximately 7 miles from Pine Springs, Texas. They were on rocks of a jutting escarpment of limestone near a stream" (Pilsbry and Cheatum 1951:90).

**Guadalupe Park Distribution.**—Apparently limited to McKittrick Canyon.

**Comments.**—*H. oritis* differs (by type definition) from *H. m. montivaga* in being more robust, longer (height, 14 to 20 mm), and with one or more whorls being smooth. In one large population (in McKittrick Canyon proper) over 40% of the specimens conformed to *H. m. montivaga*. The *oritis* characters showed up in 10 % of a population of *H. m. montivaga* located in the canyon, with the spring forming the south end of Upper Dog Canyon.

*Holospira danielsi* Pilsbry and Ferriss, 1915

**General Distribution.**—Dragoon Mountains of Arizona.

**Guadalupe Park Distribution.**—McKittrick Canyon.

**Comments.**—One specimen was taken from drift at the mouth of McKittrick Canyon by Cheatum and Fullington in 1970 and was reported in Cheatum et al. (1972). I have always been a little dubious of this specimen due to the distance from the type locality and because there is but one specimen. However, the species may actually occur in the Guadalupes and no one has discovered the population. Pilsbry (1946:137) cites the habitat as ". . . they live on the most exposed, hottest slopes, often in great profusion. . . ." He also states that they live under dead agaves, stones, and sotols. No one, as yet, has investigated this type of habitat in the Guadalupe Mountains.

Due to the extent of this survey, which has been the most thorough of all molluscan investigations in the Guadalupe Mountains thus far, several statements may be made concerning the *Holospira* species complex or at least the problem itself may be better defined.

Suspicion as to the validity of such species as *H. montivaga* form *brevaria*, *H. pityis*, and *H. oritis* have been voiced by several authors (Bequaert 1966; Cheatum and Fullington 1973:40, Bequaert and Miller 1973:142). With this in mind, emphasis during this investigation was placed on large population analysis rather than upon simple species collecting by a few individuals. Unfortunately, time has not permitted necessary anatomical analysis.

In all examined populations of *Holospira m. montivaga*, the range of shell characters (height, number, and coarseness of ribs) included that of *H. m.* form *brevaria* and vice versa. Several characters (some smooth whorls and height of at least 18 mm) for *H. oritis* were also present in a few *H. m. montivaga* populations outside McKittrick Canyon and vice versa. As stated earlier, *H. m. montivaga* decreases in height southward until, in the Pine Springs region, it becomes almost indistinguishable from *brevaria* except for the finer striations. Populations of *H. pityis* are much more restricted from The Bowl southward. McKittrick Canyon and Pine Springs Canyon appear to be "melting pots" for the characteristics which are used to distinguish species of *Holospira*. Thus, the problem becomes more question of which environmental pressures are operating on gene expression in the Guadalupe *Holospira*. The limited area of the Guadalupe Mountains should make them an excellent "laboratory" to further examine this problem.

Excluding *H. danielsi*, all Guadalupean *Holospira* species probably should be synonymized under the earliest named *H. m. montivaga*. The separate species have been retained in this study for locality retention purposes in order to assist future investigations on this complex.

Family Bulimulidae

*Rabdotus* (*Bulimulus*) *dealbatus dealbatus* (Say)

*Bulimulus dealbatus pecosensis* Pilsbry and Ferriss, in King (1948:145).

*Bulimulus dealbatus neomexicanus* Pilsbry, in Bequaert (1966) and Cheatum et al. (1972:8).

**General Distribution.**—Northern Mexico east of Sierra Madre Oriental; northward through Texas to eastern Oklahoma and Kansas; southwestern Missouri eastward to Alabama; disjunct populations in the San Andreas, Sacramento, and Guadalupe mountains of New Mexico and Texas (Fullington and Pratt 1974:16).

**Guadalupe Park Distribution.**—Common over the mountains from 5000 ft to over 8000 ft elevation; found in almost every type of habitat from dry, barren exposure to the high forested ravines. Pilsbry (1946:13) mentions that he and Ferriss collected it in 1922. King (1948:145) reported it being high up on the south wall of Pine Springs Canyon. Bequaert (1966) examined specimens collected by Monroe L. Walton in 1952 at the ruins of the old Butterfield Stage Coach Station, Pine Springs. Bequaert also found it living in South McKittrick Canyon. Field parties from the Dallas Museum of Natural History found it at almost every collecting site.

**Comments.**—*R. dealbatus neomexicanus* is considered a large *R. d. dealbatus* (Fullington and Pratt 1974:16).

*Rabdotus* (*Bulimulus*) *dealbatus durangoanus* (Martens, 1893)

*Bulimulus dealbatus pasonis* Pilsbry, in Bequaert (1966).

*Rabdotus dealbatus durangoanus* (Martens) in Fullington and Pratt (1974).

**General Distribution.**—From the Sacramento Mountains, New Mexico, south through Trans-Pecos Texas into Mexico (Fullington and Pratt 1974).

**Guadalupe Park Distribution.**—Pilsbry (1946:19), accompanied by C. Harvey in 1935, collected this species from the southern flank of Signal Peak (old name for Guadalupe Peak), south end of the Guadalupe Mountains, 6500 ft. The Dallas Museum of Natural History collected it in Bone Canyon, elevation 5300 ft.

**Comments.**—This small form of *R. dealbatus* (as also suggested by Bequaert 1966) is probably more common around the flanks of the Guadalupes than records indicate. It generally lives under dead sotol and arborescent yuccas on arid, barren low slopes. Fullington and Pratt (1974:16) state that it occurs sympatrically with *R. d. dealbatus* in the Guadalupes.

Family Thysanophoridae (Sagdidae)

*Thysanophora hornii* (Gabb)

**General Distribution.**—Northern Mexico, north to southeastern Arizona, southern New Mexico, and southwestern Texas (Fullington and Pratt 1974:27).

**Guadalupe Park Distribution.**—King (1948:145) reported this species as a fossil from a clay deposit in Bell Canyon. Bequaert (1966) took it from drift in Bell Canyon and found it living in McKittrick Canyon. The Dallas Museum of Natural History collected it at Smith Spring, elevation 6000 ft.

**Comments.**—This is not a common species and generally prefers dry, hot rocky areas although Fullington and Pratt (1974:27) state that in the mountains of Trans-Pecos Texas, it inhabits Pinyon–Oak–Juniper Woodland at higher elevations. A related western species, *Microphysula ingersolli* (Bland), should occur in the Guadalupes but has not been collected thus far.

Family Endodontidae

*Helicodiscus nummus* (Vanatta)

**General Distribution.**—Texas, from the Balcones escarpment southward and westward to the Guadalupe Mountains; one locality in Indiana (Pilsbry 1946:639).

**Guadalupe Park Distribution.**—Sparsely distributed from canyons at south end of Upper Dog Canyon (6500 ft) to the Aspen Grove (7750 ft). It has not been previously reported from the Guadalupe Mountains.

**Comments.**—The *Helicodiscus* complex has become almost bewildering with the recent addition of several new species and the elevation of several subspecies to specific rank by various authors. This tiny species (diameter, 1.3 to 1.5 mm) is difficult to separate from other immature

smooth-shelled *Helicodiscus*. It is interesting that *H. nummus* occurs only at higher elevations in the Guadalupes, whereas elsewhere in Texas, it appears to be a lower, moist, woodland form.

*Helicodiscus singleyanus singleyanus* (Pilsbry)

**General Distribution.**—New Jersey to South Dakota, Colorado, Arizona, New Mexico, and Texas; also Florida to Louisiana (Pilsbry 1948:636).

**Guadalupe Park Distribution.**—Bequaert (1966) collected the first reported specimen in South McKittrick Canyon (5300 ft). The Dallas Museum of Natural History collected it from the canyons at the south end of Upper Dog Canyon (6300 to 6500 ft). I also have identified several fossil specimens from Sloth Cave.

**Comments.**—This is a common snail in Texas.

*Helicodiscus eigenmanni* Pilsbry, 1890

*Helicodiscus arizonensis* (*H. eigenmanni arizonensis*) Pilsbry and Ferriss, in Cheatum et al. (1972).

**General Distribution** (includes the distribution of *H. e. arizonensis*).—South Dakota to Arizona, New Mexico, Texas, and Mexico (Pilsbry 1948:630).

**Guadalupe Park Distribution.**—Drift in McKittrick Canyon, otherwise sparsely distributed over the mountains in the wooded ravines only at elevations of 6500 to over 8000 ft. Dallas Museum of Natural History localities include Pipeline Canyon, Smith Spring Canyon, near top of El Capitan, Aspen Grove, Upper Dog Canyon area, Blue Ridge area.

**Comments.**—Bequaert and Miller (1973:85–87) also have relegated *H. e. arizonensis* to synonomy. They added that *H. eigenmanni* might be only a southwestern subspecies of *H. parallelus*.

*Discus cronkhitei* (Newcomb 1865)

**General Distribution.**—Canada and most of the United States (Pilsbry 1948:602–603).

**Guadalupe Park Distribution.**—As a fossil, north side of Pine Springs Canyon, 1 mi. W Pine Springs (King 1948:145), McKittrick Canyon drift (Cheatum et al. 1972), and Sloth Cave on the west side. Field parties from the Dallas Museum of Natural History found it living from Upper Dog Canyon to The Bowl and Blue Ridge at elevations over 6500 ft.

**Comments.**—Although this species is a relatively common fossil across Texas, this is the first report of this species as Recent for the state. At least six sampled populations contained specimens with smooth bases and slightly more elevated spires conforming to *Discus shmekii* (Pilsbry). This situation apparently is common as other malacologists have observed it as well.

*Punctum minutissimum* (Lea)

**General Distribution.**—Maine to Florida, west to Oregon and New Mexico (Burch 1962:80).

**Guadalupe Park Distribution.**—The Dallas Museum of Natural History collected this tiny species in densely wooded ravines from Upper Dog Canyon southward to the Aspen Grove but only at elevations over 6600 ft.

**Comments.**—This is the first report of this species for West Texas either as Recent or fossil. Mr. Lloyd Pratt (pers. comm.) has collected it alive in Tarrant County, Texas.

*Punctum vitreum* H. B. Baker 1930

**General Distribution.**—From New Jersey through most of the southeastern states to northeastern Mexico (Baquaert 1966).

**Guadalupe Park Distribution.**—Bequaert (1966) reported this species living in South McKittrick Canyon.

**Comments.**—The museum has not collected *P. vitreum* in the park. Because most of our work has been concentrated at higher elevations where *P. minutissimum* occurs, it may be that *P. vitreum* inhabits the lower levels.

Family Zonitidae

*Zonitoides arboreus* (Say, 1816)

**General Distribution.**—North American continent to Costa Rica.

**Guadalupe Park Distribution.**—As a fossil in Pine Springs Canyon, and at the east side of Bell Canyon (King 1948:145). The Dallas Museum of Natural History found living specimens generally distributed at elevations above 6300 ft. Cheatum et al. (1972) reported it as Recent for

Culberson County. The localities were McKittrick Canyon, Pine Springs Canyon, Smith Spring Canyon, and The Bowl.

**Comments.**—The probable reason that *Z. arboreus* was not reported as living in the Texas Guadalupes until 1972 is that until the museum began investigating the mountains in 1969, no one, except Pilsbry and Ferriss in 1922, collected higher than the base of the mountains.

*Glyphyalinia indentata paucilirata* (Morelet, 1851)

*Glyphyalinia indentata* (Say), in Cheatum et al. (1972).

**General Distribution.**—Central and southern United States southward to Guatemala (Pilsbry 1946:291).

**Guadalupe Park Distribution.**—Very general over the mountains at all elevations. King (1948:145) reported it as a fossil in Pine Springs Canyon. Bequaert (1966) collected washed up specimens in Bell Canyon in 1958 and live in McKittrick Canyon. The Dallas Museum of Natural History found it at most collecting sites.

**Comments.**—Cheatum et al. (1972) placed *G. i. paucilirata* as a synonym under *G. i. indentata*. *G. i. paucilirata* is characterized externally by a much wider umbilicus. The Guadalupe shells conform quite well to this character and, thus, the subspecies is retained here. However, as with several other gastropod species, *G. i. paucilirata* may prove to be a western form of *G. i. indentata*.

*Nesovitrea* sp.

**Comments.**—A small zonitid was collected at several localities. It compares in external form with *Nesovitrea binneyana occidentalis* (H. B. Baker), and is the same type of shells identified by Cheatum et al. (1972) as *Glyphyalinia roemeri* (Pilsbry and Ferriss). Until this series has been more carefully examined, it is best to leave it unnamed for the present.

*Euconulus fulvus* (Muller, 1974)

**General Distribution.**—General throughout the cold temperate parts of Europe, Asia, and North America; in the southwestern United States, restricted to mountains above 5000 ft (Bequaert 1966).

**Guadalupe Park Distribution.**—Bequaert (1966) first recorded it as living in South McKittrick Canyon. The Dallas Museum of Natural History has found it to be distributed generally over the mountains at elevations above 6300 ft.

**Comments.**—*E. fulvus* is a fairly common fossil in Texas and as far as is presently known, it is extant within the state only in the Guadalupe and Chisos mountains (Cheatum et al. 1972).

*Striatura meridionalis* (Pilsbry and Ferriss, 1906)

**General Distribution.**—Widespread in the southeastern United States, northward to New Jersey, westward to Arizona, and southward into northwestern Mexico (Bequaert 1966).

**Guadalupe Park Distribution.**—Bequaert (1966) was the first to report this species in the Guadalupe Mountains. His specimens came from South McKittrick Canyon. The Dallas Museum of Natural History collected it over most of the mountains at elevations above 6500 ft.

**Comments.**—Cheatum et al. (1972) reported it as a fossil from the Guadalupes. It is always found in the high, densely wooded canyons under humus.

*Vitrina pellucida alaskana* Dall, 1905

**General Distribution.**—Alaska to California, Arizona and New Mexico, eastward to South Dakota (Bequaert and Miller 1973:73–74).

**Guadalupe Park Distribution.**—Very sparsely distributed over the mountains at elevations over 7000 ft.

**Comments.**—This is the first report of *V. p. alaskana* for Texas and the Guadalupe Mountains. It was collected at most of our sites but only in low numbers. Bequaert and Miller (1973:73–74) placed *V. alaskana* Dall (Pilsbry 1946) as a subspecies of *V. pellucida* (O. F. Muller 1774) of the Old World.

*Hawaiia minuscula minuscula* (Binney)

**General Distribution.**—North American Continent.

**Guadalupe Park Distribution.**—General over the mountains at elevations above 6200 ft.

**Comments.**—Cheatum et al. (1972), without realizing, gave the first report of this very com-

mon species for the Guadalupes. Since that report, we have found it to be common at higher elevations and as a fossil from Sloth Cave.

*Hawaiia minuscula neomexicana* (Cockerell and Pilsbry, 1900)

**General Distribution.**—Scattered localities in Texas, New Mexico, and Mexico.

**Guadalupe Park Distribution.**—King (1948:145) reported this species as a fossil from the north side of Pine Springs Canyon. Bequaert (1966) found it in drift from Bell Canyon at Highway 180 and living in South McKittrick. I found it living at scattered localities across the mountains at elevation above 6200 ft and as a common fossil from Sloth Cave.

**Comments.**—Bequaert (1966) feels that this subspecies may be just a slight variance of *H. m. minuscula*. However, in a mixed lot, they are easily separable.

*Nesovitrea electrina* (Gould, 1841)

**General Distribution.**—Alaska, through Canada to Virginia, south to New Mexico and northeastern Arizona (Bequaert and Miller 1973:67–68).

**Guadalupe Park Distribution.**—Spottily distributed over the mountains at elevations over 6300 ft. This is the first report of this species as living in Texas, although it is a common fossil.

**Comments.**—I am not following Bequaert and Miller (1973:67–68) in placing *electrina* (elevated by Pilsbry 1946:256 to specific rank) as a subspecies of the Holarctic *N. hammonis* at this time.

Family Limacidae

*Deroceras laeve* (Müller, 1774)

**General Distribution.**—Arctic Region to Central America (Bequaert and Miller 1973:68–69).

**Guadalupe Park Distribution.**—Upper Pine Springs Canyon and Choza Spring.

**Comments.**—This is the first report of a slug in the Guadalupe Mountains.

Family Polygyridae

*Ashmunella rhyssa rhyssa* (Dall)

**General Distribution.**—Living specimens known from the Sacramento Mountains, New Mexico (Metcalf and Fullington, in litt.).

**Guadalupe Park Distribution.**—As a fossil from Pine Springs Canyon.

**Comments.**—Dr. A. L. Metcalf informed me that he recently collected this species in an alluvial deposit where he also collected a new, very small *Ashmunella* that we are currently describing.

*Ashmunella kochi amblya* Pilsbry, 1940

**General Distribution.**—Guadalupe Mountains: Type Locality, "Guadalupe Mountains, east and southeast of Orange, New Mexico, from Pine Springs Canyon, above Walter Glover's House (Pilsbry and Ferriss, November 2–11, 1922)" (Pilsbry 1940:977). Bequaert (1966) stated that in the Harvard Museum of Comparative Zoology there are paratypes (of the original lot, received from Pilsbry) labeled more precisely, "Canyon south of the summit of PX trail, east of Orange." However, no altitude was given. Also found in western foothills of San Andreas Mountains and Organ Mountains, New Mexico (Bequaert 1966).

**Guadalupe Park Distribution.**—General over the mountains at elevations over 7000 ft. Mainly in the wooded canyons but almost as readily found in the craggy limestone outcrops nearly devoid of vegetation. King (1948:145) reported it as living on the upper south wall of Pine Springs Canyon and as a fossil from the north side of Pine Springs Canyon. M. L. Walton (1963:126) also recorded it as living 1½ mi. up Pine Springs Canyon.

**Comments.**—*A. kochi amblya* is distributed in the Texas Guadalupes from Guadalupe Peak north to the ridge that transversely bisects the mountains which includes Lost Peak and the north side of McKittrick Ridge. Spire height, shell diameter, and teeth structure are highly variable. Shells from the Blue Ridge area populations conform perfectly to *A. kochi kochi* Clapp which is known from only one locality—Black Mountain, at the south end of San Andreas Mountains at 6800 ft, Dona Ana County, New Mexico (Pilsbry 1940:979). *A. kochi amblya* should probably be synonomized under *A. kochi kochi*.

*Ashmunella edithae* Pilsbry and Cheatum, 1951

**General Distribution.**—Texas Guadalupe Mountains: Type Locality "Guadalupe Range, near the top of the mountain up Pipeline Canyon, Pine Springs, Texas" (Pilsbry and Cheatum 1951:88).

**Guadalupe Park Distribution.**—The distribution of *A. edithae* in the mountains is unclear at present.

**Comments.**—*Ashmunella edithae* should probably be synonomized with *A. kochi amblya* for several reasons. The original description by Pilsbry and Cheatum (1951:88) matches perfectly the description of *A. carlsbadensis*, as does their illustration. I have collected the entire length of Pipeline Canyon twice and have collected nothing but *A. kochi amblya*. This fact leads to the main problem—the type locality. Pilsbry and Cheatum cite the locality as "Pipeline Canyon." I have shells listed as paratypes from Cheatum's personal collection with the locality cited as "Guadalupe Mountains on trail to Guadalupe Springs at base of El Capitan Mountain" (E. P. Cheatum, June 1950). Cheatum and his wife Edith (who collected the shells) both have told me that she went up the trail to Guadalupe Peak and not Pipeline Canyon. The three shells listed as paratypes are perfect *A. kochi amblya*, which makes one suspicious of mixed labels. The illustrations of *A. kochi amblya* and *A. edithae* in Cheatum and Fullington (1971) are also remarkably similar. I believe that Edith collected *A. kochi amblya* and that Dr. Pilsbry simply had a lapse concerning *A. carlsbadensis*. Besides, no one at that time had collected *A. carlsbadensis* previously in Texas. Dr. Cheatum indicated that he collected in McKittrick Canyon. It may be that he picked up *carlsbadensis* there and in the process of shipping the material to Dr. Pilsbry, mixed these shells and Edith's material from wherever she collected them.

*Ashmunella carlsbadensis* Pilsbry, 1932

**General Distribution.**—Guadalupe Mountains of New Mexico and Texas: Type Locality, "A cave in Dark Canyon, southwest of Carlsbad, from the surface to a depth of two feet (E. B. Howard)" Pilsbry (1940:978).

**Guadalupe Park Distribution.**—This species has a strange distribution in the Texas Guadalupes. The Dallas Museum of Natural History collected it from the heavily wooded canyons of Upper Dog Canyon (7400 ft), and along the eastern flanks from McKittrick Canyon to Bone Canyon (5400 ft) on the west, except in the Pine Springs Canyon area. While *A. kochi amblya* occupies the high central areas, *A. carlsbadensis* encircles the mountains, inhabiting the lower level, rocky outcroppings. It appears to be tolerant of xeric conditions, whereas *A. kochi amblya* is not. Altitude is not a prohibitive factor as we found it in the limestone outcroppings along the summit of the eastern escarpment (8200 ft). It was found sympatrically with *A. kochi amblya* at only one locality—near the junction of Pipeline Canyon and The Bowl where the forest borders the edge of the escarpment.

**Comments.**—The relationship of *A. kochi amblya* and *A. carlsbadensis* is interesting in that the two are sympatric at only one place (thus far investigated) in the mountains. The problem needs further investigating before a definitive statement may be made. In 1972, the late Dr. Cheatum and I collected a series of small *Ashmunella* along the east-facing cliffs of the Sierra Diablos which lie just south of the Guadalupes that, cursorily, appear to be small *carlsbadensis*, but some evidence indicates that they may be a new species.

In view of the fossil *Ashmunella* collected by Dr. A. L. Metcalf, and the unknown species from Sloth Cave, the whole Guadalupe *Ashmunella* complex appears to be highly dynamic.

*Ashmunella* spp.

**Comments.**—Two small species of fossil *Ashmunella* have been collected recently in the Guadalupes—one by Dr. A. L. Metcalf from Pine Springs Canyon which we are in the process of describing and the second was taken from Sloth Cave but cannot be described until whole specimens are exhumed.

Family Succineidae

*Succinea luteola* Gould, 1848

**General Distribution.**—Louisiana, Texas, New Mexico, Arizona, and Mexico (Pilsbry 1948:829).

**Guadalupe Park Distribution.**—King (1948:145) reported this species as a fossil from Pine Springs Canyon and from Bell Canyon. The Dallas Museum of Natural History collected throughout the mountains dead shells that conform to *S. luteola*, but no live specimens were taken.

**Comments.**—Due to the current state of confusion over succineid taxonomy, a conservative approach to this group has been taken in this report.

*Succinea* sp.

**Comments.**—An unusual series of fossil succineids were taken from Sloth Cave. These require further study and will be described at a later date.

Family Cionellidae

*Cionella lubricella* (Porro)

*Cionella lubrica* (Müller 1774), in Bequaert (1966),

**General Distribution.**—A worldwide genus with all North American forms referred to as *Cionella lubrica* (Pilsbry 1948:1047). Current consensus is that at least five species occur in North America (including Mexico) (F. W. Grimm, 1974 in litt., and Leslie Hubricht 1974 pers. comm.), and that the range of *C. lubricella* covers the area of this report.

**Guadalupe Park Distribution.**—General over the mountains at all elevations where enough vegetation is present to maintain a layer of leaf litter.

**Comments.**—Bequaert (1966) first reported this species from the Guadalupe Mountains as a possible fossil from drift in Bell Canyon. Cheatum et al. (1972) reported it living in the Guadalupes. The Dallas Museum of Natural History found it to be one of the most common species in the park. Bequaert and Miller (1973:72) reported it living in McKittrick Canyon (as *Cochlicopa lubrica*).

Family Pupillidae

*Gastrocopta armifera* (Say, 1821)

**General Distribution.**—Canada, eastern United States to Colorado, New Mexico, and Texas (Cheatum and Fullington 1973:10).

**Guadalupe Park Distribution.**—Bequaert (1966) first collected this species from drift in Bell Canyon at Highway 180 as a fossil; Cheatum et al. (1972) reported it living in McKittrick Canyon. Metcalf (1975, pers. comm.) found it as a fossil in Pine Springs Canyon.

**Comments.**—Field parties of the Dallas Museum of Natural History did not find *G. armifera* alive during the July investigation, thus its distribution in the park remains unknown. Evidence indicates that this species is losing ground in the West. Bequaert and Miller (1973:172) indicate that it no longer lives in Arizona, but that there are numerous fossil localities. This situation also holds true for New Mexico and Texas.

*Gastrocopta procera procera* (Gould, 1840)

**General Distribution.**—Eastern United States, west to the Dakotas, south to the Rio Grande, with only spotty records in New Mexico and Arizona.

**Guadalupe Park Distribution.**—One colony was found by the museum (July 1974) in one of the head canyons of Upper Dog Canyon, elevation 6200 ft.

**Comments.**—This is the first report of *G. p. procera* in the park. In the western United States, it is not considered a native snail by Bequaert and Miller (1973:90–91).

*Gastrocopta pentodon* (Say, 1821)

**General Distribution.**—Northeastern Canada, the eastern half of the United States (as far west as Colorado), and northeastern Mexico (Bequaert 1966).

**Guadalupe Park Distribution.**—Bequaert (1966) reported the first specimens from McKittrick Canyon. Cheatum et al. (1972) also reported it from McKittrick Canyon. During July 1974, the Dallas Museum of Natural History found it spottily across the mountains at elevations 6200 to 7500 ft.

**Comments.**—Bequaert and Miller (1973:88–90) placed *G. tappaniana* (Adams) under the synonomy of *G. pentodon*.

*Gastrocopta pilsbryana* (Sterki, 1890)

**General Distribution.**—In the mountains of New Mexico, Arizona, Mexico, and one locality in southwestern Utah (Bequaert and Miller 1973:158–159), Franklin Mountains (Metcalf and Johnson 1971:98), and Guadalupe Mountains, Texas (Cheatum et al. 1972), as fossils.

**Guadalupe Park Distribution.**—Bequaert (1966) presented the first report for the park and for Texas when he found it living in South McKittrick Canyon. Cheatum et al. (1972) reported it as

a fossil from the Guadalupes. The Dallas Museum of Natural History found it to be common across the park at elevations over 6500 ft.

**Comments.**—At present, the Guadalupe Mountains are the easternmost limit for this western mountain-dwelling species.

*Gastrocopta ashmuni* (Sterki, 1898)

**General Distribution.**—Arizona, New Mexico, northern Mexico, and Trans-Pecos Texas.

**Guadalupe Park Distribution.**—Mead in 1969 (*in* Bequaert and Miller 1973) reported it from South McKittrick Canyon as did Cheatum et al. (1972). The Dallas Museum of Natural History also found it only in McKittrick Canyon. Fossil specimens were taken from Sloth Cave.

**Comments.**—Generally, this species lives in protected areas of low, rocky hills, usually at elevations between 3000 and 6000 ft. This type of habitat has not been fully investigated in the Guadalupes. When the area has been more fully covered, *G. ashmuni* will probably turn up in more places than just McKittrick Canyon.

*Gastrocopta contracta* (Say, 1822)

**General Distribution.**—Southeastern Canada, widespread over most of the eastern United States, west to the Dakotas, south to northern Mexico; in the Southwest, Trans-Pecos Texas and eastern New Mexico.

**Guadalupe Park Distribution.**—Bequaert (1966) first reported it from flood debris in Bell Canyon in 1958. Later, he found it living in South McKittrick Canyon. The Dallas Museum of Natural History found it distributed across the mountains at elevations above 6300 ft.

**Comments.**—Bequaert and Miller (1973:91) consider *G. contracta* to be a post-Pleistocene invader of the Southwest.

*Gastrocopta pellucida* (Pfeiffer, 1841)

*Gastrocopta pellucida hordeacella* (Pilsbry 1890), in Bequaert (1966).

**General Distribution.**—A common snail in the southern United States from New Jersey to southern California; southward to Central America (Bequaert 1966).

**Guadalupe Park Distribution.**—In 1958, Bequaert collected the first Guadalupe specimens from drift in Bell Canyon. Later, he took live specimens from South McKittrick Canyon, elevation 5300 ft. We found only two colonies, one at The Bowl (8200 ft) and the other at Smith Spring (6000 ft).

**Comments.**—Bequaert and Miller (1973:79–81) synonomized *G. pellucida hordeacella* and *G. parvidens* under *G. pellucida.*

*Pupilla muscorum muscorum* (Linne, 1758)

**General Distribution.**—Widespread throughout temperate Europe, Asia, and North America; in North America as far south as the mountains of New Mexico (as Recent) (Bequaert 1966). Often found as a fossil in Texas.

**Guadalupe Park Distribution.**—King (1948:145) has reported the only instance of this species in the park. It was found in a fossilferous layer on the north side of Pine Springs Canyon, 1 mi. W of Pine Springs, Texas.

**Comments.**—*P. m. muscorum* is considered a mountain-dwelling snail in the west and probably will be found alive in the park. It and *P. blandi* apparently were eliminated from the Great Plains just before or after the Bradyon interval (Leonard and Frye 1962:27).

*Pupilla blandii* (Morse, 1865)

**General Distribution.**—Throughout the Rocky Mountains, from Alberta to Arizona and New Mexico (at high altitudes) according to Bequaert (1966).

**Guadalupe Park Distribution.**—Bequaert (1966) first reported this species in the park from drift in Bell Canyon, which he considered fossil. Cheatum and Fullington (1973:23) collected shells in McKittrick Canyon drift with the dried animal still within the shell. The museum did not collect this species at the higher elevations.

**Comments.**—See comments under *Pupilla sonorana.*

*Pupilla sonorana* (Sterki, 1899)

**General Distribution.**—New Mexico and west Texas.

**Guadalupe Park Distribution.**—In 1969, Mead (*in* Bequaert and Miller 1973) first reported this

species from South McKittrick Canyon. The Dallas Museum of Natural History found it to be common over the entire park at elevations above 6300 ft.

**Comments.**—*Pupilla sonorana* and *P. blandii* are probably the same species; the only difference is in size and the compression behind the lip of *sonorana*. In most populations sampled, there were specimens that conformed to both species, except for size. As most fell into the height range (2.5 to 3.25 mm) of *P. sonorana*, for the present I am classifying them as *P. sonorana*. However, I also firmly feel (as do Bequaert and Miller 1973) that *P. blandii* and *P. sonorana* are conspecific.

*Pupoides albilabris* (Adams, 1841)

**General Distribution.**—Southern Ontario; the United States westward to Colorado, Utah, and Arizona; northern Mexico, Cuba, Haiti, Puerto Rico, and Bermuda (Pilsbry 1948:921).

**Guadalupe Park Distribution.**—In drift at Delaware Creek at State Highway 652 (Cheatum et al. 1972).

**Comments.**—It is amazing that this ubiquitous gastropod has not been collected in the park more often than just the one record indicates.

*Pupoides hordaceus* (Gabb, 1866)

**General Distribution.**—Colorado, New Mexico, Arizona, Wyoming, and Utah (Bequaert and Miller 1973:58–59). It occurs only as a fossil in Texas and Kansas.

**Guadalupe Park Distribution.**—Presumably as a fossil from drift at Delaware Creek at State Highway 652 crossing (Cheatum et al. 1972).

**Comments.**—This species is yet to be collected as Recent in the Guadalupe Mountains. It prefers arid plateaus and xeric foothills and does not occur in the higher elevations according to Pilsbry (1948:924). This type of habitat in the park has not been fully explored as yet.

*Vertigo milium* (Gould, 1840)

**General Distribution.**—Recent from southern Ontario, south to Florida, west to Minnesota, South Dakota, northern Colorado, east Kansas to east-central Texas; only as a fossil westward through Arizona (with a few exceptions), no reports from New Mexico (Bequaert and Miller 1973:95–95).

**Guadalupe Park Distribution.**—Drift specimens from McKittrick Canyon (Cheatum et al. 1972).

**Comments.**—The specimens collected in McKittrick Canyon appear much too fresh to be classified as fossil, though they might well be. *V. milium* is another eastern Nearctic species that appears to be losing ground in the West. Areas such as the Guadalupe Mountains offer the last suitable habitats for this tiny snail in the West.

*Vertigo gouldii arizonensis* Pilsbry and Vanatta, 1900

**General Distribution.**—Arizona, New Mexico, and northern Mexico (Bequaert and Miller 1973:186–187).

**Guadalupe Park Distribution.**—Aspen Grove area to the northernmost edge of Blue Ridge at elevations over 7500 ft.

**Comments.**—This is the first report of this subspecies for Texas and for the Guadalupes.

*Vertigo ovata* (Say, 1822)

**General Distribution.**—Throughout most of temperate North America, becoming sporadic in the Rocky Mountain states (Bequaert and Miller 1973:92–94).

**Guadalupe Park Distribution.**—Bequaert (1966) first reported *V. ovata* as a fossil from drift in Bell Canyon. Cheatum et al. (1972) reported it as Recent from drift in Delaware Creek at State Highway 652. I have reexamined the shells and they do appear very fresh, but they could very well be sub-Recent.

**Comments.**—With further investigation, living material will most likely be found in the park.

Family Valloniidae

*Vallonia perspectiva* Sterki, 1893

**General Distribution.**—Common throughout most of the southern United States; north to New Jersey and westward to North Dakota and Arizona (Bequaert and Miller 1973:96–98).

**Guadalupe Park Distribution.**—Bequaert (1966) first collected this species as a fossil in South

McKittrick Canyon at 5300 ft. Cheatum et al. (1972) reported it as Recent from drift in McKittrick Canyon. Bequaert and Miller (1973:26) stated that Miller in 1969 also found it living in South McKittrick Canyon. During July 1974, the Dallas Museum of Natural History found it commonly distributed throughout the park at elevations over 6300 ft in the forested ravines.
**Comments.**—In Texas, *V. perspectiva* is known as living only in Terrell County, Chisos Mountains in Brewster County, and Franklin Mountains in El Paso County (Fullington and Pratt 1974:29).

*Vallonia cyclophorella* Sterki, 1893

**General Distribution.**—A western montane snail from Washington to Arizona and New Mexico, a few relictal colonies in sheltered canyons along the eastern escarpment of the High Plains (Fullington and Pratt 1974:28).
**Guadalupe Park Distribution.**—King (1948:145) reported it as a fossil from Pine Springs Canyon.
**Comments.**—*V. cyclophorella* is another western species that apparently spread eastward during the Pleistocene and now is losing ground as the areas east of the Rockies become more arid.

*Vallonia gracilicosta* Reinhardt, 1883

**General Distribution.**—Rocky Mountain Region to New Mexico; only as a fossil in Arizona and previously in Texas.
**Guadalupe Park Distribution.**—Cheatum et al. (1972) found fossil specimens in drift in Cherry Canyon at State Highway 180. Metcalf (pers. comm.) found it as a fossil in Pine Springs Canyon. The museum collected specimens from Upper Pine Springs Canyon (6600 ft) and along the Guadalupe Peak trail (7500 ft).
**Comments.**—This is the first report of *V. gracilicosta* as Recent for both Texas and the park. The specimens from Upper Pine Springs Canyon could be questionable as being Recent or fossil, but the Guadalupe Peak shells are bright and fresh.

*Vallonia parvula* Sterki, 1893

**General Distribution.**—Southern Ontario to South Dakota, south to Iowa, Oklahoma, and the Texas Panhandle (Fullington and Pratt 1974:29).
**Guadalupe Park Distribution.**—Fossil shells from drift in Delaware Creek at State Highway 652 (Cheatum et al. 1972).
**Comments.**—This species is listed with reservation. The shells from the only locality in the park have disappeared and cannot be reverified. They may have been young *V. gracilicosta*.

Family Strobilopsidae

*Strobilops labyrinthica* (Say, 1817)

**General Distribution.**—Southern Maine and Quebec; south through Minnesota, Nebraska, and Kansas; east of the Great Plains to Oklahoma, Arkansas, Georgia, and Alabama (Fullington and Pratt 1974:25).
**Guadalupe Park Distribution.**—Living specimens were collected in McKittrick Canyon by Cheatum et al. (1972).
**Comments.**—Only one other locality of living *S. labyrinthica* is known in Texas (Harris County). The species is known from several Pleistocene sites in Texas. Thus it is another northern species that is becoming extinct in the Southwest.

Family Oreohelicidae

*Oreohelix soccorensis soccorensis* Pilsbry, 1905

*Oreohelix yavapai compactula* Cockerell, in King (1948:145), from the north side of Pine Springs Canyon, 1 mi. W Pine Springs (fossil).
**General Distribution.**—Known as Recent only in the Gallinas Mountains, New Mexico; as a fossil in the San Andreas and Sacramento mountains in New Mexico, and the Franklin, Hueco, and Guadalupe mountains in Texas (Metcalf, per. comm.).
**Guadalupe Park Distribution.**—Metcalf (pers. comm.) has collected fossil shells in Pine Springs Canyon, in addition to King's (1948) report. This species was abundant in Sloth, Upper Sloth, and Dust caves.

**Comments.**—I have examined one *Oreohelix soccorensis* shell from the Guadalupe Peak area brought to me by a group of young people without more information than the above. The shell looks very fresh. Although the outer surface shows evidence of weathering, the interior is completely devoid of dirt and has only fungul mycelia in it. However, temerity and lack of better collecting site data force me to include it as a fossil.

## DISCUSSION

Sixty-one species of land and freshwater mollusks are presently known from the Guadalupe Mountains National Park, Texas; 54 are Recent and 7 are fossil forms. Doubtless, many more species will be discovered with further investigation. However, enough species are known now to enable us to understand something of the mountains' molluscan fauna.

Apparently, the mountains have stood for a long time period as an "island" for periodic molluscan movements in relation to climatic changes. With the current southwestern drying trend, the mountains offer a last refuge for many of the more temperate species. It may be that even these "refuges" are losing species. The fossil record of the Guadalupes is still too poorly known for definite statements on this problem.

Seventeen species in the Guadalupes currently have a more northerly or wide distribution (*Pisidium casertanum, Lymnaea humilis, Helisoma trivolvis trivolvis, Gyraulus parvus, Helicodiscus singleyanus singleyanus, Discus cronkhitei, Zonitoides arboreus, Euconulus fulvus, Hawaiia minuscula minuscula, Nesovitrea electrina, Deroceras laeve, Gastrocopta contracta, Pupilla muscorum muscorum, Pupoides albilabris, Vertigo milium,* and *Strobilops labyrinthica*). Based on Southwestern fossil evidence, most of these species are rapidly losing ground in the area or are already known only as fossils (*N. electrina, D. cronkhitei, S. labyrinthica*, and *E. fulvus*).

Twelve species inhabit only the Southwest (*Physa virgata, Metastoma roemeri roemeri, Rabdotus dealbatus dealbatus, R. dealbatus durangoanus, Thysanophora hornii, Helicodiscus nummus, Glyphyalinia indentata paucilirata, Hawaiia minuscula neomexicana, Succinea luteola,* and *Cionella lubricella*). It is interesting to note that several southwestern genera (*Polygyra, Helicina*, and *Euglandina*) apparently have never reached the Guadalupes, while some almost strictly Mexican genera such as *Humboldtiana* and *Thysanophora* have made the transition.

Species from the Rocky Mountain molluscan fauna, as defined by Bequaert and Miller (1973:12), invaded the Guadalupes during cooler Pleistocene periods. Most of these species (*Holospira danielsi, Helicodiscus eigenmanni, Gastrocopta pilsbryana, Gastrocopta ashmuni, Pupilla blandi, Pupilla sonorana, Pupoides hordeaceus, Vallonia cyclophorella, Vallonia gracilicosta, Vitrina pellucida alaskana,* and *Oreohelix soccorensis soccorensis*) are found only at the higher elevations in the Guadalupes. An unanswered question is why several of these forms are now apparently extinct in the mountains (*Oreohelix* and *Pupoides hordeaceus*) and why other forms such as *Sonorella* and *Radiodiscus* never became established. It should also

be stated that forms such as *Sonorella* and *Humboldtiana* do not fossilize due to their thin shells and the elevations which they inhabit.

The Guadalupes harbor only six species that inhabit the southeasterly to south-central United States (*Striatura meridionalis, Gastrocopta armifera, Gastrocopta procera procera, Gastrocopta pentodon, Gastrocopta pellucida*, and *Vallonia perspectiva*). The mountains are the westernmost limits for several of these species.

Nine species are endemic, or nearly so, to the Guadalupe Mountains as follows: *Humboldtiana ultima, Ashmunella carlsbadensis, Ashmunella kochi amblya, Ashmunella edithae, Holospira montivaga montivaga, H. montivaga* form *brevaria, H. pityis, H. oritis*, and *Ashmunella* sp. nov. It should be understood, however, that, with further investigation, this number of species probably will be reduced through synonymy.

All of the aquatic species represented are adventive and widespread in North America. Thus far, very few fossil aquatic species are recorded. Apparently, the stream systems of the Guadalupes have always had relatively sharp inclines with rapid run-off, and the Guadalupes never established much of a lasting, aquatic molluscan fauna.

In conclusion, the Guadalupe Mountains have stood as a crossroads for periodic North American areal molluscan movements. Most representative species of these areas still inhabit the Guadalupes, though many forms have ceased to inhabit the surrounding areas. Although the molluscan fauna is stratified, the majority of the species occur at elevations over 6500 ft in the wooded canyons. It should be noted here that most population localities are somewhat vaguely referred to in this report for protective purposes. The Guadalupe Mountains, due to their unique molluscan fauna and their relatively small size, offer themselves as a tremendous "laboratory" for solving existing molluscan problems. For this reason, as well as others, additional care must be exercised to sustain the fragile populations.

Identified specimens have been catalogued into the Dallas Museum's molluscan collections and a duplicate set has been deposited with the National Park Service at Carlsbad, New Mexico.

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# Plusiotis woodi *and* Plusiotis gloriosa *(Scarabaeidae); First Report of the Guadalupe Mountains National Park, Texas*

RICHARD W. FULLINGTON and DON HARRINGTON,
Dallas Museum of Natural History, Texas

Two species of a basically Mexican beetle genus, *Plusiotis*, were collected in the Texas Guadalupe Mountains during 20 to 25 July 1974. *Plusiotis gloriosa* LeConte and *Plusiotis woodi* Horn were collected in abundance by the Dallas Museum of Natural History staff.

*Plusiotis gloriosa* was taken from juniper trees in McKittrick Canyon, Upper Dog Canyon, and Pine Springs Canyon. Elytra were quite common in raccoon scat as were juniper seeds. Most specimens were taken late in the afternoon and around lights at night at elevations above 5000 ft (1500 m). However, no specimens were found above 6500 ft (1950 m).

*Plusiotis woodi* proved to be even more abundant than *P. gloriosa*. Large mating groups were observed in clumps of oak and desert walnut in Pine Springs and McKittrick canyons. No specimens were observed above 6000 ft (1800 m) elevation and no elytra were found in animal scat.

The genus *Plusiotis* is mainly Mexican in distribution, with only 4 of the 55 known species occurring in the United States. *P. gloriosa* is known from the Davis Mountains, Texas, to Pena Blanca, Arizona, and southward into Mexico. *P. woodi* occurs only in the Davis Mountains, Texas, and at Pinos Altos in the Mexican state of Chihuahua (Anon. 1973). Their discovery in the Guadalupe Mountains greatly extends the range of these two species northward and probably represents the extent of their range in the United States.

The activity of both species is highly moisture dependent (Cazier 1951). It was thought that they were strictly nocturnal until Young (1951) studied the habits of *P. gloriosa* in Arizona. He found that they actively fed during a 24-hour period as long as the humidity was high. Rain fell nearly every day of our stay in the Guadalupes and the sky was overcast, thus creating excellent

conditions for the beetles to emerge from the ground where they burrow during dry periods.

For several reasons, care should be exercised in protecting these two species. They are highly prized by professional and amateur collectors and even though during short, wet periods they appear very abundant, the populations could quickly be depleted. Second, as Young (1951) postulated, these species are relicts from a cooler, wetter era of the Southwest. He felt that many more species were present in the United States until the climate in the area began drying. Thus, *P. gloriosa* and *P. woodi* represent "living fossils" in the mountains and merit protection.

Specimens have been deposited in the Dallas Museum's Entomology Collection and with the National Park Service, Carlsbad, New Mexico.

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We wish to express our gratitude to the museum staff who accompanied us to the Guadalupes. Our thanks, too, to the park staff who often had "prowlers" around their lighted window screens.

# *Notes on the Bionomics and Nest Structure of* Pogonomyrmex maricopa *(Hymenoptera: Formicidae)*

JAMES V. MOODY and DAVID E. FOSTER, Texas Tech University and Museum, Lubbock

*Pogonomyrmex maricopa* Wheeler is a widely distributed harvester ant common to semi-arid areas of Texas, New Mexico, Arizona, and northern Mexico (Cole 1968). Colonies of *P. maricopa* are characterized by dome-shaped mounds surrounded by large bare areas. The species commonly occurs in sandy, silt, and loam soils on flat or gently sloping areas. They infrequently occupy rocky areas or steep inclines.

A number of workers have studied harvester ants with the objective of control or eradication. The bionomics of a related species, *Pogonomyrmex occidentalis* (Cresson), has been studied (Lavigne 1969; Rogers 1974). The only noneconomic works on *P. maricopa* deal specifically with oxygen consumption under laboratory conditions (Ettershank and Whitford 1973) and home range orientation (Hölldobler 1974).

A study was initiated in 1973 to examine the bionomics of *P. maricopa* in the valley floor habitats of Guadalupe Mountains National Park. The study is being conducted in two phases. Phase one, presently underway, is a study of nest and colony activities, including nest structure, reproductive cycle, foraging behavior, and the effect of abiotic factors on foraging. Phase two will focus on the energetic requirements of the species.

**STUDY AREA.** The study area chosen for phase one is the floor of West Dog Canyon along the northern boundary of the park. The site was chosen for the following reasons: its vegetative cover approximates that found on most valley floors within the park; it has numerous ant colonies; a deep ravine runs through the center of the site that facilitates excavation of adjacent colonies; the site is easily accessible.

**METHODS.** Observations were made and colonies were excavated during

April, May, June, July, August, and October 1974. Colonies chosen for excavation were located within 5 ft (150 cm) of the ravine. They were reached by digging laterally from the ravine wall toward the colony. Nest structure was mapped and the number of eggs, larvae, pupae, workers, and inquilines in each chamber was recorded.

Foraging activity periods and rates were determined by selecting three colonies for observation during their above-ground activity period each day. Foraging ants leaving the mound during a 5-minute period were counted at hourly intervals. The soil surface temperature during each count period was recorded.

Forage materials gathered were determined by aspirating each returning forager into an empty vial; aspirated ants generally responded by dropping their booty. The booty of each ant was placed in a separate envelope. One hundred returning ants were taken during the July, August, and October study periods. Booty was separated into six categories—dry twigs, dirt and pebbles, seeds, living plant material, arthropod parts, and bird feces.

The influence of abiotic factors on above-ground activity was observed during all phases of the study. Initial observations suggested that above-ground activities of *P. maricopa* are influenced largely by temperature.

**RESULTS AND DISCUSSION.** *Pogonomyrmex maricopa* constructs a dome-shaped mound surrounded by a bare area of 4 to 10 ft (120 to 300 cm) in diameter. The mound is constructed from excavated soil supplemented with twigs, pebbles, and miscellaneous particles returned by foraging workers. Completed mounds stand 12 to 18 in. (30 to 45 cm) high and range from 24 to 30 in. (60 to 75 cm) in base diameter.

Very young colonies lack the characteristic mound and bare area. They surround their nest entrance with twigs and debris. As excavation and expansion proceed, the mound slowly becomes more typical in appearance. Mounds are evident in second year colonies. The development of the bare area corresponds with the construction of the mound.

The nest entrance is located usually 2 to 3 in. (5 to 7.5 cm) above the base of the east-facing mound surface. Occasionally, a nest has two separate entrances. If so, they are close together and open into the same gallery. The entrance is roughly circular and large enough to accommodate two or three ants simultaneously. The position of the entrance facilitates warming in the early morning and shading in the late afternoon. This allows workers to begin foraging early in the morning and to resume foraging earlier in the afternoon.

In 1974 severe drought conditions existed until July, disrupting normal mound maintenance. During the drought period, many nest entrances were broken open, exposing entire galleries. Such openings never were closed at the end of daily above-ground activity. After the advent of rains in July, entrances were repaired. Subsequently, all entrances were closed each day when foraging was terminated.

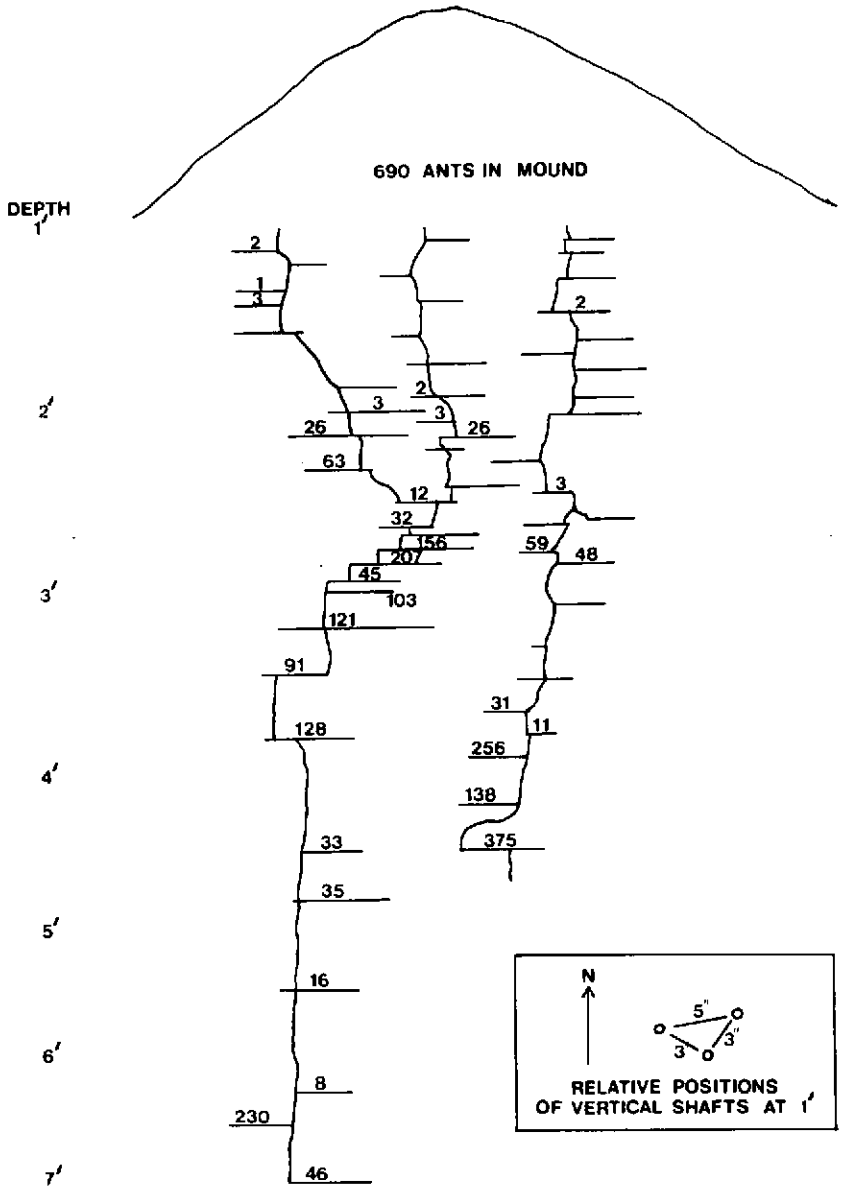


Fig. 1. Nest structure and underground distribution of *P. maricopa* in West Dog Canyon, Guadalupe Mountains National Park, 1974.

The mound and the first 12 to 16 in. (30 to 40 cm) below it are honeycombed with dome-ceilinged, flat-floored chambers. Below the honeycombed area, two or three main vertical shafts extend downward to a depth

of 42 to 78 in. (105 to 195 cm) below the mound entrance (Fig. 1). The distance between chambers along the first foot of the vertical shafts is usually less than 2 in. (5 cm). At lower depths, the chambers are separated by as much as 10 to 12 in. (25 to 30 cm). Vertical shafts usually dead end, but sometimes merge with an adjacent shaft. The largest chambers were found in the mound and near the bottom of the nest.

TABLE 1. Population of *Pogonomyrmex maricopa* nests excavated in West Dog Canyon, Guadalupe Mountains National Park, 1974.

| Population of Nest | 20 April | 11 May | 9 June | 9 July | 7 August | 19 October |
|---|---|---|---|---|---|---|
| Eggs | 40 | 121 | 73 | 103 | 3 | 0 |
| Larvae | 51 | 328 | 278 | 1331 | 470 | 46 |
| Pupae | 0 | 0 | 83 | 1104 | 393 | 0 |
| Workers | 13,816 | 5932 | 1505 | 3148 | 3442 | 2958 |
| Total | 13,907 | 6381 | 1939 | 5789 | 4308 | 3004 |

Although colonies with approximately equal mound and base area size were selected for excavation, populations varied greatly (Table 1). There seems to be no correlation between mound size and ant numbers in colonies 2 years old or older. Growing colonies sometimes abandon nests in favor of nearby, larger vacant nests. The age structure of each nest population excavated was recorded (Table 1). Reproductive activity had begun prior to the first excavation as indicated by the presence of eggs and larvae in the nest. Pupae were encountered first on 9 July; no teneral adults were present. It is interesting to note that egg production peaked during June. The number of both larvae and pupae were greatest in July. Winged adults were present in July and appeared above ground in large numbers at the time of the first rains. Reproduction declined sharply during the latter part of the summer as reflected by egg, larval, and pupal populations encountered during August. By October, the only immatures present were a few larvae scattered throughout the nest. The nest excavated on 19 October 1974 (Fig. 1) was typical both in structure and population distribution.

All arthropods encountered during nest excavation were collected and returned to the laboratory. Many were common associates of ants (Wilson 1971). Inquilines covered in the following discussion are recorded from the nest of *Pogonomyrmex* spp. for the first time. Two species of beetles, *Echinocoleus* n. sp. (Coleoptera: Leptodiridae) and *Limulodes* n. sp. (Coleoptera: Limulodidae), were encountered in the deeper areas of every nest. Both species usually were found in galleries packed with eggs and larvae. *Limulodes* were found clinging to many of the eggs and larvae. *Echinocoleus* specimens were found running about the gallery floors.

Abandoned trash and storage galleries in the honeycomb area occasionally were inhabited by larvae of *Collops* sp. (Coleoptera: Malachiidae). *Collops* larvae are predaceous and probably feed on scavengers associated with these galleries. Another insect found in the honeycomb area was the larva of *Gonasida elata* (LeConte) (Coleoptera: Tenebrionidae), which apparently spends its entire larval life burrowing through the mound.

Foraging activity is affected strongly by surface temperature. The nest entrance usually is uncovered and the first workers emerge when the surface temperature at the nest opening reaches 21 to 23° C. Activity increases until the surface temperature reaches 40 to 45° C and decreases sharply at temperatures above 46° C. Activity is reduced greatly at temperatures above 57° C.

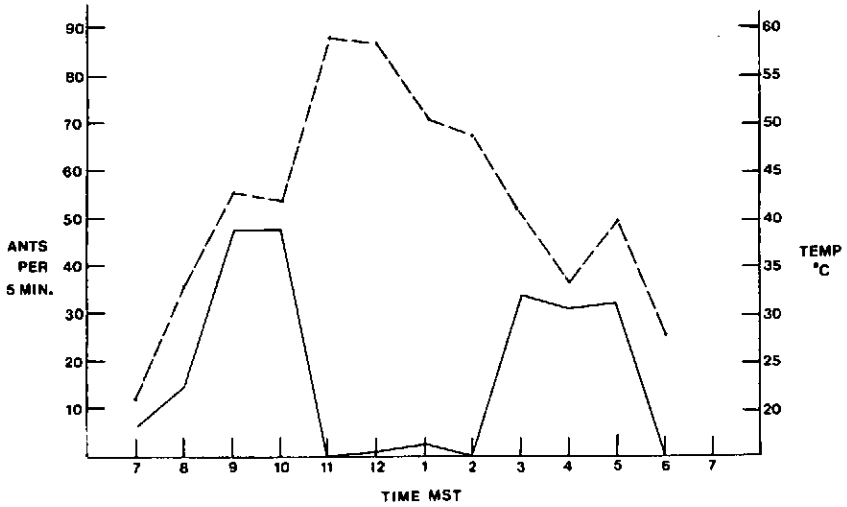


**Fig. 2.** Foraging activity and soil temperatures at hourly intervals on a clear day in West Dog Canyon, Guadalupe Mountains National Park, 5 July 1974. Dashed line, temperature; solid line, numbers of ants.

On clear days foraging usually was terminated by 11 a.m. and began again when temperatures dropped to the 48 to 52° C range (Fig. 2). Afternoon activity ceased when temperatures dropped to the upper 20s. This bimodal pattern of daily activity did not occur on cloudy days when the soil surface was exposed only to brief periods of direct sunlight (Fig. 3).

It was noted on several occasions that rain caused the cessation of foraging activity. During light rain, workers stopped leaving the mound; foragers returning with booty were unaffected. During heavy rains, foragers returned

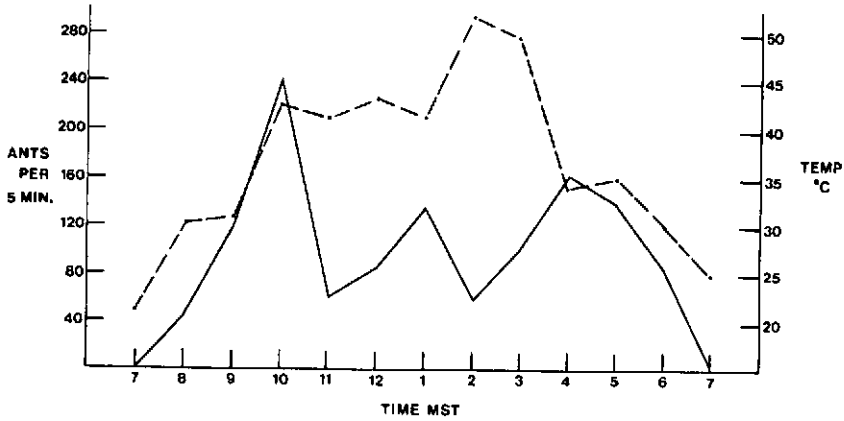


**Fig. 3.** Foraging activity and soil temperatures at hourly intervals on a cloudy day in West Dog Canyon, Guadalupe Mountains National Park; 6 July 1974. Dashed line, temperature; solid line, numbers of ants.

directly to the nest. Termination of light rain brought a return of normal foraging activity. During the first drought-breaking rains of July, large numbers of workers massed around their nest entrances, where they imbibed water for several minutes at a time. Such behavior did not occur during subsequent rains in July and August.

Foraging patterns suggest that populations in the study area forage from their mounds in all directions. Ants generally cross the bare area by fairly well-defined routes, which lead in four or five directions. Beyond the bare area, movement becomes less directional. Foraging distances sometimes extend as far as 41 ft (12.3 m) from the nest entrance. However, most forage excursions did not extend more than 16 to 20 ft (4.8 to 6 m) from the entrance. Foraging is terminated when the first acceptable booty is encountered. Returning ants usually follow a more direct route.

Booty returned by foraging ants during the early afternoons of 9 July, 3 August, and 18 October were collected and analyzed. On 9 July a few days after the rainy season had begun, insect parts comprised 35% of the material returned, whereas seeds accounted for 54%. Twigs and pebbles accounted for only 8%. On 3 August, seeds and insect parts accounted for only 32% of the booty; twigs and pebbles comprised 68%. Mound repair appeared to be the prime function of workers visible during the study period. On 18 October, the colony was engaged in gathering provisions. Sixty-two percent of the material returned was seeds, whereas insect parts comprised only 2%. Twigs and pebbles accounted for 35%.

Observations made over the entire season suggest that seeds are gathered whenever they are available, and that most plants within the forage range are utilized. Insect parts comprise a substantial part of the forage material only after the initial summer rains, which trigger a flush of insect emergence.

Twigs, dirt, and pebbles are gathered most frequently during late afternoon. These materials are applied directly to mound-building or repair.

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# *Limnology of McKittrick Creek, Guadalupe Mountains National Park*

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McKittrick Creek is an unusual aquatic ecosystem. It is a completely isolated system surrounded by the Chihuahuan Desert and arid mountains of southern New Mexico and western Texas. Such isolation has resulted in relatively little human impact until its inclusion into Guadalupe Mountains National Park. McKittrick Creek is a significant part of the park which has been described as "an island in the sky." Within this canyon, several small, relict communities persist. Such isolated systems have much appeal to the scientist concerned with community evolution and dynamics. The imminent threat to such microcosmic natural laboratories by park development and visitor use prompted the aquatic surveys reported here. Financial support for this second visit to the canyon was provided by the National Park Service preliminary to development of the Master Plan.

## DESCRIPTION OF THE CREEK-CANYON HABITAT

McKittrick Creek is a small, discontinuous, spring-fed stream with two main branches. Situated primarily in the sharp limestone canyons of Guadalupe Mountains National Park, Culberson County, Texas, with a small section in Lincoln National Forest, Eddy County, New Mexico, the principal direction of flow is easterly, cutting through the Permian limestone of the Guadalupe escarpment where surface flow ends (Fig. 1). This aquatic system provides a unique and isolated resource in the midst of an arid region. The creek and its several associated springs and seeps produce a moderation of the canyon climate that permits more water-requiring species of terrestrial life to exist. In the protected canyon, woody vegetation includes *Juniperus, Quercus, Acer, Juglans, Pinus,* and *Arbutus*. Some stream-side alligator junipers and ponderosa pines reach diameters of 1 m.

For the purpose of this study, the McKittrick Creek system is divided into three naturally identifiable zones. These are as follows: North McKittrick Creek, with surface water flow in both New Mexico and Texas and its south fork with the principal spring originating here; South McKittrick Creek, from the confluence with North McKittrick Creek to its large headwater

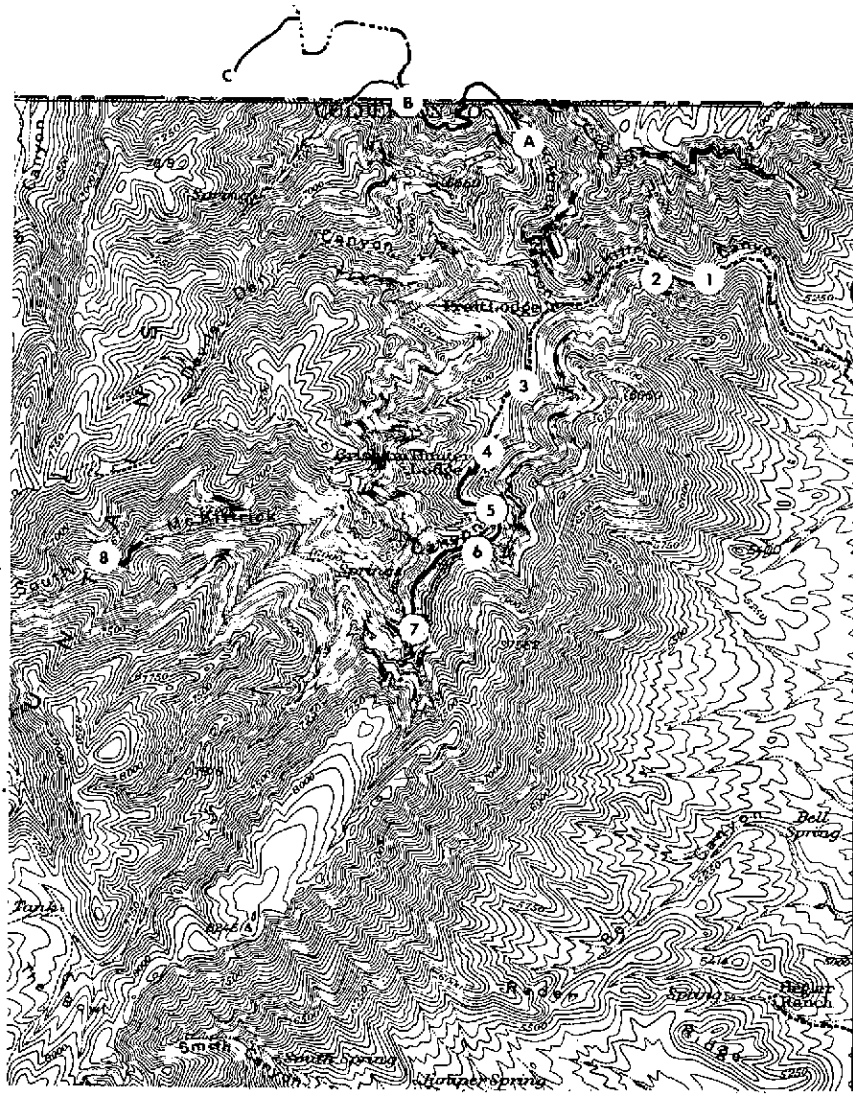


Fig. 1. Map of the McKittrick Creek portion of Guadalupe Mountains National Park, Texas, and adjacent parts of New Mexico showing location of sampling sites.

tanks; and McKittrick Creek downstream from the confluence of the north and south forks to a point of final subterranean disappearance. A wind-mill well is at the mouth of the canyon and assumed to be pumping from the subsurface creek flow.

Surface flow is usually over a travertine bed of varying thickness, and the intermittent creek flow is usually associated with breaks in this bed. Regions of surface flow are indicated in Fig. 1.

I have defined three physically as well as biologically different habitats in McKittrick Creek. The first, identified as a run, is a reach of water of up to 15 cm deep. It has a smooth surface film or, at most, evenly spaced swells. The usual bottom substrate in a run is cobblestone from 5 to 10 cm diameter. Macro-algae, principally *Spirogyra*, are often attached. Finely divided organic detritus is deposited among the stones. The second habitat type, the riffle, has a steeper gradient than the run. The water depth is usually less than 5 cm. The substrate grades from 15 cm diameter cobblestones at the head to small gravel or even sand at the tail. Riffles are quite short, rarely exceeding 2 m in length. They are typically free of attached macro-algae and organic matter deposits. A pool, the third habitat type, does not indicate standing water, but defines a wider and deeper portion with slow, usually imperceptible current. These range up to 5 m in width and 2 m in depth. The substrate grades from sand to silt. Large deposits of fine organic detritus are present. The bottom frequently has well-developed beds of *Chara* with marl formations.

The stream-bed gradient is slight in the lower canyon as it is in North McKittrick Creek up to the south fork, and in South McKittrick Creek up to the abandoned Grisham-Hunter Lodge (Fig. 1). The water course of North McKittrick Creek (Stations A and B, Fig. 1) below the south fork is the most exposed in a broad, open canyon. The south fork of North McKittrick Creek is well shaded by woody and herbaceous vegetation with maidenhair ferns (*Adiantium capillus*) providing much cover. Protective stream-side vegetation of the main canyon and of the portion of South McKittrick Creek below the Grisham-Hunter Lodge is dominated by saw-grass (*Cladium jamaicense*) as well as deciduous trees. Above this point, South McKittrick Creek has less protection by woody vegetation but several reaches flow among large boulders and are shaded with maidenhair fern.

## METHODS

Data and observations contained herein are based on a series of visits. The first was November 1967, followed by visits in May 1969, April 1971, and November 1972.

Collection stations were selected to provide a sampling of each major habitat type as well as stream portions having real or potential human impact.

Most chemical analyses were done in the field using the Engineer's Laboratory, Hach Chemical Co. Specific conductance and total residue were determined according to *Standard Methods for the Examination of Water and Waste Water* (Am. Public Health Assoc. 1965, 1971). Iron, copper, lead, and zinc contents were determined by atomic absorption and total organic carbon, by combustion and infrared analysis.

TABLE 1. Chemical characteristics of McKittrick Creek, Guadalupe Mountains National Park, as mg $l^{-1}$.

| Chemical Characteristics | Date | Station 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | A | B | C Spring | C Spring pool |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Temperature (°C) | 5/69 | 26 | 20 | 18 | 20 | 21 | | | | 14 | 25 | 16 | 18 |
| | 4/71 | | | 14 | | 14 | | 16 | 10 | 14 | 20 | 15 | 15 |
| | 11/72 | | | | | | | 3 | | | | | |
| pH | 5/69 | 8.7 | 8.5 | 7.7 | 8.0 | 8.3 | | | | 8.0 | 9.0 | 7.5 | 8.0 |
| | 4/71 | | | 6.8 | | 7.5 | | 7.4 | 7.0 | 8.0 | 8.1 | 7.5 | |
| | 11/72 | | | | | | | 7.5 | | | | 7.0 | |
| Total alkalinity | 5/69 | 256 | 272 | 264 | 262 | 252 | | | | 296 | 280 | 330 | 440 |
| | 4/71 | | | 250 | | 250 | | 250 | 250 | 265 | 280 | 325 | 440 |
| Total hardness | 5/59 | 272 | 312 | 300 | 300 | 272 | | | | 300 | 270 | 350 | 350 |
| | 4/71 | | | 270 | | 270 | | 250 | 250 | 250 | 270 | 310 | 290 |
| Calcium | 5/69 | 72 | 78 | 82 | 75 | 72 | | | | 94 | 70 | 116 | 128 |
| Oxygen | 5/69 | | 6.0 | 7.0 | 8.0 | 6.5 | | | | | 8.2 | 7.2 | 8.2 |
| | 4/71 | | | 6.6 | | 9.0 | | | 0.2 | 8.4 | | | 9.2 |
| Specific Conductance @ 18°C | 5/59 | 450 | 350 | 490 | 480 | 300 | | | | | 440 | 520 | 340 |
| $SO_4$ | 5/69 | 12.0 | 12.4 | 11.6 | 8.8 | 9.2 | | | <5 | | 9.2 | 8.8 | 6.8 |
| $SiO_2$ | 4/71 | 6.8 | 6.8 | 7.2 | 6.4 | 6.4 | | | | | 8.8 | 6.8 | 6.8 |
| $NO_3$-N | 7/71 | | | 0.35 | | 0.10 | | 0.10 | 0.10 | | | | |
| | 11/72 | | | | | | | | | | | 38.0 | |
| $PO_4$-P | 4/71 | | | 0.05 | | 0.01 | | | | | | | |

TABLE 1. (continued)

| Chemical Characteristics | Date | Station 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | A | B | C Spring | C Spring pool |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Fe | 11/72 | | | | | | 0.07 | 0.06 | | | | 0.04 | |
| Cu | 11/72 | | | | | | 0.02 | 0.02 | | | | 0.02 | |
| Pb | 11/72 | | | | | | <1 | <1 | | | | <1 | |
| Zn | 11/72 | | | | | | 0.005 | 0.001 | | | | 0.001 | |
| Total residue | 5/69 | 14.2 | | 15.6 | 14.3 | 21.7 | | | | | 25.6 | 30.8 | 14.5 |
| Total organic carbon | 11/72 | | | | | | 18 | 13 | | | | 12 | |

Quantitative benthos samples were by Surber sampler with 3 square ft sampled at each station. Qualitative samples were by sweep net and hand-picking. Fishes were collected by habitat seine. Plankton from the rock tanks were collected with a 20-mesh Wisconsin net. Identification of most of the vascular aquatic plants and aquatic-associated plants was confirmed by Helen and Donovan Correll. Mosses were identified by L. J. Gier.

## RESULTS AND DISCUSSION

### Physical and Chemical Properties

Because of the intermittent nature of McKittrick Creek, water temperatures do not have a continuous, gradual rise downstream. The spring source of North McKittrick Creek's south fork (station C) was cool at 15 and 16° C. In the open, shallow, travertine-lined tanks downstream (station B), this rose to 20 and 25° C, then dropped, after further subterranean flow, to 14° C at the last downstream station (A) (Table 1). This same irregular pattern of temperature was followed in South McKittrick Creek.

The water chemistry reflects the limestone substrate of the region. This is a well-buffered calcium carbonate-magnesium carbonate system with a greater calcium to magnesium ratio in the water of South McKittrick Creek than in North McKittrick Creek. Bicarbonate is the principal anion in both creeks. In the more exposed waters, high rates of photosynthesis deplete the carbon dioxide-bicarbonate system with a consequent rise in pH and the production of the insoluble carbonate ion resulting in heavy marl formation. Sulfate, the other anion present in significant quantities, is slightly more abundant in South McKittrick Creek water than in North McKittrick Creek water.

Dissolved oxygen concentrations at all sampling stations, except the uppermost tank at station 8 of South McKittrick Creek, were always considerably greater than those shown to cause stress on any forms of aquatic life. This is to be expected in the relatively cool, shallow, and flowing water. However, when taken as a percentage of saturation, South McKittrick Creek waters always were less saturated than North McKittrick Creek waters, suggesting a greater organic matter load in the former. No diel oxygen studies (the reported data being for mid-day) were conducted. Consequently, I do not know if oxygen concentrations are significantly lowered at night. However, the biota present demonstrate that any decrease is not to a critical concentration.

The uppermost rock tank at station 8 of South McKittrick Creek had a mid-afternoon oxygen concentration of 0.2 mg $l^{-1}$. Because of its location and morphometric configuration, this station collected large quantities of organic matter. The orientation of the vertical canyon walls coming directly out of the water provides almost constant shading and protection from the wind. Other physical and chemical conditions associated with this sheltered, organic-rich system were the lower temperature, low pH, and higher free carbon dioxide.

Nitrogen, phosphorus, and occasionally carbon and silica are of concern to limnological investigations because of their confirmed role as elements often, or occasionally, limiting the quantity of biological production. In well-buffered carbonate systems such as these, carbon is probably always superabundant. Dissolved silica also was present in relatively high quantities, although there is little information available on limiting effects of silica concentrations especially in streams. These concentrations, 6.4 to 8.8 mg $l^{-1}$, are similar to those shown to be limiting in a central Texas reservoir (Kimmel and Lind 1972). However, they are approximately four times greater than the ambient concentrations of Douglas Lake, Michigan, which I found to cause no limitation (Lind, unpublished). The dissolved silica concentration of any water is inversely related to the population size of active diatoms. Though not sampled, diatom populations in both forks of McKittrick Creek were large, as evidenced by the color and texture of the rock and travertine substrate. It is probable that a large portion of the silica present in these samples was tied up in the silicon tests of active diatoms. The high concentration of dissolved silica at station B probably indicated the decline of a large diatom population in the travertine runs immediately upstream.

Nitrate–nitrogen concentrations increased downstream in South McKittrick Creek from undetectable at the upper rock tank to 0.35 mg $l^{-1}$ at station 3 below the Grisham–Hunter Lodge. The threefold increase at station 3 over station 5 above the lodge causes one to suspect human sources, possibly septic seepage associated with the lodge. The high concentration of nitrate–nitrogen in the spring water of North McKittrick Creek is not unusual for many springs of the region. Three nearby springs on the east face of the Guadalupe Mountains were analyzed during the 1971 study. These, Manzanita,Choza, and Upper Pine springs, had nitrate-nitrogen concentrations of 20, 50, and 50 mg $l^{-1}$, respectively. These concentrations approach or exceed the recommended drinking water limit of 45 mg $l^{-1}$ established by the American Public Health Association (1971). Smith Spring, which presently is diverted into Manzanita Spring, had a much lower nitrate–nitrogen content of 0.46 mg $l^{-1}$.

Phosphate-phosphorus concentrations were measured at stations 3 and 5 to gather further data on possible human impact. The results were similar to those of nitrate–nitrogen. The downstream station had a phosphorus concentration 5 times greater than the upstream.

Little is known about normal concentrations of heavy metals in nonpoluted waters. Riley (1939, cited by Hutchinson 1957) found the range of copper of Connecticut lakes to be from 0.009 to 0.215 mg $l^{-1}$. Atkins (1933, cited by Hutchinson 1957) found 0.0 to 0.036 mg $l^{-1}$ in several English rivers. A small central Texas reservoir had a mean concentration of 0.06 mg $l^{-1}$ (Lind 1974). Several springs in Big Bend National Park, Texas, had copper concentrations of 0.03 to 0.04 mg $l^{-1}$ and Tornillo Creek had a range from 0.02 to 0.03 mg $l^{-1}$ (Lind and Bane, unpublished). It is probable that the value of 0.02 mg $l^{-1}$ for all sampled stations in the McKittrick Creek system

is not exceptional. Hutchinson (1957) cited several authors regarding the toxic copper concentrations for a variety of aquatic life. The McKittrick Creek values are all less than any reported toxic concentration.

Hutchinson (1957) suggested that zinc, though little studied, is probably present in quantities equal to or greater than copper. The zinc concentration of McKittrick Creek waters is less than copper and of the same order of magnitude and in the same copper: zinc ratio as found by Morita (1955, cited by Hutchinson 1957) for high Japanese lakes. The small central Texas reservoir had a mean zinc concentration of 0.1 mg $l^{-1}$ (Lind 1974) or approximately double the copper concentration. Concentrations in Tornillo Creek were 0.01 to 0.02 mg $l^{-1}$, one order of magnitude greater than in McKittrick Creek. It appears from this that ambient zinc concentrations in McKittrick Creek are exceptionally low. The concentration of lead was below the detection limits of our instrumentation (1 mg $l^{-1}$). This is consistent with very limited data available on this element. The total iron values, 0.02 mg $l^{-1}$, are, as with zinc, approximately one order of magnitude low when compared to data for Swedish lakes (0.09 to 0.160 mg $l^{-1}$) (Rodhe 1948), for Lindley Pond, Connecticut (0.170 mg $l^{-1}$) (Hutchinson 1957), for a small central Texas reservoir (0.30 mg $l^{-1}$) (Lind 1974), and for Tornillo Creek (0.1 to 0.2 mg $l^{-1}$) (Lind and Bane, unpublished).

## The Biota

The aquatic and streamside flora of the creek is varied, most are perennials. The transition from aquatic-associated plants of the narrow canyon floor to the xerophytic forms of the canyon sides is abrupt. The criterion for inclusion as an aquatic associated plant in Table 2 was the listing of that taxon in *Aquatic and Wetland Plants of Southwestern United States* (Correll and Correll 1972).

TABLE 2. Stream-side and aquatic plants of McKittrick Canyon, Guadalupe Mountains National Park.

| | |
|---|---|
| *Equisetum laevigatum* (Horsetail) | *Agrostis semiverticillata* (Bentgrass) |
| *Adiantum capillus* (Maidenhair fern) | *Leersia* sp. (Cutgrass) |
| *Bryum turbinatum* (Turbin moss) | *Glyceria striata* (Fowl Manna-Grass) |
| *Hygroamblystegium irriguum* (Spring moss) | *Rorippa naturtium-aquaticum* (Water Cress) |
| *Potomogeton illinoensis* (Pondweed) | *Aquilegia chrysantha* (Columbine) |
| *Eleocharis montevidensis* (Spike rush) | *Galium microphyllum* (Bedstraw) |
| *Cladium jamaicense* (Sawgrass) | *Valeriana texana* (Valerian) |
| *Carex microdenta* (Sedge) | *Senecio* sp. (Groundsel) |
| *Carex hystericina* (Porcupine sedge) | *Najas* sp. (Water nymph) |
| *Juncus interior* (Rush) | *Spirogyra* sp. |
| *Juncus dudleyi* (Rush) | *Chara* sp. (Stonewort) |
| | *Nitella* sp. (Stonewort) |

TABLE 3. Occurrence of noninsect fauna of McKittrick Creek, Guadalupe Mountains National Park. Quantitative data are numbers per square meter. X indicates occurrence in nonquantitative samples. Composite data from 1967–1971, not all taxa were found on each sample date.

| Taxon | North McKittrick Creek | McKittrick Creek (Station 2) | South McKittrick Creek | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | Station 3 | | | Station 4 | Station 5 | Qualitative unspecified |
| | | | Pool | Riffle | Run | | | |
| Coelenterata | | | | | | | | |
| *Chlorohydra* sp. | | | | | | | | X |
| Turbellaria | | | | | | | | |
| *Dugesia tigrina* | X | 64 | 43 | 118 | | 462 | 376 | |
| Nematomorpha | | | | | | | | |
| *Gordius* sp. | | | | | | | | X |
| Annelida | | | | | | | | |
| Oligochaeta | | | | 11 | | | 22 | |
| Mollusca | | | | | | | | |
| Physidae | | | | | | | | X |
| Crustacea | | | | | | | | |
| Ostracoda | | 75 | 1343 | | 2 | 2388 | | |
| Amphipoda | | | | | | | | |
| *Hyalella azteca* | X | 75 | 32 | 366 | 312 | 161 | | |
| Copepoda | | | | | | | | |
| *Ectocyclops phaleratus* | | | | | | | | X |
| Cladocera | | | | | | | | |
| *Daphnia pulex* | | | | | | | | X |
| *Ceriodaphnia quadrangula* | | | | | | | | X |

TABLE 3. (continued)

| Taxon | North McKittrick Creek | McKittrick Creek (Station 2) | South McKittrick Creek | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | Station 3 | | | Station 4 | Station 5 | Qualitative unspecified |
| | | | Pool | Riffle | Run | | | |
| Acari | | | | | 11 | 11 | 11 | |
| Vertebrata | | | | | | | | |
| *Rana* sp. | X | | | | | | | X |
| *Lepomis cyanellus* | X | | | | | | | X |
| *L. auritus* | | | | | | | | X |
| *Salmo gairdneri* | | | | | | | | X |

With a few exceptions, the fauna is typical of more northerly, spring-fed streams. This supports the hypothesis of a relict biota, left in isolation by the northerly retreat of montane climates and associated biotic communities. The three species of fish (Table 3) were apparently imported by the earlier landowners for sport fishing. The yellow-belly sunfish (*Lepomis auritus*) is at the limit of its known natural range. The green sunfish (*L. cyanellus*) was probably a contaminent of this sunfish stocking. The rainbow trout (*Salmo gairdneri*) has been successful in the creek although not reaching large sizes. Populations of trout were found at the lower downstream stations where the water temperatures exceed those in which trout are capable of effective reproduction. It is probable that these represent a downstream wash at periods of high water, and the spawning must be restricted to the colder upstream portions.

The rock tanks at the head of South McKittrick Creek with cold, some with low oxygen waters, though depauperate in benthos, had an interesting plankton fauna. Quantative samples were not taken but dense populations of three species were present. *Ectocyclops phaleratus* stores large quantities of orange-yellow oil droplets. This is in the same manner as arctic copepods as well as those observed by me in alpine lakes of the Rocky Mountains. This is not to be confused with a pink carapace pigmentation also observed in some high-altitude species. This oil pigmentation, as well as the dense population, contributes an orange hue to the water which may at first be attributed mistakenly to organic matter stain. It would be extremely interesting to determine the source of inoculation of these plankton into this uppermost tank.

Several detritus-associated taxa are common in the tanks and pools holding leaf litter. Ostracods are abundant, especially at station 4 where the population exceeded 2300 organisms $m^{-2}$ (Table 3). This is also the station that experiences the suspected nutrient enrichment. Station 4 also had the maximum planaria population density. The amphipod, *Hyalella azteca*, was present throughout except at the lowermost station 5. The horsehair worm, *Gordius* sp., is restricted to organic rich pools of middle to upper South McKittrick Creek and has been found in small numbers on each of the sampling dates.

The insect fauna (Table 4) collected consisted primarily of larval or pupal stages. With a few exceptions, no effort to identify beyond family was made. Seven families of Diptera were found in South McKittrick Creek and five, in the smaller North McKittrick Creek. At least five recognizable genera of Tendipedidae (Chironomidae) were found. *Simulium* sp. populations in the riffles were large, exceeding 18,000 organisms $m^{-2}$ at station 3. Tendipedids were found throughout the system, with one genus being found in substantial numbers at all quantitative stations.

Trichoptera were present in all but the swiftest water throughout. Two, *Notiomxia* sp. and Genus A (Ross), were found only in North McKittrick

TABLE 4. Occurrence of insect fauna in McKittrick Creek, Guadalupe Mountains National Park. Quantative data as numbers per square meter. X indicates occurrence in nonquantative samples. Composite data from 1967-71, not all taxa were found on each sample date.

| Taxon | North McKittrick Creek | McKittrick Creek (Station 2) | South McKittrick Creek | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | Station 3 | | | Station 4 | Station 5 | Qualitative unspecified |
| | | | Pool | Riffle | Run | | | |
| Diptera | | | | | | | | |
| Tipulidae | | | | 194 | | | 97 | |
| Heleidae | | | 226 | | | 97 | | |
| Simulidae | | | | | | | | |
| *Simulium* sp. | X | | | 18,127 | | 75 | 3270 | |
| Tendipedidae | X | | | | | | | |
| Genus A | | 312 | 2905 | 161 | 118 | 1005 | 226 | |
| Genus B | | 172 | 75 | 22 | 11 | | 54 | |
| Genus C | | | 22 | | 11 | 54 | 688 | |
| Genus D | | 11 | | | 22 | 172 | 129 | |
| Genus E | | | | | | 43 | 43 | |
| Tabanidae | | | | | | | | |
| *Tabanus* sp. | X | 22 | | 22 | | 22 | | |
| Stratiomyiidae | | | | | | | | |
| *Euparyphus* sp. | X | | | | | | | |
| Ceratopogonidae | | | | | | | | |
| *Probezzia* sp. | X | | | | | | | |
| Trichoptera | | | | | | | | |
| Calamoceratidae | | | | | | | | |
| *Notiomxia* sp. | X | | | | | | | |
| Psychomyiidae | X | 688 | | 656 | | 269 | 344 | |
| Odontoceridae | | | | | | | | |
| Genus A (Ross) | X | | | | | | | |

TABLE 4. (continued)

| Taxon | North McKittrick Creek | McKittrick Creek (Station 2) | South McKittrick Creek: Station 3: Pool | Station 3: Riffle | Station 3: Run | Station 4 | Station 5 | Qualitative unspecified |
|---|---|---|---|---|---|---|---|---|
| Helicopsychidae | | | | | | | | |
| *Helicopsyche* sp. | | | | 430 | | | | |
| Limnephilidae | | | | | | | | |
| *Hesperophylac* sp. | X | | | | | | | X |
| Hydroptilidae | | | | | | | | |
| *Agraylea* sp. | | 172 | 129 | 11 | | 882 | 32 | |
| *Hydropsyche* sp. | | | | | | | | X |
| Leptoceridae | | | | | | | | |
| *Athripsodes* sp. | | | 32 | 86 | 32 | | | |
| Odonata | | | | | | | | |
| Zygoptera | | | | | | | | |
| Agrionidae | | | | | | | | |
| *Argia* sp. | X | 97 | 97 | 64 | 22 | 376 | 581 | |
| Coenogrionidae | | | | | | | | |
| *Archilestes* sp. | X | | | | | | | |
| Anisoptera | | | | | | | | |
| Libellulidae | X | 11 | | | | 11 | | |
| Hemiptera | | | | | | | | |
| Belostomatidae | | | | | | | | |
| *Belostoma* sp. | X | | | | | | | X |
| Ephemeroptera | | | | | | | | |
| Baetidae | | | | | | | | |
| *Baetis* sp. | X | | 215 | | 11 | 323 | 527 | |
| *Choroterpes* sp. | X | 32 | 75 | 75 | 11 | 129 | 118 | |

TABLE 4. (continued)

| Taxon | North McKittrick Creek | McKittrick Creek (Station 2) | South McKittrick Creek | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | Station 3 | | | | | |
| | | | Pool | Riffle | Run | Station 4 | Station 5 | Qualitative unspecified |
| Coleoptera | | | | | | | | |
| Psephenidae | | | | | | | | |
| *Psephenus* sp. | | | | | | | | X |
| Chrysomelidae | | | | | | | | |
| *Neohaemonia* sp. | X | | | | | | | |
| Elmidae (adults) | | | | | | 11 | | |
| Curculionidae | | | | | | 22 | | |
| Georyssidae | | | | | | | | |
| *Georyssus* sp. | X | | | | | | | |

Creek. *Helicopsyche* sp., *Hydropsyche* sp., *Agraylea* sp., and *Athripsodes* sp. were present only in South McKittrick Creek. Damselflies (Zygoptera) and dragonflies (Anisoptera) were found in both systems. *Archilestes* sp. was found only in North McKittrick Creek, whereas *Argia* sp. was common in both systems. The seclusion of dragonfly larva in bankside vegetation and the method of sampling could have led to the low population estimates of the libellulids. Baetid mayflies (Ephemeroptera) were in all stream zones, with *Choroterpes* sp. present at all quantitative stations. Larval and adult beetles were present throughout in the qualitative samples as was the hemipterian, *Belostoma* sp. Subsequent to my last collection, Harley P. Brown (pers. comm.) has collected in the lower canyon and has identified three dryopid beetles (*Helichus confluentus, H. saturalis*, and *H. triangularis*), four elmids (*Elsianus* sp., *Heterelmus obesa, Microcylloepus* sp., and *Neoelmis* sp.), one limnichid (*Lutrochus luteus*), and representatives of Gerridae, Naucoridae, and Veliidae.

The occurrence of several southerly range extensions of insects supports the concept of a relict fauna. *Psephenus* sp. is normally found to the northeast of the McKittrick region. The odontocerid caddisfly, known only as Genus A by Ross, has been described only from northern California, and the georyssid colopteran, *Georyssus* sp., is reported from the northern Rocky Mountains.

TABLE 5. Mean, maximum, and minimum species diversity of six quantitative sampling stations, 1969 and 1971, McKittrick Creek, Guadalupe Mountains National Park.

| Sampling Station | 1969 | | | 1971 | | |
|---|---|---|---|---|---|---|
| | Mean | Maximum | Minimum | Mean | Maximum | Minimum |
| A | – | – | – | 2.5 | 3.2 | 0.2 |
| C | – | – | – | 2.5 | 4.0 | 0.2 |
| 2 | 2.9 | 3.8 | 0.5 | – | – | – |
| 3 (riffle) | 1.7 | 3.9 | 0.1 | 2.9 | 3.6 | 0.2 |
| 4 | 3.0 | 4.3 | 0.3 | – | – | – |
| 5 | 2.6 | 4.1 | 0.2 | 3.0 | 3.6 | 0.2 |
| 7 | – | – | – | 2.0 | 3.1 | 0.1 |

Species diversity indices reflect community stability. A low index suggests either a youthful, very small, or a disturbed system. Disturbances, natural or manmade, tend to bring about a decrease in the index. Most diversity data for McKittrick Creek (Table 5) are rather high, especially considering the small size of the creek habitats. Because benthos are relatively permanent (until their life cycle is complete) inhabitants of stream systems, they are continuous monitors of any stresses placed on the system. Changes in their diversity provide a means to detect stresses that may be missed by periodic sampling of biological, chemical, or physical parameters.

Stations 3 and 5 were sampled for diversity in both 1969 and 1971. There was a slight (though probably insignificant, cf. maximum and minimum) increase in 1971. The increase at station 3 in 1971 may be attributed to the fact that this riffle is immediately below a ford crossing used by occasional jeep traffic up to about 1970. It is advisable to continue monitoring for changes in diversity as an expression of environmental degradation.

The standing crop of stream organisms is not usable for evaluation of water quality because large populations of more tolerant organisms may exist even under stress. However, it does provide insight to the quantity of organic nutrients available. These may be available as either allochthonous detritus or autochthonous production. Generally, small aquatic ecosystems are more dependent upon the former. This is probably true of McKittrick Creek as the canyon topography provides "funneling" of the downhill-moving plant production to the stream. However, the large beds of stream-side *Cladium jamaicense*, *Chara* sp., and *Spirogyra* sp. in the pools and runs, as well as the large diatom populations, each contribute significantly to the food base.

No biomass data on benthos were gathered. Numeric standing crop data were high. The mean for all South McKittrick Creek stations is approximately 7000 organisms/$m^{-2}$, with a maximum for station 3 of 20,000 organisms/$m^{-2}$. These numbers are high when compared with data given by Macan (1963) who reported mean numeric standing crops of English streams to be from 3000 to 5000 organisms/$m^{-2}$.

The results of these studies confirm that the McKittrick Creek ecosystem is a unique and valuable resource. The opportunity for scientific discovery here is great. Sound, carefully regulated research activities should be encouraged as there is yet much to know about the structure and dynamics of this stream.

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# *The Quaternary Vertebrate Fauna of Upper Sloth Cave, Guadalupe Mountains National Park, Texas*

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Upper Sloth Cave is located in the extreme northwestern corner of Culberson County, Texas, at an elevation of 2000 m and approximately 2.5. mi. northwest of Guadalupe Peak. Vertebrate material obtained from excavations of Upper Sloth Cave provides an excellent opportunity to study the vertebrate faunal evolution of the southern Guadalupe Mountains from approximately 13,000 years Before Present (BP) to the present. A previous excavation of Upper Sloth Cave, then called High Cave (Mera 1938), yielded few vertebrate remains, but some perishable archaeological material was found. Previous work in the southern Guadalupe Mountains has shown that the Sangamonian-Wisconsian faunas contained extinct genera such as *Nothrotherium* (Ayer 1936; Van Devender et al. 1977a) and extant genera such as *Marmota* (Stearns 1942; Schultz and Howard 1935) and *Sorex* (Harris 1970b; Logan 1975) that are found only farther north, at higher elevations, or in more mesic habitats than now exist in the southern Guadalupe Mountains.

## METHOD OF STUDY

The bones of the vertebrates were identified to the lowest possible taxonomic level. Specific identifications of most mandibles and maxilla with teeth were possible. Because of the extremely fragmentary nature of most of the postcranial material, identifications were not attempted except on the Serpentes.

The habitat preferences and environmental interpretations are based on modern literature reports regarding the species represented in the cave deposits.

The vertebrate specimens are cataloged in the vertebrate paleontological collections of The Museum of Texas Tech University (TTU-P), Lubbock,

under the locality number TTU–TEX–2. The molluscan fauna (Table 1) is deposited at the Dallas Museum of Natural History.

TABLE 1. Mollusca from Upper Sloth Cave.

| Taxa | Depth in cm | | | |
|---|---|---|---|---|
| | 0–10 | 10–20 | 20–30 | 30–40 |
| *Discus cronkhitei* | X | | | |
| *Gastrocopta ashmuni* | | X | | |
| *G. pellucida parvidens* | | X | | |
| *Glyphyalinia indentata paucilrata* | X | X | X | |
| *Helicodiscus eigenmanni* | X | | | |
| *H. s. singleyanus* | | X | X | X |
| *Holospira pityis* | X | | X | |
| *Holospira* sp. (immature) | X | X | | |
| *Metastoma roemeri roemeri* | X | X | | X |
| *Oreohelix socorroensis socorreonsis* | | X | | |
| *Oreohelix* sp. | X | X | | |
| *Pupilla blandii* | | X | | |
| *Pupilla* sp. (immature) | X | X | X | |
| *Rabdotus* sp. (immature) | X | | | |
| *Succinea* sp. (immature) | | X | | |
| *Vallonia* sp. (immature) | | X | | |

## PRESERVATION OF BONE

The bones of Upper Sloth Cave are well preserved with little or no mineralization, but with a high degree of breakage. The fragmentary nature of the bones and the fact that very little material present is larger than a jackrabbit suggest that the major bone accumulations were by small mammalian carnivores and predatory birds, although some of the mammals, such as *Neotoma* and *Bassariscus*, certainly live in and around the cave today.

## STRATIGRAPHY

Two trenches were excavated in the front chamber of Upper Sloth Cave (Fig. 1) during the summer of 1974. Due to the very different nature of the deposits, the only correlation between the two trenches is based upon the appearance of *Sorex cinereus* and *Cryptotis parva* in the 30 to 40 cm level of trench 1 and in the 10 to 20 cm level of trench 2 (Table 2). The 30 to 40 cm level of trench 1 has been radiocarbon dated at 11,760±610 BP (A–1519), on artiodactyl fecal pellets from an adjacent, but previously excavated, trench (Van Devender et al. 1977a).

Trench 1, located near the west wall, shows the following stratigraphic units. Unit 1 is from the surface to a depth of 15 cm where it makes a hummocky and somewhat blended contact with unit 2. Unit 1 is composed

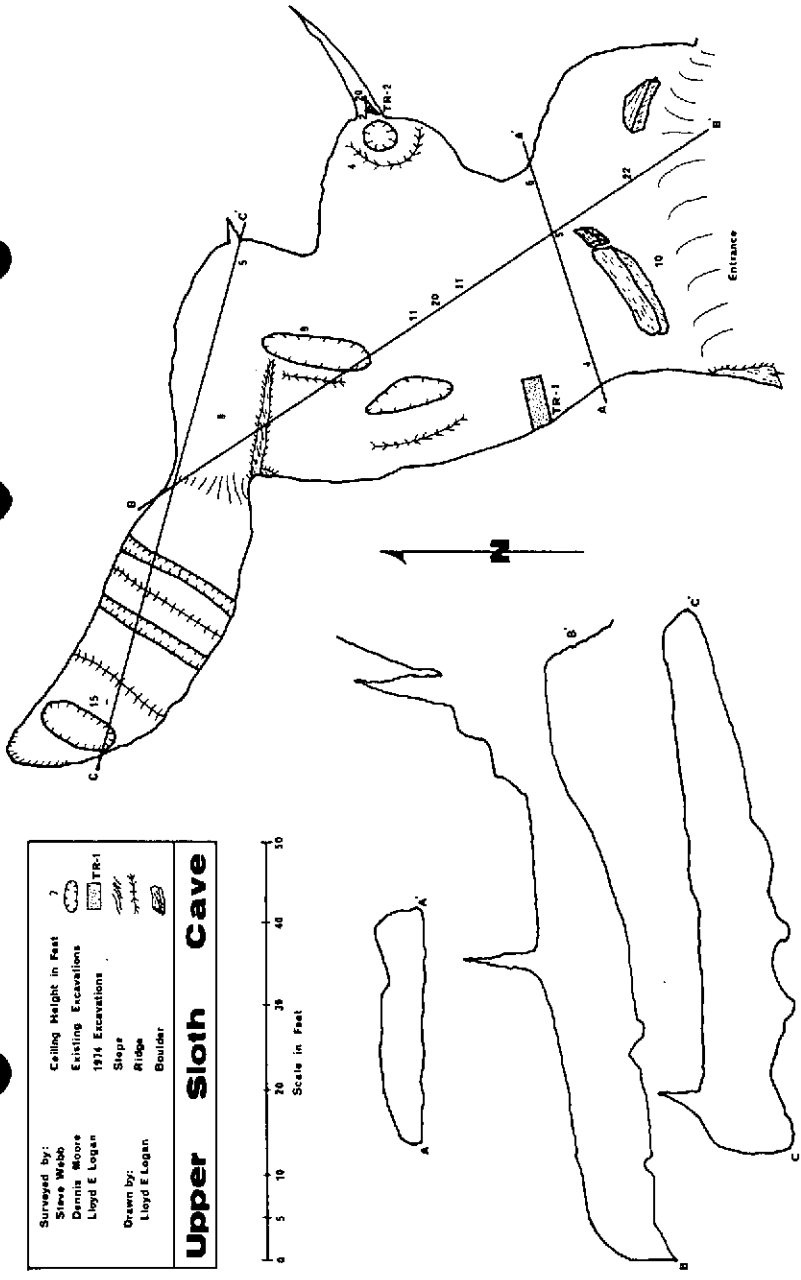


**Fig. 1.** Map of Upper Sloth Cave (GUMO Cave-08), Guadalupe Mountains National Park, Texas.

TABLE 2. Mammals from Upper Sloth Cave.

| Taxa | Depth in cm | | | | |
|---|---|---|---|---|---|
| | Trench 1 | Trench 2 | | | |
| | | 0–10 | 10–20 | 20–30 | 30–40 |
| *Sorex cinereus* | 30–40 | | X | | |
| *Cryptotis parva* | 10–20 | | X | | |
| | 30–40 | | | | |
| *Notiosorex crawfordi* | | X | X | X | X |
| *Myotis velifer* | | X | | | |
| *Myotis* sp. | | X | | | |
| *Lasionycteris noctivagans* | | | X | | |
| *Eptesicus fuscus* | | | X | X | |
| *Plecotus townsendi* | | X | | | |
| *Antrozous pallidus* | | X | | X | |
| *Nothrotherium shastense* | 25–45 | | | | |
| *Sylvilagus* sp. | | X | X | | |
| *Lepus* sp. | | X | | | |
| *Marmota flaviventris* | | | X | | |
| *Spermophilus variegatus* | | X | X | | |
| *Thomomys bottae* | | X | X | | |
| *Pappogeomys castanops* | | X | | | |
| *Peromyscus* spp. | | X | X | X | X |
| *Peromyscus eremicus* | | X | X | | |
| *Neotoma cinerea* | | X | X | X | |
| *Neotoma mexicana* | | X | X | X | X |
| *Neotoma albigula* | | | X | | |
| *Neotoma micropus* | | | X | | |
| *Microtus mexicanus* | | X | X | X | X |
| *Bassariscus astutus* | | X | X | | |
| *Mustela frenata* | | Surface of a spoil heap near trench 2 | | | |
| *Felis concolor* | | X | | | |

of many cobble and gravel-sized limestone fragments, much plant material, limited archaeological material in the form of quids and charcoal fragments, and much fine grey dust. Small artiodactyl fecal pellets are present, but other vertebrate material is sparse. Unit 2 differs from unit 1 in that the archaeological material and most plant material are absent. The dust is more of a reddish tan, but not the typically red clays of most cave deposits. Unit 2 lies from 15 to 25 cm below the modern surface of the cave and makes a rather sharp but hummocky contact with unit 3. Unit 3 lies from 25 to 45 cm below the surface and is composed primarily of dung balls of *Nothrotheriops shastense* (Shasta ground sloth) in various stages of decomposition (Van Devender et al. 1977a). The majority of identifiable vertebrate remains found in this trench are from stratigraphic unit 3 at the 30 to 40 cm level and consist primarily of mandibles of *Sorex cinereus* and *Cryptotis parva*. Also present in unit 3, and increasing in mass toward the center of the chamber,

are sticks and small logs of *Pinus edulis* (limber pine). Unit 3a is an apparently wind-accumulated layer of leaf litter at the 40 to 45 cm level. This unit is present only in a local area in the east end of the trench directly under the largest concentration of small pine logs. One partial skull and associated mandibles of *Sorex cinereus* were recovered from this unit. Unit 4 consists of limestone cobbles averaging 20 cm in diameter, with the reddish dust filling the cracks between the rocks. Little vertebrate material was recovered from the 45 to 70 cm levels. Trench 1 was terminated at this level.

Trench 2, located at the mouth of a small passage on the east side of the main chamber (Fig. 1), contains the following stratigraphic units. Unit 1, from the surface to 6 or 7 cm, is composed of a dry, grey dust mixed with many pieces of broken flowstone. Fragmentary vertebrate material is extremely abundant. Unit 2 is a calcite cement layer up to 3 cm thick along the walls of the passage, but interrupted toward the center of the passage. Some vertebrate material is incorporated within the cemented matrix. Unit 3 is from 6 to 10 cm below the surface of the trench to a depth of approximately 40 cm, and is composed of a typically reddish and slightly damp clay fill with many gravel-sized limestone fragments. Vertebrate material is extremely common throughout the trench, but nearly all of it is of a fragmentary nature.

## SPECIES ACCOUNTS

### **Sceloporus poinsetti** Baird and Girard, Crevice Spiny Lizard

*Material.*—Right dentary (TTU-P-8312); right maxilla (TTU-P-8313).
*Discussion.*—*S. poinsetti* is a relatively common lizard in the vicinity of Upper Sloth Cave and is found throughout the rocky, arid areas of the southern Guadalupe Mountains. *S. poinsetti* does not indicate any change from present environmental conditions.

### **Sceloporus undulatus** (Latreille), Eastern Fence Lizard

*Material.*—Two right dentaries (TTU-P-8315-8316); seven left dentaries (TTU-P-8317-8323); four left maxilla (TTU-P-8324-8327); five right maxilla (TTU-P-8328-8332).
*Discussion.*—*S. undulatus* has previously been reported only twice from prehistoric localities in the southwestern United States (Holman 1970; Gehlbach and Holman 1974). *S. undulatus* is an abundant lizard in the vicinity of Upper Sloth Cave and occurs in all biomes of the southern Guadalupe Mountains. This species is not useful as an ecological indicator because of its ecological plasticity.

### **Urosaurus ornatus** Baird and Girard, Tree Lizard

*Material.*—Four left maxilla (TTU-P-8334-8337); five right maxilla (TTU-P-8338-8342); seven left dentaries (TTU-P-8343-8349); six right dentaries (TTU-P-8350-8355).
*Discussion.*—*U. ornatus* occurs in a wide variety of habitats in the southern Guadalupe Mountains today and is extremely common in the vicinity of Upper Sloth Cave. The wide range of habitats occupied by this species makes it nearly useless for climatic interpretations.

**Eumeces** cf. **E. multivarigatus** Hallowell, Many-lined Skink

*Material.*—Fragmentary left maxilla (TTU-P-8375).
*Discussion.*—*E. multivarigatus* has previously been reported from Pratt Cave (Gehlbach and Holman 1974) where it represented the first record of the species from a southwestern prehistoric locality. *E. multivarigatus* is a fairly common inhabitant in some portions of the southern Guadalupe Mountains and does not indicate any climatic change.

**Thamnophis** sp. Fitzinger

*Material.*—One precaudal vertebrae (TTU-P-8368).
*Discussion.*—*Thamnophis* is generally considered to be primarily a mesic-adapted genus (Raun 1965; Gehlbach and Holman 1974). The presence of this genus on the west face of the Guadalupe Mountains indicates either more mesic conditions or transportation of the material from place of origin to place of deposition.

cf. **Diadophis punctatus** (Linnaeus), Northern Ringneck Snake

*Material.*—One precaudal vertebrae (TTU-P-8372).
*Discussion.*—*D. punctatus* is usually considered a woodland species (Raun 1965). This single specimen (Table 3) may represent transportation from the forested area approximately 450 m above the cave, or it may represent a depression of the woodlands to the elevation of the cave as suggested by Van Devender et al. (1976b)

TABLE 3. Reptiles from Upper Sloth Cave.

| Taxa | Depth in cm | | | |
|---|---|---|---|---|
| | 0–10 | 10–20 | 20–30 | 30–40 |
| *Sceloporus poinsetti* | X | X | | |
| *Sceloporus undulatus* | X | X | X | |
| *Sceloporus* sp. | X | X | X | |
| *Urosaurus ornatus* | X | X | X | |
| *Eumeces multivarigatus* | | | X | |
| *Eumeces* sp. | X | | | |
| *Thamnophis* sp. | | X | | |
| *Diadophis punctatus* | | | X | |
| *Coluber* or *Masticophis* | X | X | | |
| *Opheodrys vernalis* | X | | | |
| cf. *Salvadora* | X | | | |
| *Elaphe subocularis* | X | X | X | |
| *Arizona elegans* | X | | | |
| *Trimorphodon biscutatus* | X | | | |
| *Crotalus* sp. | X | X | X | |
| Unidentified snake | X | X | X | X |

**Coluber** Linnaeus or **Masticophis** Baird and Girard

*Material.*—Four precaudal vertebrae (TTU-P-8370); two precaudal vertebrae (TTU-P-8371).
*Discussion.*—We are unable to assign these vertebrae to either *Coluber* or *Masticophis* with certainty. *M. flagellum* and *M. taeniatus* are found in the immediate vicinity of Upper Sloth Cave, with the latter species being the more abundant. Brattstrom (1964) reported *Coluber constrictor* from late Wisconsin deposits of south-central New Mexico, but this species has not

been reported from the southern Guadalupe Mountains. No change from present climatic conditions is indicated by this material.

**Opheodrys vernalis** (Harlan), Smooth Green Snake

*Material.*—Three precaudal vertebrate (TTU-P-8367).
*Discussion.*—In Texas, *O. vernalis* presently is known only from Ellis, Bosque, Austin, and Matagorda counties (Raun 1965). These specimens are the first Texas records of *O. vernalis* west of the Edwards Plateau and the first confirmed record for the Guadalupe Mountains. The presence of *O. vernalis* in the southern Guadalupe Mountains has been suspected for several years, based on a description given to Dr. John Mecham by a rancher in the Guadalupe Mountains of southern New Mexico (John Mecham, pers. comm.) In the western United States, *O. vernalis* inhabits damp, grassy environments such as stream borders, meadows, and rocky habitats interspersed with grass (Stebbins 1966). The presence of this species indicates a more mesic environment than presently occurs in the vicinity of the cave or possibly transportation from place of origin.

cf. **Salvadora** sp. (Baird and Girard)

*Material.*—One precaudal vertebrae (TTU-P-8373).
*Discussion.*—*S. grahamiae* was observed within 0.5 mi. of Upper Sloth Cave during the period of excavation. The presence of this genus does not indicate any change in climatic conditions.

**Elaphe** cf. **E. subocularis** (Brown), Trans-Pecos Rat Snake

*Material.*—24 precaudal vertebrae (TTU-P-8364); 10 precaudal vertebrae (TTU-P-8365); one precaudal vertebrae (TTU-P-8366).
*Discussion.*—Raun (1965) listed *E. subocularis* from the Guadalupe Mountains and stated that the preferred habitat is rocky areas at higher elevations, a condition that closely matches the area surrounding Upper Sloth Cave. The presence of this species in the deposits does not indicate any change from the present climatic conditions.

**Arizona elegans** Kennicott, Glossy Snake

*Material.*—Two precaudal vertebrae (TTU-P-8369).
*Discussion.*—*A. elegans* is a common inhabitant of the desert shrub community immediately to the southwest and approximately 500 m lower in elevation than the cave. This xeric-adapted species indicates no change from present climatic conditions.

**Trimorphodon biscutatus** Cope, Texas Lyre Snake

*Material.*—Five precaudal vertebrae (TTU-P-8374).
*Discussion.*—Raun (1965) listed *T. vilkinsoni* (= *T. biscutatus vilkinsoni*) from the Trans-Pecos region of Texas, but excluded the Guadalupe Mountains. These specimens represent the first known occurrence of *T. biscutatus* from the Guadalupe Mountains. The preferred habitat is rocky, arid, or semi-arid regions where it feeds primarily on lizards (Raun 1965). No change in climatic conditions is indicated by this species.

**Crotalus** sp. Linnaeus

*Material.*—27 precaudal vertebrae (TTU-P-8360); 13 precaudal vertebrae (TTU-P-8361); seven precaudal vertebrae (TTU-P-8362); one precaudal vertebrae (TTU-P-8363); two precaudal vertebrae (TTU-P-8377).
*Discussion.*—*C. atrox, C. molussus*, and *C. lepidus* are all found in the immediate vicinity of Upper Sloth Cave. Based on the large size of the vertebrae, these specimens most probably represent *C. atrox* or *C. molossus*. Rattlesnakes frequently are found around the entrances of caves and their presence in the deposit was expected. Due to the wide range of habitats occupied by this genus, *Crotalus* is of little use as an ecological indicator.

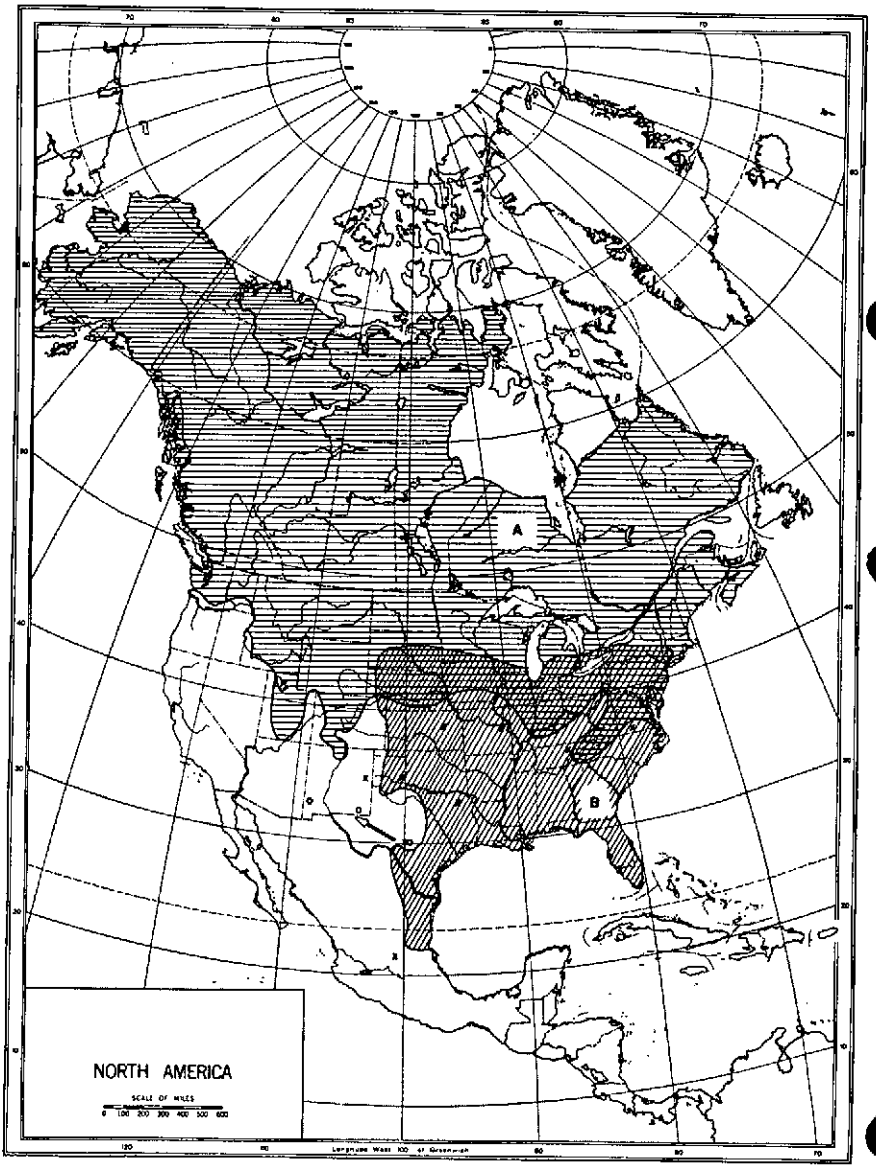


**Fig. 2.** Recent distribution (A) and Pleistocene occurrences (x) of *Sorex cinereus* and Recent distribution (B) and Pleistocene occurrences (O) of *Cryptotis parva*.

cf. **Tympanuchus** sp. (Linnaeus)

*Material.*—One fragmentary sternum (TTU-P-8396).

*Discussion.*—This fragmentary sternum closely resembles *Tympanuchus* sp., but is too

fragmentary to permit specific identification. *T. pallidicinctus* presently occurs in limited numbers on the plains to the east of the Guadalupe Mountains. This genus does not indicate any change from present climatic conditions.

### Passeriformes

*Material.*—Abundant material.
*Discussion.*—These bones represent at least three taxa of passeriform birds. The majority of the bones are of young birds and are incompletely ossified, making further identifications uncertain.

### **Sorex cinereus** Kerr, Masked Shrew

*Material.*—Skull and Mandibles (TTI-P-8273); two, $R_1$-$M_3$ (TTU-P-8274-8275); three, $LI_1$-$M_3$ (TTU-P-8276-8278); $LI^1$-$P^4$ (TTU-P-8279); $LM^{1-3}$ (TTU-P-8280); $LM_{1-3}$ (TTU-P-8281); $LP^4$-$M^2$ (TTU-P-8282); $RI_1$-$M_2$ (TTU-P-8283); $LI_1$-$P_1$ (TTU-P-8284); $LM_{1-2}$ (TTU-P-8285); $RI_1$-$M_1$ (TTU-P-8286).
*Discussion.*—*Sorex cinereus* is differentiated from other members of the genus by a shorter and much shallower dentary, a shorter molar row, and a lower coronoid (Findley 1953). The closest occurrence of *S. cinereus* today is in northern New Mexico (Fig. 2), a distance of approximately 300 mi. Specimens from the cave deposit agree closely with a modern specimen (MALB-2684) from San Miguel County, New Mexico, that is deposited in the collections of the Museum of Arid Lands Biology, the University of Texas at El Paso. *Sorex cinereus* "prefers mesic and hydric communities from which it rarely wanders" (Findley 1953). The presence of this species in the deposits is an indicator of more mesic conditions than presently occur in the southern Guadalupe Mountains.

### **Cryptotis parva** (Say), Least Shrew

*Material.*—$RI_1$-$M_3$ (TTU-P-8287); $LI_1$-$M_2$ (TTU-P-8288); $RI_1$-$M_1$ (TTU-P-8289); $LI_1$-$P_4$ (TTU-P-8290).
*Discussion.*—*C. parva* has been reported from Dry Cave, Eddy County, New Mexico, by Harris et al. (1973), associated with a radiocarbon date of 10,730±150 BP. This date compares favorably with the date 11,760±610 BP (A-1533) obtained from the 23 to 30 cm level of trench 1. This is the first record of *Cryptotis parva* from the Trans-Pecos of Texas and represents a former range extension of at least 200 mi. to the southwest of its present range (Fig. 2). The presence of *C. parva* in the deposits is an indicator of at least slightly more mesic conditions than now exist in the area.

### **Notiosorex crawfordi** (Coues), Desert Shrew

*Material.*—Two, $RI_1$-$M_1$ (TTU-P-8291-8292); two, $LI_1$-$M_3$ (TTU-P-8293-8294); rostrum with $RI_1$-$M_3$, $LI_1$-$M_1$ and $M_3$ (TTU-P-8295); $RM_{1-2}$ (TTU-P-8296); $LM_{1-2}$ (TTU-P-8297); $RM_{1-3}$ (TTU-P-8298); $RP_4$-$M_3$ (TTU-P-8299).
*Discussion.*—Specimens from Upper Sloth Cave do not differ significantly from recent specimens from Garza County, Texas. *N. crawfordi* possibly occurs in the vicinity of the cave today although no specimens are known from the Guadalupe Mountains National Park. Desert shrews are known from a variety of habitats and thus are relatively useless as climatic indicators.

### **Myotis velifer** (J. A. Allen), Cave Myotis

*Material.*—$LM_{2-3}$ (TTU-P-8300).
*Discussion.*—*M. velifer* is larger than other American members of the genus, with the exception of the extinct *M. magnimolaris* (Choate and Hall 1967). *M. velifer* is differentiated from *M. magnimolaris* by a slightly less massive mandible and slightly smaller dentition; the greatest crown length of *M. magnimolaris* has a range of 1.50 to 1.65 mm and a mean of 1.57 mm (Choate and Hall 1967). TTU-P-8300 has a crown length of 1.47 mm on the $M_3$ and is assigned

to *M. velifer* on this basis. *M. velifer* is a common inhabitant of caves in a wide variety of habitats and thus is not useful as an ecological indicator.

### Myotis sp. Kaup

*Material.*—$LP_4$-$M_3$ (TTU-P-8301); $RP_4$-$M_3$ (TTU-P-8302).
*Discussion.*—Several species of small *Myotis* are found in the immediate vicinity of the cave today and are extremely difficult to differentiate on the basis of fragmentary material. The presence of a small *Myotis* in the fauna does not reflect any change in the environmental conditions.

### **Lasionycteris noctivagans** (Le Conte), Silver-haired Bat

*Material.*—$LC_1$-$M_3$ (TTU-P-8303).
*Discussion.*—*L. noctivagans* is a migratory, tree-dwelling bat that is also known to occupy caves, mines, and buildings (Schwartz and Schwartz 1959). Although *L. noctivagans* is presently an uncommon bat in the Trans-Pecos, its presence in the deposits does not necessarily reflect any change in climatic conditions in the area.

### **Eptesicus fuscus** (Beauvois), Big Brown Bat

*Material.*—Edentulous left mandible (TTU-P-8304); $LM_{2-3}$ (TTU-P-8305).
*Discussion.*—The material from Upper Sloth Cave closely resembles a modern specimen from Jeff Davis County, Texas. *E. fuscus* commonly inhabits caves, especially in the winter, and has been observed hibernating in nearby caves. Its presence is not unexpected and indicates no climatic change.

### **Plecotus townsendii** (Cooper), Townsend's Big-eared Bat

*Material.*—$LM_{2-3}$ (TTU-P-8306); $RM_{2-3}$ (TTU-P-8307).
*Discussion.*—The above-mentioned specimens do not differ significantly from Recent specimens collected in Upper Sloth Cave. During the period of 20 July 1974 to 17 August 1974, Upper Sloth Cave was the site of a nursery colony of *P. townsendii* consisting of approximately 50 individuals. Its presence in the deposit was not unexpected. The presence of *P. townsendii* does not indicate any change in climatic conditions.

### **Antrozous pallidus** (Le Conte), Pallid Bat

*Material.*—$LC_1$-$M_2$ (TTU-P-8308); $LM_3$ (TTU-P-8309); $RM_2$ (TTU-P-8310).
*Discussion.*—*A. pallidus* is a rather common inhabitant of caves and mine shafts in the southwestern United States, thus its occurrence in the deposits was expected. No change in climatic conditions is indicated by this species.

### **Nothrotherium shastense** Sinclair, Shasta Ground Sloth

*Material.*—Abundant dung balls from the 25 to 45 cm level of trench 1 are referred to this species (TTU-P-8259).
*Discussion.*—The dung of *N. shastense* is known from only six other North American sites—Rampart Cave and Mauv Caves in the Grand Canyon of Arizona; Gypsum Cave, Nevada; Aden Crater, New Mexico; Williams Cave and Lower Sloth Cave, Guadalupe Mountains National Park, Texas. Radiocarbon dates available for these locations are all 11,000 YBP or older and agree closely with the date of 11, 760±610 YBP (A-1533) on artiodactyl fecal pellets associated with the sloth dung (Van Devender et al 1976a). No bones of *N. shastense* have been recovered from Upper Sloth Cave, but the dung balls agree closely in size and texture with the dung balls from the other North American sites (Paul Martin, pers. comm.). *N. shastense* is the only extinct species represented in the deposits of Upper Sloth Cave.

**Sylvilagus** sp. Gray

*Material.*—Two, $LP_3$ (TTU-P-8379-8380); two, $RP_3$ (TTU-P-8381-8382).
*Discussion.*—*S. floridanus* and *S. auduboni* both presently occur in the southern Guadalupe Mountains, with the latter species being more abundant. The presence of this genus gives no indications of climatic conditions due to the wide variety of habitats in which it is found today.

**Lepus** cf. **L. californicus** Gray, Black-tailed Jackrabbit

*Material.*—$LP_3$ (TTU-P-8378).
*Discussion.*—*L. californicus* is a common inhabitant of grasslands and desert areas of the southwestern United States (Burt and Grossenheider 1964) and is a common inhabitant of the shrub-desert community to the southwest of Upper Sloth Cave. This species does not indicate any change in climatic conditions.

**Marmota flaviventris** (Audubon and Bachman), Yellow-bellied Marmot

*Material.*—$RP_4$ (TTU-P-8255).
*Discussion.*—The present closest occurrence of *M. flaviventris* to Upper Sloth Cave is in the high mountain forests of northern New Mexico (Fig. 3). *M. flaviventris* has previously been reported from Burnet Cave (Murray 1957) and Dry Cave (Harris 1970b). Murray (1957) attributed the presence of this species at Burnet Cave to the movement of the forests southward and to a lower elevation than where they presently occur. This interpretation is supported by plant macrofossils and pollen samples from the southern Guadalupe Mountains (Van Devender et al. 1976a). In a study of a late Pleistocene fauna from north-central New Mexico, Harris and Findley (1964) pointed out that *M. flaviventris* occurs in other habitats and its presence in conjunction with nonforest forms, as in Dry Cave (Harris 1970b), may indicate an open habitat that now exists even farther to the north. Harris (1970a) suggested that a minimum winter rainfall of at least 2 in. would probably provide enough green fodder to carry *M. flaviventris* through the spring dry season. *M. flaviventris* is an indicator of a more mesic environment than presently occurs in the southern Guadalupe Mountains.

**Spermophilus variegatus** (Erxleben), Rock Squirrel

*Material.*—Two $LP^4$-$M^3$ (TTU-P-8244-8245); four, $RM_{1\ or\ 2}$ (TTU-P-8246-8249); two, $LM_1$ (TTU-P-8250, 8254); $LM^1$ (TTU-P-8251); $RP^4$ (TTU-P-8252); R and L $P^4$-$M^2$ (TTU-P-8253).
*Discussion.*—The material referred to this species is indistinguishable in size and morphology from modern specimens from Culberson County, Texas. *S. variegatus* is a common inhabitant of rocky areas throughout the southern Gaudalupe Mountains, and has been observed in the immediate vicinity of Upper Sloth Cave. This species is of little value as a climatic indicator.

**Thomomys bottae** (Eydoux and Gervais), Botta's Pocket Gopher

*Material.*—Four, $LP_4$ (TTU-P-8384-8386, 8390); three, $RP_4$ (TTU-P-8392-8393, 8387); two, $LM^{1\ or\ 2}$ (TTU-P-8388-8389); $RM^{1\ or\ 2}$ (TTU-P-8391).
*Discussion.*—*T. bottae* is the most abundant pocket gopher in the higher elevations of the Guadalupe Mountains today. *T. bottae* occupies valleys and mountain meadows of the southwestern United States, where it prefers a loamy soil, but it also occurs in sandy or rocky soil (Burt and Grossenheider 1964). This species is of little value as a climatic indicator.

**Pappogeomys castanops** (Baird), Yellow-faced Pocket Gopher

*Material.*—$LP_4$ (TTU-P-8383).
*Discussion.*—*P. castanops* is found primarily on the high plains and in mountain basins (Blair et al. 1957) and is found in the Guadalupe Mountains today. This species is of little use as a climatic indicator.

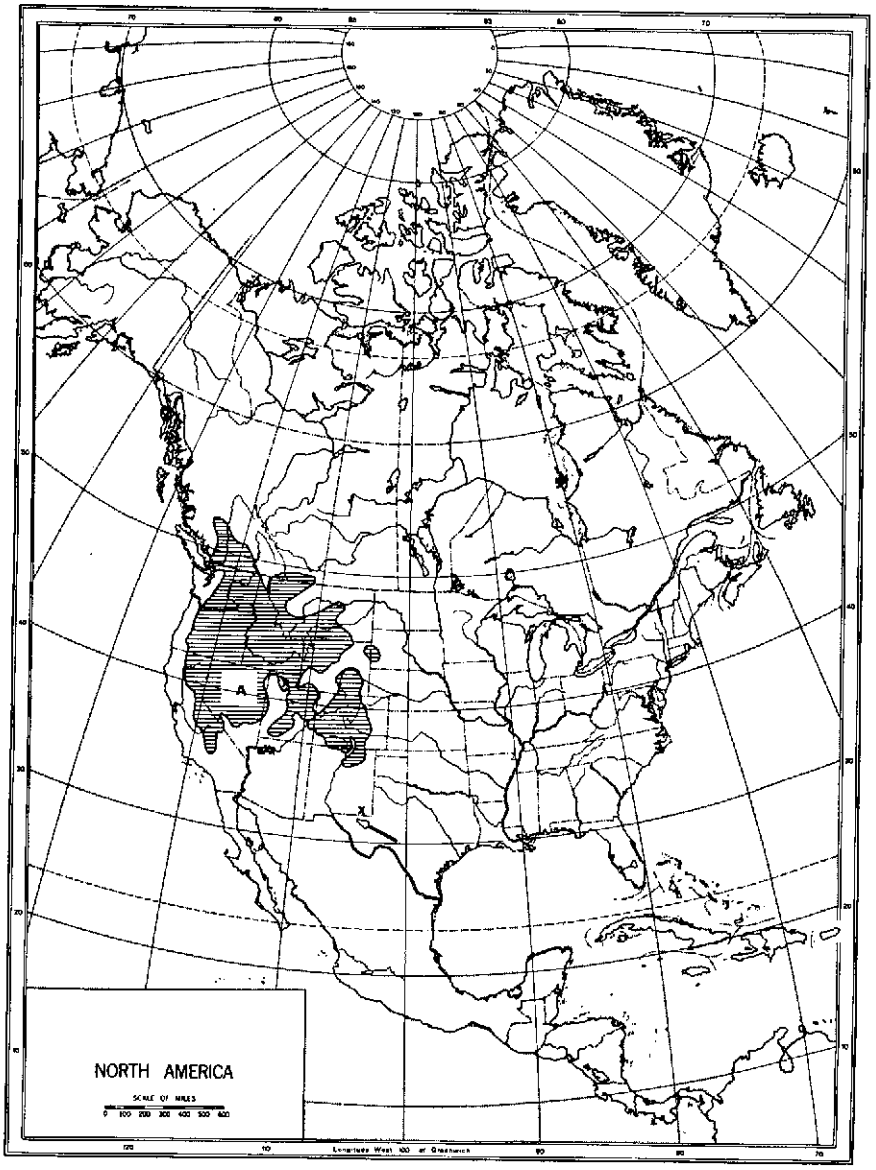


**Fig. 3.** Recent distribution (A) and Pleistocene occurrences (x) of *Marmota flaviventris.*

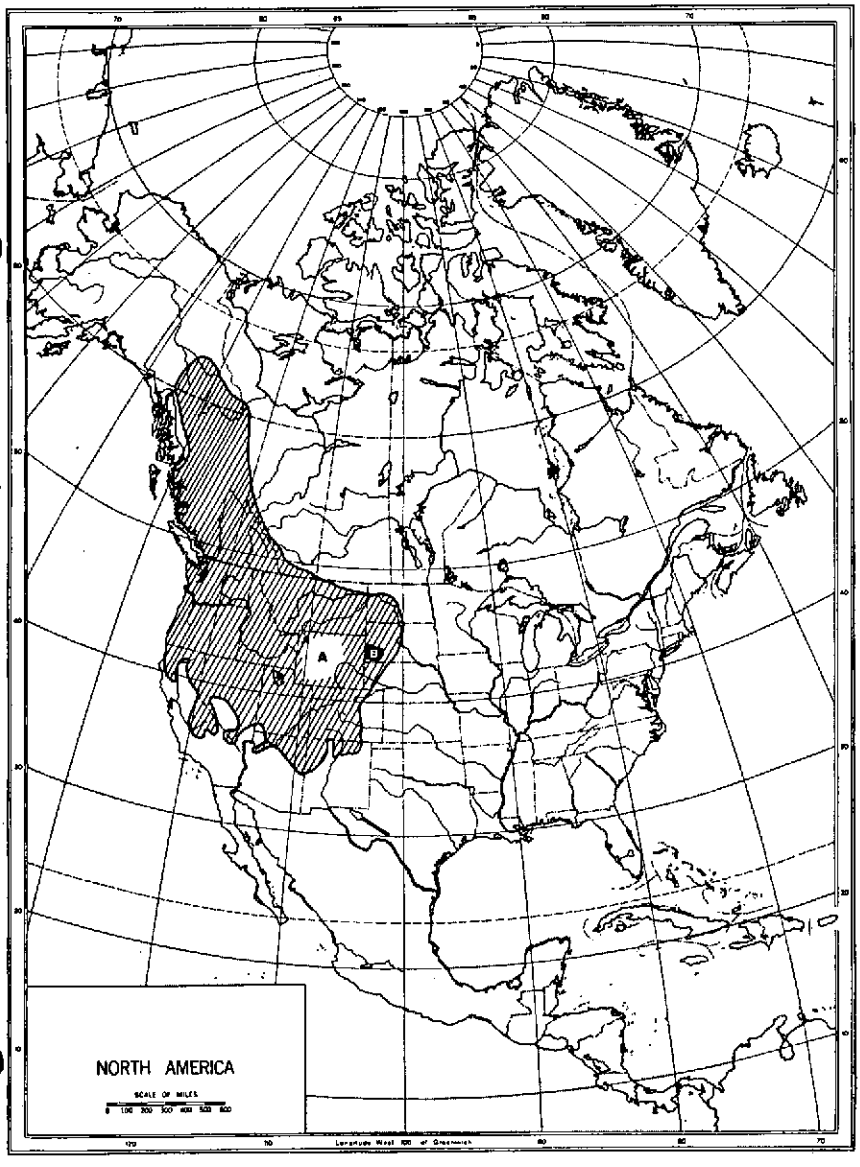


**Fig. 4.** Recent distribution (A) of *Neotoma cinerea* and present area of sympatry (B) for *Sorex cinereus, Cryptotis parva, Marmota flaviventris,* and *Neotoma cinerea.*

**Peromyscus** spp. Gloger

*Material.*—Abundant fragmentary material.
*Discussion.*—*P. eremicus, P. leucopus, P. maniculatus, P. boylei, P. truei, P. difficilis*, and *P. pectoralis* all presently occur in the southern Guadalupe Mountains (Genoways et al. 1977). Of these seven species, only *P. eremicus* can be identified to species with any degree of certainty on the basis of fragmentary material. *P. eremicus* is differentiated from the other six species by the lack of, or, at the most, rudimentary accessory cusps in the two principal outer angles of the $M^1$ and $M^2$ (Hall and Kelson 1959). Due to the extreme range in habitats occupied by members of this genera and the difficulty of distinguishing the various species, *Peromyscus* are nearly useless as climatic indicators.

**Peromyscus eremicus** (Baird), Cactus Mouse

*Material.*—$RM^{1-2}$ (TTU-P-8394); $RM^1$ (TTU-P-8395).
*Discussion.*—Characters to differentiate *P. eremicus* have already been discussed in the previous account of *Peromyscus* spp. *P. eremicus* is an inhabitant of deserts from central Mexico through the southwestern United States (Blair et al. 1957). The presence of this species in the fauna does not indicate any change from present climatic conditions.

**Neotoma cinerea** (Ord), Bushy-tailed Woodrat

*Material.*—$RM^1$ (TTU-P-8264); $RM_2$ (TTU-P-8265); $LM_1$ (TTU-P-8266); three, $LM_2$ (TTU-P-8267-8270); $RM_2$ (TTU-P-8271); $LM_{1-2}$ (TTU-P-8272).
*Discussion.*—*N. cinerea* is differentiated from *N. mexicana* on the basis of accessory cusps developed in the re-entrant angles of some of the teeth (Lundelius 1976), a condition found in 50% of the Recent specimens of *N. cinerea* examined and lacking in all Recent specimens of *N. mexicana* examined.

*N. cinerea* is essentially a boreal animal and is found at higher latitude or higher elevations today (Hall and Kelson 1959). The present closest population of *N. cinerea* to Upper Sloth Cave is in the mountains of north-central New Mexico (Fig. 4). The presence of *N. cinerea* in the fauna is an indicator of cooler and/or more mesic conditions than now exist in the southern Guadalupe Mountains.

**Neotoma mexicana** Baird, Mexican Woodrat

*Material.*—Abundant isolated teeth from all levels of trench 1 and trench 2.
*Discussion.*—*N. mexicana* is identified on the basis of dentine tracts on the anteroexternal sides of the $M_1$ that extend from one-fourth to one-third the distance from the root to the crown of an unworn tooth. The dentine tracts on the $M_2$ are shorter (Lundelius 1977).

This species is very common among the limestone ledges and cliff faces that dominate the west face of the Guadalupe Mountains. *N. mexicana* is not useful as a climatic indicator.

**Neotoma micropus** (Hartly), Southern Plains Woodrat

*Material.*—$LM_1$ (TTU-P-8400).
*Discussion.*—Dalquest et al. (1969) separated *N. micropus* from *N. albigula* on the width of the second lophid of the $M_1$. They found that this measurement in *N. albigula* was always less than 1.94 mm whereas in *N. micropus* this measurement was always greater than 1.94 mm. This criterion was followed in the identification of the *Neotoma* from Upper Sloth Cave. When these two species are sympatric, *N. albigula* is restricted to rocky areas and *N. micropus* is restricted to more open areas (Finley 1958). *N. micropus* presently occurs in the flats in the western portion of the park.

**Neotoma albigula** (Baird), White-throated Woodrat

*Material.*—Two, $LM_1$ (TTU-P-8401-8402); $RM_1$ (TTU-P-8403).
*Discussion.*—Criteria for identification and habitat preferences were discussed in the preced-

ing account of *N. micropus*. *N. albigula* occurs at middle to lower elevations in the park at present.

**Microtus mexicanus** (Saussure), Mexican Vole

*Material.*—Abundant isolated teeth.
*Discussion.*—*M. mexicanus* presently occurs in grassy meadows in the higher elevations of the southern Guadalupe Mountains and is common in local areas. The presence of this species in the fauna does not indicate any significant change in climatic conditions.

**Bassariscus astutus** (Lichtenstein), Ringtail

*Material.*—$LP_3$ (TTU-P-8256); $LM_1$ (TTU-P-8257).
*Discussion.*—*B. astutus* is an inhabitant of the more rocky areas of the southern Guadalupe Mountains where it feeds on a wide variety of small mammals, birds, insects, and plants. This species does not indicate any change in climatic conditions.

**Mustela frenata** (Lichtenstein), Long-tailed Weasel

*Material.*—$RP_3$-$M_3$ (TTU-P-8258).
*Discussion.*—*M. frenata* has not been taken from the Guadalupe Mountains National Park in Recent times (Genoways et al. 1977) although it occurs widely in the United States and Mexico. It has been recorded from Culberson County (Davis 1966:87). *M. frenata* is found in a variety of habitats and is therefore not useful as an ecological indicator.

**Felis concolor** Linnaeus, Mountain Lion

*Material.*—$RdP_3$ (TTU-P-8311).
*Discussion.*—*F. concolor* presently occurs in limited numbers in the southern Guadalupe Mountains. The presence of this species in the deposit was not unexpected and gives no information concerning climatic conditions.

## CLIMATIC INTERPRETATIONS

Upper Sloth Cave provides a good record of faunal transition from a more mesically adapted vertebrate community to the present more xerically adapted vertebrate community. Five taxa of xerically adapted vertebrates are found in the 0 to 10 cm level of trench 2, whereas only two taxa of mesically adapted vertebrates occur in this level. The 10 to 20 cm level of trench 2 presents the opposite picture, with five taxa of mesically adapted vertebrates and only two taxa of xerically adapted vertebrates still present in the deposit. In the 20 to 30 cm level, one additional taxon of mesically adapted vertebrate is gained, whereas all xerically adapted vertebrates are absent. This drop in the number of mesically adapted taxa can probably be attributed to the relatively small amount of matrix removed from the 20 to 30 level of trench 2 because of the configuration of the cave walls at this depth. The actual numbers of specimens obtained also follow the trends discussed above.

If we assume that *Sorex cinereus, Cryptotis parva, Marmota flaviventris*, and *Neotoma cinerea* existed contemporaneously in the vicinity of Upper Sloth Cave and look for a modern area of sympatry, we find that the eastern portion of the Black Hills of South Dakota is the only area where these four taxa presently occur together. The elevation of the Black Hills is

similar to that of Upper Sloth Cave and the vegetation of the Black Hills is similar to that proposed for the southern Guadalupe Mountains by Van Devender et al. (1976b). On the basis of the previously discussed floral and faunal similarities, we are therefore postulating that approximately 11,000 years ago the climatic conditions in the southern Guadalupe Mountains may have been similar to the climatic conditions existing in the Black Hills of South Dakota today.

This more xeric trend in the southern Guadalupe Mountains may have begun approximately 11,500 years ago and been a contributing factor in the extinction of the Shasta Ground Sloth, *Nothrotherium shastense*, or it may not have started until as late as 5000 years ago as suggested by Van Devender and Worthington (1977). Lack of a radiocarbon date directly associated with the deposits in trench 2 precludes a more definite timetable.

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# *Environmental Implications of Herpetofaunal Remains from Archeological Sites West of Carlsbad, New Mexico*

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This report is to demonstrate the usefulness of herpetofaunal remains in reconstructing archeological environments. In and near caves and rock-shelters predators leave a concentrated sample of whatever prey species are abundant locally. Three such sites in the hills west of Carlsbad, Eddy County, New Mexico, have yielded a wealth of faunal remains, and among the smallest bones are those of amphibians and reptiles.

In the arid Southwest the archeological remains of salamanders, turtles, and snakes are relatively uninformative. The tiger salamander, *Ambystoma tigrinum*, is widespread and only suggests general proximity to a pond or streamcourse. Finding any other species of salamander is unlikely. Turtle remains in archeological sites are environmentally unreliable because the human residents may have carried them great distances for uses other than food. Snakes often make up a major part of archeological herpetofauna; unfortunately most species are relatively wide-ranging, so their remains say little about local conditions. Accordingly, this report is limited to the two groups that seem most useful as indicators of past conditions, the anurans (frogs and toads) and the lizards.

The oldest of the three sites is Honest Injun Cave, which is located on the West Fork of the Little McKittrick Draw at 1115 m (3660 ft) elevation (Fig. ). It is situated about 12 m up a terraced, west-facing, limestone cliff, extends in horizontally for about 12 m, and has about 60 cm of loose dust and rock debris on the floor. A radiocarbon date of 2930 ± 60 years BP (980 B.C.; WIS-598) was obtained from woven artifacts found near the middle of the cave and about 25 cm below the surface. Depthwise, the artifacts tended to be concentrated in the middle third, but occupants had churned the fill to some extent. Three carapace fragments of a western box turtle, *Terrapene ornata*, all from a single individual judging by color and size, had been scattered at least 15 cm vertically and 3 m horizontally. Roughly 100 m

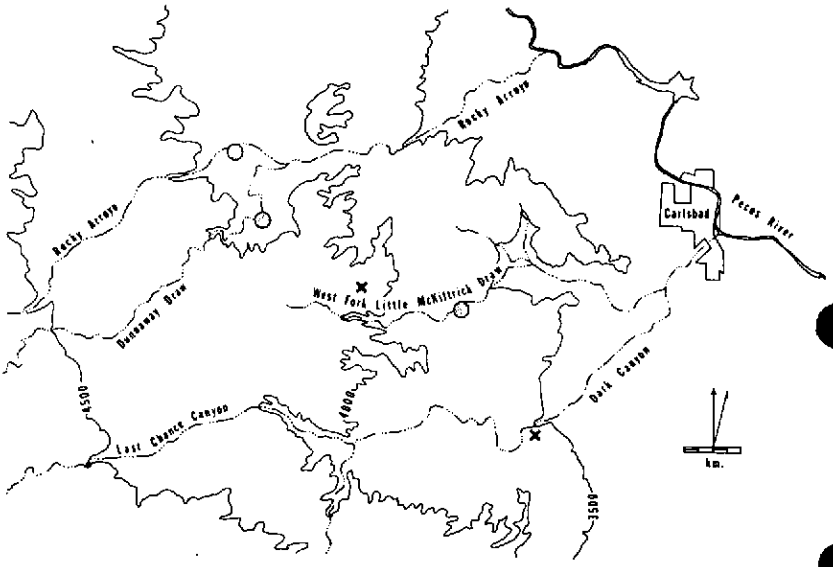


FIG. 1. Map of the area west of Carlsbad, New Mexico, showing the distributions of the following archeological sites (shaded dots) and paleontological sites (crosses): Ellis, Roberts Rockshelter, Dry Cave, Honest Injun Cave, and Dark Canyon Cave (reading from upper left to lower right). The elevational contours, abstracted from USGS maps, are in feet above mean sea level.

downcanyon is an arroyo-bottom pool; although never seen completely dry, its water is foul when low. Except for the Little McKittrick floodplain, the surrounding area within 5 km is almost entirely rolling, rocky hills.

The second site is Roberts Rockshelter located on Dunnaway Draw at 1183 m (3880 ft) elevation. The shelter is situated in the lower part of a west-facing, limestone cliff which is about 8 m high. It is adjacent to an arroyo-bottom pool, which usually has some water but has been seen completely dry. A radiocarbon date of 1075 ± 50 years BP (A.D. 875; WIS–579) was based on charcoal found 90 cm down in the midden adjacent to the shelter. The deposit was entirely outside the shelter, had a maximum depth of about 110 cm next to the shelter, and became thinner as one moved away from the cliff, with bare rock benches rimming the pool. Raptors have used the shelter and nearby ledges as evidenced by the thousands of small bones recovered from roughly a cubic meter of deposit, and the deposit being richest within one meter of the cliff. A similar number of bones was recovered from deposit disturbed by illegal artifact hunters (the "back dirt" of "pot hunters").

Third, the Ellis site consists of two small shelters in a low, west-facing bluff on the south side of Rocky Arroyo at 1173 m (3850 ft) elevation. The shelters are both about 1 m high and extend horizontally 4 m and 2 m, respectively, into the loosely cemented conglomerate just under a relatively hard top

stratum. Radiocarbon dates of 815 ± 50 years BP (A.D. 1135; WIS–577) and 810 ± 55 years BP (A.D. 1140; WIS–578) were obtained from charcoal found 23 cm and 45 cm below the surface of the midden deposit just outside each shelter. The fill in the shelters was 50 cm and 30 cm deep. Test trenches were dug in the fill and extended outward through the midden of each shelter. As the shelters were only 51 m apart and so similar in age and design, their herpetofaunal data are pooled in this report. Occupants had churned the fill as evidenced by two bones of the barking frog, *Hylactophryne augusti*, evidently from one individual, one bone being on the surface and the other at least 28 cm down in the 50-cm fill. Both the Roberts and Ellis sites are in a shallow valley, Indian Basin, the topography of which is a mixture of relatively level areas and low, rolling hills.

Because the deposits of all the sites were more or less disturbed, stratigraphic data are not presented. In treating data for whole sites, it is assumed that the proportion of bones from historic times is relatively insignificant. Taking relative recoverability into account, the archeological samples are viewed as a fair measure of the prehistoric relative abundance of the various species, before modern environmental alteration.

For comparison with archeological abundance, qualitative estimates of present relative abundance (PRA) within 5 km of each site are given with the archeological data in Tables 1 and 2. These estimates are based on four summers of field work (1970–73) and the museum records of Carlsbad Caverns National Park, Eastern New Mexico University, the University of Kansas, and the University of New Mexico. All archeological herpetofauna is being held for further study and eventually will be deposited in the Laboratory for Environmental Biology of the University of Texas at El Paso.

Of the anuran and lizard species now in the general area but not found in the archeological sites, four are so small that recovery of their delicate bones was unlikely with the single, dry, flyscreen sieves (1 to 1.5-mm mesh) that were used (layered wet screens, down to 0.5-mm mesh, would have been better). The four species are: the cricket frog, *Acris crepitans* (which, because of its limitation to the immediate vicinity of permanent water, was not seen or heard near any of the sites); the green toad, *Bufo debilis*; the tree lizard (a misnomer in New Mexico as most are found on large rocks), *Urosaurus ornatus*; and the many-lined skink, *Eumeces multivirgatus*. The last two are scarce and most often found near springs and permanent streams.

The only relatively large species[1] not found in the sites was the bullfrog, *Rana catesbeiana*, which is suspected to have invaded the Pecos River in historic times (Raun and Gehlbach 1972:10). Although this species was reported by Wiley (1972) from a Pleistocene deposit in Dark Canyon Cave (Fig. 1), personal reexamination of the material negates that record.

[1]The plains leopard frog, *Rana blairi*, may inhabit the Pecos Valley as far south as Artesia, roughly 43 km NNE of the Ellis site; it seems to be separable osteologically from the Rio Grande leopard frog, *R. berlandieri*.

University of Texas 41228–509 consists of two third vertebrae, one from a large (roughly 11 cm) Woodhouse's toad, *Bufo woodhousei*, and the second from a smaller (roughly 7 cm) toad, *Bufo* sp. (possibly *B. woodhousei*, but the bone is in poor condition).

## ANURANS

The red-spotted toad, *Bufo punctatus* (Table 1), locally prefers rocky slopes. The rocky terrain around Honest Injun explains both its archeological and modern abundance. Although now common in the Indian Basin, it seems to have been relatively scarce there 800 years ago, a change presumably due to overgrazing and consequent soil erosion.

The Texas toad, *Bufo speciosus*, is fairly restricted to valleys with some grass and soil. In the Indian Basin its archeological abundance contrasted to its present-day rarity suggests considerable erosion and vegetational alteration. The relative abundance of *B. speciosus* compared to *B. punctatus*, wherever sympatric, seems a sensitive indicator of the relative abundance of grass and soil. (Many bones could only be assigned to species groups, so when some were determined to a particular species and none to other closely related species, all were pooled for estimating the minimum number of individuals represented.)

Woodhouse's toad, *Bufo woodhousei*, is now absent from Eddy County, with the exception of the Pecos floodplain from Lake McMillan northward (25 airline km northeast of Ellis). It favors sandy soil, relatively mesic conditions, and is now generally confined to river valleys in the Southwest. It has been reported from Pleistocene deposits (Fig. 1) in Dry Cave (Holman 1970) and Dark Canyon Cave (Wiley 1972). The remains in Honest Injun Cave

TABLE 1. Archeological and present anuran faunas of three sites west of Carlsbad, New Mexico. Archeological items include fragments, whole bones, and groups of co-adherent bones. MNI are the minimum number of individuals represented by the recovered items. Estimates of present relative abundance (PRA) within 5 km of each site are very common (vc), common (c), scarce (s), rare (r), and absent (a).

| Anuran species | Honest Injun | | | Roberts | | | Ellis | | |
|---|---|---|---|---|---|---|---|---|---|
| | Items | MNI | PRA | Items | MNI | PRA | Items | MNI | PRA |
| *Bufo debilis* | | | s | | | c | | | c |
| *Bufo punctatus* | 51 | 10 | vc | 9 | 3 | c | 4 | 2 | c |
| *Bufo* small species | 4 | | | | | | 2 | | |
| *Bufo speciosus* | | | a | 9 | 10 | r | | | s |
| *Bufo* large species | 17 | | | 67 | | | 7 | 3 | |
| *Bufo woodhousei* | 6 | 6 | a | | | a | | | a |
| *Hylactophryne augusti* | 1 | 1 | a | | | a | 2 | 1 | a |
| *Rana berlandieri* | | | r | 1 | 2 | r | | | r |
| *Rana* small species | | | | 1 | | | | | |
| *Scaphiopus couchi* | 2 | 1 | a | 161 | 17 | r | 46 | 8 | s |
| *Spea hammondi* | | | c | 30 | 23 | c | 1 | 2 | c |
| *Spea* species | 4 | 1 | | 196 | | | 9 | | |

suggest a slightly wetter climate and locally marshy conditions along the Little McKittrick Draw, probably in post-Wisconsin times and possibly as recent as 3000 years ago. The absence of this species from the Indian Basin deposits indicates attainment of the present, relatively dry climate prior to 1000 years ago.

The barking frog, *Hylactophryne augusti*, is rare in New Mexico. Of the five modern specimens (all in the University of New Mexico herpetology museum), four are from east of Roswell and one is from 19 airline km northwest of Carlsbad. All were collected on grassy benches adjacent to cliffs along the Pecos River. Two archeological bones from Ellis and one from Honest Injun suggest some grass on the benchland above each bluff. More important to their distribution seems to be their ability to find moisture in limestone cracks and caves, and their apparent near extinction in the Carlsbad area suggests a lowering of the ground moisture.

The Rio Grande leopard frog, *Rana berlandieri*, is a member of the recently redefined *Rana pipiens* complex (Pace 1974). All species of leopard frogs indicate permanent water somewhere in the general vicinity; this species may indicate a relatively warm climate. In 1973 four live frogs at the Honest Injun pool and two at the Roberts pool were a surprise because none had been seen there in three previous summers. These vagrants probably moved in during a rainy period; their presence seemed ill-fated, as most biological range-expanding efforts must be. The source of the Honest Injun frogs is unclear, possibly a spring-refugium somewhere upcanyon. The frogs at the Roberts pool most likely came from spring-fed pools about 10 km downcanyon. In general, ranid frogs breed only in permanent water, whereas spadefoot toads breed only in temporary water. Honest Injun yielded no ranid bones and six spadefoot bones to suggest ephemerality of the local pool. The ephemerality of the Roberts pool is certified by a scarcity of ranid remains, two bones, and an abundance of spadefoot remains, 560 bones, which were found at all depths in the deposit. Arroyo-bottom and rain pools around Ellis are highly ephemeral, and that seems to have been the case for at least the last 800 years.

Couch's spadefoot toad, *Scaphiopus couchi*, prefers short-grass and desert grasslands with deep, sandy alluvium. It is now common in the relatively level parts of the Pecos Valley but seems to be absent from the Honest Injun area and scarce in the Indian Basin. Its archeological presence in Honest Injun suggests the occurrence of some grassland in the vicinity, most likely on the Little McKittrick floodplain. In the Indian Basin the archeological abundance of this species is evidence for a relatively extensive grassland and deep soil prior to modern grazing.

The western spadefoot toad, *Spea*[2] *hammondi*, locally appears to prefer

[2]Most authors have treated *Spea* as a subgenus or synonym of *Scaphiopus*; *Spea* is used here as a valid genus because most skeletal elements can be determined to either *Spea* or *Scaphiopus* (a practical matter in working with herpetofaunal remains), and because the magnitude of the osteological differences is viewed as justification for full generic rank.

hilly terrain with sandy or gravelly substrate. However this may be a marginal habitat, unsuitable for the larger *S. couchi* which may displace *S. hammondi* from the Pecos Valley. The greater abundance of *S. hammondi* bones in Roberts as compared to Ellis probably reflects the terrain around each site, Ellis having relatively more flat land. The abundance of both *S. couchi* and *S. hammondi* in the Indian Basin sites indicates, in prehistoric times, both grassland in the relatively level areas and open desert vegetation on the hillsides.

## LIZARDS

Whiptail lizards, *Cnemidophorus* sp. (Table 2), of this region include five species. Arranged by body size from smallest to largest, they are *C. inornatus, C. gularis, C. exsanguis, C. tigris,* and *C. tesselatus*. Lack of adequate comparative material has prevented specific identification of remains. However, with considerable overlap among the ranges of these species, use can be made of the observation by Asplund (1974:695) that "the larger species tend to be restricted to habitats that are shaded, relative to the open habitats of smaller species." Of the minimum of four individuals represented by remains from Honest Injun, two were small and two were medium to large; of the eight from Roberts, four were small; and of the four from Ellis, three were small. Presence of medium to large species in all three sites indicates the occurrence of some brush, sotol, or other shade-providing vegetation in the general vicinity of all three sites.

The Texas banded gecko, *Coleonyx brevis*, is found in arid regions where there are fractured rock outcrops. The apparent low frequency of remains is probably due largely to the difficulty of recovering their delicate bones.

TABLE 2. Archeological and present lizard fauna of three sites west of Carlsbad, New Mexico. Abbreviations as in Table 1.

| Lizard species | Honest Injun | | | Roberts | | | Ellis | | |
|---|---|---|---|---|---|---|---|---|---|
| | Items | MNI | PRA | Items | MNI | PRA | Items | MNI | PRA |
| *Cnemidophorus* species | 9 | 4 | vc | 31 | 8 | vc | 7 | 4 | vc |
| *Coleonyx brevis* | | | s | | | s | 1 | 1 | s |
| *Crotaphytus collaris* | 28 | 5 | c | 77 | 13 | c | 8 | 2 | c |
| *Eumeces obsoletus* | 6 | 2 | r | 15 | 4 | r | | | r |
| *Holbrookia texana* | 5 | 3 | c | 29 | 11 | c | 1 | 1 | c |
| *Phrynosoma cornutum* | 6 | 2 | a | 39 | 6 | r | 7 | 2 | r |
| *Phrynosoma douglassi* | 14 | 4 | a | | | a | | | a |
| *Phrynosoma modestum* | 4 | 1 | c | 278 | 47 | c | 6 | 3 | c |
| *Sceloporus poinsetti* | 58 | 16 | c | 44 | 8 | s | | | r |
| *Sceloporus* large species | 7 | | | 5 | | | | | |
| *Sceloporus undulatus* | 11 | 5 | vc | 26 | 7 | c | 16 | 6 | vc |
| *Urosaurus ornatus* | | | r | | | r | | | a |
| *Uta stansburiana* | | | a | 1 | 1 | r | | | r |

The collared lizard, *Crotaphytus collaris*, ranges from hot desert to pinyon–juniper woodland, wherever it can find rocks for lookouts and open areas for running. As noted by Gehlbach and Holman (1974:196), this species may have been in the aboriginal diet. Consequently their remains are relatively uninformative.

The Great Plains skink, *Eumeces obsoletus*, is relatively riparian, and some riparian vegetation is suggested by their remains in Honest Injun and Roberts. Their absence from Ellis could be due to sampling error, as the small deposits yielded a minimum of only 19 lizards.

The greater earless lizard, *Holbrookia texana*, prefers open stands of desert vegetation with plenty of bare ground for running. On study plots in Big Bend National Park, Degenhardt (1977) found this species was eliminated by dense growth of grass where the ground formerly had been relatively bare due to grazing. The abundance of their remains in Roberts and presence in the other sites indicate an open nature of some portion of the local vegetation, especially near Roberts. The open desert vegetation of the hill slopes probably has changed little in historic times.

The Texas horned lizard, *Phrynosoma cornutum*, favors grasslands with a relatively warm climate and soft, sandy soil. It is also found in disturbed areas that used to be grassland. It is fairly common in the Pecos Valley, but a specimen from 11 km east of Ellis is the closest modern record to the Indian Basin[3]. Its archeological presence in all three sites indicates some grassland with soft soil to have been near all three sites.

The short-horned lizard, *Phrynosoma douglassi*, favors grasslands with loose soil but with cooler and wetter climatic conditions. Its range extends north into Canada where it inhabits the valleys between mountain ranges, and south into Mexico where it is confined to the higher elevations of the Sierra Madre Occidental. In the Guadalupe Mountains of Texas and New Mexico this species is scarce and only known from above 1800 m elevation. It is also known from Pleistocene deposits in Dry and Dark Canyon caves at 1280 m and 1067 m elevation, respectively (Holman 1970; Wiley 1972). Therefore the remains in Honest Injun Cave indicate a slightly cooler and wetter climate, probably post-Wisconsin and possibly as recent as 3000 years ago. The absence of this species from the Indian Basin deposits indicates warmer, drier times by 1000 years ago.

The round-tailed horned lizard, *Phrynosoma modestum*, prefers a warm climate and a substrate of loose sand or gravel, with little or no grass. It is now common on the hills west of Carlsbad but seems generally absent from the Pecos floodplain, which is in direct contrast to the distribution of *P. cornutum*. The few bones in Honest Injun and Ellis suggest some loose

[3]In June 1976, a specimen (UNM 31935) was found in the Indian Basin, dead on state road 137 about 1.3 km southeast of the Roberts site.

gravel and open desert vegetation locally, but these bones could be of relatively recent origin. The wealth of remains in Roberts probably represents concentration via raptors and their pellets. A ratio of 6 *P. cornutum* to 47 *P. modestum* indicates strongly that the hills around Roberts were much as they are today, with loose gravel and open desert vegetation, and that the prehistoric grassland was relatively limited to the floodplains.

Not only are the massive skull bones of the horned lizards relatively durable and recoverable, but they are also highly identifiable to species. Therefore the genus *Phrynosoma* is particularly useful as an indicator of past conditions. The three species of this region form a gradient of environmental preferences with *P. douglassi* favoring moderately cool, mesic grassland, *P. cornutum* preferring warmer, drier grassland, and *P. modestum* favoring desert with little or no grass.

The crevice spiny lizard, *Sceloporus poinsetti*, is generally restricted to outcrops of large, fractured rock, individuals usually remaining close to a crevice retreat. The relative number of their bones in the three sites corresponds well with the relative abundance of nearby suitable habitat.

The eastern fence lizard, *Sceloporus undulatus*, locally favors dense plants such as yucca, agave and sotol, especially in association with loose rocks and crevices. The ratio between *S. poinsetti* and *S. undulatus* in Honest Injun is biased by the greater recoverability of the bones of the larger species, *S. poinsetti*. Both species now live in the vicinity of Honest Injun, but *S. undulatus* is far more abundant. The quantity of *S. undulatus* remains from the Ellis shelters reflects its modern abundance along the bluff and suggests the presence of bushes and other dense plants on the bluff face in prehistoric times.

The side-blotched lizard, *Uta stansburiana*, locally seems to prefer loose sand and open vegetation. It is common in the sand hills east of the Pecos, less common on old sandbars of the Pecos riverbed, and a single specimen from 3 km east of Ellis seems to approximate the present limit of its distribution into the limestone hills west of the Pecos. The single bone from Roberts could be of relatively recent origin, and its singularity indicates the local area to have been marginal or unsuitable for this species in prehistoric times.

## SUMMARY

Species-by-species discussion of the anurans and lizards represented in three archeological sites in southeastern New Mexico, paints a detailed picture of environmental conditions as they were in prehistoric times, prior to overgrazing of delicate desert grassland by domestic livestock.

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# *The Biogeographical Relationships of the Amphibians and Reptiles of the Guadalupe Mountains*

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The Guadalupe Mountains of southern New Mexico and adjacent Texas possess an unusually rich and diverse herpetofauna. This is undoubtedly due in large part to the unusual diversity of habitats within the region, but it may also reflect the strategic location of the mountains with respect to biogeographic regions. The Guadalupes are essentially an extension of the more prominent Sacramento Mountains that lie immediately to the northwest, and as such are subject to some biotic influence of the southern Rocky Mountain system. However, the southern Great Plains lie to the east of the mountains, and the great Chihuahuan Desert stretches away to the south. Also, the Pecos River is located only a few miles to the east, and could act as an avenue for the intrusion of some more aquatic species.

The purposes of this paper are to provide a brief summary of the amphibians and reptiles that occur in the Guadalupe Mountains and their immediate vicinity and to analyze the faunal elements represented in the herpetofauna and their relative importance. Needless to say, any conclusions relative to the biogeographic position of the area that are based on the herpetofauna alone may not apply to other groups.

## THE HERPETOFAUNA

Bailey (1905) briefly described the vertebrate fauna of the Guadalupe Mountains and wrote (1928) a popular account of the animals found in the vicinity of Carlsbad Caverns. The first serious study of the amphibians and reptiles as such, however, was that of Mosauer (1932), who recorded 18 species from the area. My own field work in the Guadalupe Mountains resulted in the collection of 50 species, together with considerable relevant ecological data (Mecham 1955). Most of this information has not been published, although two taxonomic papers (Mecham 1956, 1957) were stimulated by this new material. Frederick Gehlbach has done extensive work on the ecology and distribution of the herpetofauna, but again much of this work remains unpublished. A mimeographed summary (Gehlbach 1964) of

the amphibians and reptiles of Carlsbad Caverns National Park, however, is available together with two relevant taxonomic papers (Gehlbach 1974; Gehlbach and McCoy 1965) and the contribution in this volume. Many other herpetological records are scattered through the literature. A recent review of the turtles of New Mexico (Degenhardt and Christiansen 1974) provides a useful summary of the distribution of this group in the region. Several studies on late and post-Pleistocene herpetological remains are also of some relevance. These include Holman (1970), Gehlbach and Holman (1974), and Applegarth (1977).

A list of the amphibians and reptiles known from the Guadalupe Mountains or their immediate vicinity is given below, together with brief summaries of their local distribution. Life belts in the sense of Dice (1943) have been used in a loosely descriptive sense, although it is recognized that an altitudinally based classification of habitats in the Guadalupe Mountains is unsatisfactory in some respects. The plains life belt as used here refers to habitats below roughly 4200 ft on the lower slopes and the adjacent desert plains. The roughlands belt encompasses a wide range of habitats in the mountains proper from roughly 4200 ft to 7000 ft or more, and including evergreen woodland (*sensu* Gehlbach 1967). The montane belt includes coniferous forest as may occur on the peneplane above approximately 7200 ft.

Subspecific names have not been used in this account except where relevant. Forms rare in the area (known from only one or two records) are indicated by "R." Forms indicated by an asterisk presumably do not occur within the boundaries of the Guadalupe Mountains National Park; other species listed have been reported from the park or almost certainly occur there. Distributional information is based primarily on Mecham (1955) together with published sources except as otherwise noted.

**Amphibia.** Recorded species include *Ambystoma tigrinum, Scaphiopus couchi, Scaphiopus hammondi, Scaphiopus bombifrons,* **Hylactophryne augusti* (R), *Bufo cognatus* (R), *Bufo debilis, Bufo punctatus, Bufo speciosus,***Acris crepitans*, and *Rana berlandieri*. The bullfrog, *Rana catesbeiana*, also is present in the region, but apparently is an introduction. *Ambystoma tigrinum* may occur at all altitudes in ponds or tanks. The *Scaphiopus* species, *Bufo cognatus, B. speciosus*, and *B. debilis* occur primarily in the plains life belt below 4800 ft, whereas the more rock-loving *B. punctatus* ranges from the lower altitudes to above 6000 ft. *Acris crepitans* is known only from permanent water sites on the eastern side of the range, as are southern leopard frogs (*Rana berlandieri*). *Bufo cognatus* is known from a single record south of Dell City on the southwestern side of the mountains (data of Gehlbach). The robber frog, *Hylactophryne augusti*, is known from a single specimen taken northwest of Carlsbad (Koster 1946). This was the only record of the species in New Mexico for a number of years, although another specimen has since been taken near Roswell (Zweifel 1967).

**Testudinata**. Turtles recorded include **Chelydra serpentina*, *Kinosternon flavescens*, **Chrysemys picta*, **Chrysemys scripta*, **Chrysemys concinna*, *Terrapene ornata*, and **Trionyx spiniferus*. With the exception of *Kinosternon flavescens*, which is distributed widely in association with permanent and semipermanent ponds and streams, the aquatic turtle species are essentially limited in the area to the Pecos River and to its tributary, the Black River (Degenhardt and Christiansen 1974), which extends to the eastern foothills of the mountains. The only terrestrial species, *Terrapene ornata*, is widely distributed at lower elevations.

**Lacertilia**. Species recorded include *Eumeces obsoletus, Eumeces multivirgatus, Cnemidophorus exsanguis, Cnemidophorus gularis, Cnemidophorus inornatus, Cnemidophorus tesselatus, Cnemidophorus tigris, Coleonyx brevis, Crotaphytus collaris*, **Crotaphytus wislizeni, Cophosaurus texanus, Holbrookia maculata* (R), *Phrynosoma cornutum, Phrynosoma douglassi, Phrynosoma modestum, Sceloporus poinsetti, Sceloporus undulatus, Urosaurus ornatus*, and *Uta stansburiana*.

*Holbrookia maculata* is reported here in the area for the first time. Specimens in the Texas Tech Museum collection were taken by Mr. Tony Burgess from gypsum dunes on the southwestern side on the mountains near Eclipse Well. *Cnemidophorus tigris, C. inornatus, C. gularis, Crotaphytus wislizeni*, and *Uta stansburiana* are all essentially confined to the desert plains below 4500 ft. *Cnemidophorus tigris* and *Crotaphytus wislizeni* apparently have been collected in the immediate vicinity only from mesquite dunes bordering the salt flats to the southwest. Forms such as *Coleonyx brevis* and *Phyrnosoma modestum* occur in parts of the desert plains but also penetrate lower parts of the roughlands belt. *Phrynosoma cornutum* not only occurs widely in the plains belt, but ranges to nearly 6000 ft. *Eumeces obsoletus, Cnemidophorus tesselatus, Cnemidophorus exsanguis, Crotaphytus collaris*, and the rocky adapted *Cophosaurus texanus* are all common in more open roughlands habitats to approximately 6000 ft. The saxicolous *Urosaurus ornatus* and *Sceloporus poinsetti* have extremely wide altitudinal ranges, and *S. poinsetti*, at least, ranges above 8000 ft. The ubiquitous *Sceloporus undulatus* occurs at all altitudes as does *Eumeces multivirgatus*. *Phrynosoma douglassi* occurs in evergreen woodland and coniferous forest, usually above 6000 ft. The last four species listed all occur in the coniferous forest of The Bowl.

**Serpentes**. Species recorded include *Leptotyphlops dulcis*, **Thamnophis marcianus*, **Thamnophis proximus, Thamnophis cyrtopsis*, **Natrix erythrogaster, Arizona elegans, Elaphe guttata, Elaphe subocularis, Pituophis melanoleucus, Rhinocheilus lecontei, Salvadora grahamiae, Salvadora hexalepis* (R), *Sonora episcopa, Diadophis punctatus, Gyalopion canum, Lampropeltis getulus, Lampropeltis mexicana* (R), *Masticophis flagellum, Masticophis taeniatus, Opheodrys vernalis* (?), *Heterodon*

*nasicus, Hypsiglena torquata, Tantilla atriceps, Tantilla nigriceps, Crotalus atrox, Crotalus lepidus, Crotalus molossus, Crotalus scutulatus* (R), and *Crotalus viridis.*

The inclusion of *Opheodrys vernalis* is based primarily on a recent sight record of the species in the McKittrick Canyon area by Mr. Tony Burgess, although a rancher some years ago gave the writer a good description of what apparently was this species in the vicinity of the ruins of Queen, New Mexico (northern Guadalupe Mountains, 6000 ft). The form is known as a sub-Recent fossil (Logan and Black 1977), and occurs nearby in the Sacramento Mountains. The presence of *Lampropeltis mexicana* is based on a single specimen from the vicinity of Pine Springs (Gehlbach and McCoy 1965), the northernmost record of the species. Inclusion of *Salvadora hexalepis* is based on a specimen in the collection of the Carlsbad Caverns National Park (data of Gehlbach). The listing of only one form of *Diadophis* is an over simplification. Gehlbach (1974) found evidence to indicate that small (*D. p. arnyi*) and large (*D. p. regalis*) forms both occur in the Guadalupe Mountains where they may act as distinct species. The two forms intergrade extensively in other areas of contact, however.

Distributional patterns of the snakes are complex. *Thamnophis proximus, Thamnophis marcianus, Thamnophis cyrtopsis,* and *Natrix erythrogaster* are all confined to the vicinity of permanent water at lower altitudes and drainages on the eastern or northeastern side of the mountains. *Thamnophis cyrtopsis*, a form that is less dependent on permanent water, is more characteristic of the mountains proper and is of wide occurrence. A few species are most characteristic of the plains belt and appear to invade the mountains only at lower altitudes. These include *Arizona elegans, Rhinocheilus lecontei, Heterodon nasicus, Lampropeltis getulus, Tantilla nigriceps, Crotalus viridis*, and *Crotalus scutulatus.* The last form is marginal in the area. The closest record is a specimen taken by Tony Burgess just southwest of the mountains near Eclipse Well. Two saxicolous rattlesnakes (*Crotalus lepidus* and *Crotalus molossus*) are common in the roughlands belt and extend to the highest altitudes. I have found them as high as 7400 and 8200 ft, respectively. Most of the other species of snakes appear to be distributed at lower to intermediate altitudes, spanning parts of both the roughland and plains belts. The bullsnake, *Pituophis melanoleucus*, apparently has the widest ecological tolerance of any of the snakes. I recorded one specimen as low as 3600 ft (in mesquite dunes); Mosauer (1932) found a specimen at about 8000 ft in pine-fir forest.

**Other Species.** Some additional species as yet unreported from the Guadalupe Mountains may occur there. Possibilities include *Bufo woodhousei, Rana blairi, Leptotyphlops humilis, Coluber constrictor, Lampropeltis triangulum, Thamnophis sirtalis, Trimorphodon biscutatus*, and *Sistrurus catenatus*, among others. The proximity of records for *Bufo woodhousei* strongly suggest that this species does occur in the area, at least in the

vicinity of the Pecos River. The presence of *Coluber constrictor* also is particularly likely. The form occurs nearby in the Sacramento Mountains and has recently been reported to the south in the Davis Mountains (Glidewell 1974). Stebbins (1951) indicated on a map that the canyon treefrog, *Hyla arenicolor*, is present in the Guadalupe Mountains, but this almost certainly was in error. Absence of the species, however, is puzzling in view of the seemingly optimal habitat that is present at several locations, particularly in McKittrick Canyon.

## BIOGEOGRAPHICAL RELATIONSHIPS

Dice (1943) and Blair (1950) have placed the upper parts of the Guadalupe Mountains within the Navahonian biotic province, of which they would form the southernmost extension. Lower areas were placed within the Chihuahuan biotic province. The Navahonian, as identified by Dice, is an extensive region that lies between the south-central Rocky Mountains (Coloradan biotic province) and the southwestern deserts. In a sense it is a zone of transition, and inclusion of much of the Guadalupe Mountains in this province emphasizes the northern or montane aspects of the biota. The Chihuahuan biotic province corresponds essentially to the Chihuahuan Desert, although it is more extensive than the desert proper as identified by Shelford (1963) and some other ecologists.

If the biotic province concept is accepted as a viable method of biogeographical classification, this characterization of the Guadalupe Mountains is definitely misleading as far as amphibians and reptiles are concerned. This is demonstrated by an analysis of the reported forms with respect to their occurrence in the Navahonian and Chihuahuan provinces, together with two other nearby provinces, the Kansan (corresponding essentially to the southern Great Plains) and Balconian (the Edwards Plateau of Texas). As shown by Table 1, the strongest affinities lie with the Chihuahuan, with somewhat lower but nevertheless strong affinities with the Kansan and Balconian. The lowest relationship is with the Navahonian, a finding that is highly inconsistent with the classifications of Dice and Blair. Even if the analysis is restricted to species that penetrate to higher altitudes, say above 6000 ft, the herpetofauna appears to be more Chihuahuan than Navahonian. At least 18 species occur at such altitudes. These include *Ambystoma tigrinum, Bufo punctatus, Cnemidophorus exanguis, Eumeces multivirgatus, E. obsoletus, Phrynosoma douglassi, Sceloporus poinsetti, S. undulatus, Urosaurus ornatus, Diadophis punctatus, Hypsiglena torquata, Masticophis taeniatus, Pituophis melanoleucus, Salvadora grahamiae, Thamnophis cyrtopsis, Opheodrys vernalis, Crotalus lepidus*, and *C. molossus*. Of these, 15 are important in the Chihuahuan, 13 in the Navahonian, 12 in the Balconian, and 7 in the Kansan provinces.

A somewhat different picture emerges if the amphibians and turtles, a greater proportion of which have higher water requirements, are considered separately from lizards and snakes (Tables 2 and 3, respectively). It

TABLE 1. Distribution of amphibians and reptiles of the Guadalupe Mountains in near biotic provinces.

| Biotic provinces | Important | Marginal | Total |
|---|---|---|---|
| Kansan | 40 | 4 | 44 |
| Balconian | 41 | 7 | 48 |
| Navahonian | 31 | 10 | 41 |
| Chihuahuan | 46 | 13 | 59 |

TABLE 2. Distribution of amphibians and turtles of the Guadalupe Mountains in near biotic provinces.

| Biotic provinces | Important | Marginal | Total |
|---|---|---|---|
| Kansan | 14 | 0 | 14 |
| Balconian | 14 | 2 | 16 |
| Navahonian | 6 | 3 | 9 |
| Chihuahuan | 8 | 6 | 14 |

TABLE 3. Distribution of lizards and snakes of the Guadalupe Mountains in near biotic provinces.

| Biotic provinces | Important | Marginal | Total |
|---|---|---|---|
| Kansan | 26 | 4 | 30 |
| Balconian | 27 | 5 | 32 |
| Navahonian | 25 | 7 | 32 |
| Chihuahuan | 38 | 7 | 45 |

may be seen that affinities of the amphibians and turtles are primarily with the Kansan and Balconian provinces, although the importance of the Chihuahuan province still ranks above that of the Navahonian. With respect to the snakes and lizards, the affinities are overwhelmingly with the Chihuahuan province, as would be expected in view of the xeric adaptations of many of these forms.

Another method of analysis is in terms of faunal elements, an approach that involves some arbitrary aspects but does provide a different perspective. At least seven faunal elements (or categories) appear to be represented in the Guadalupe Mountain herpetofauna. These elements (Fig. 1) are listed below.

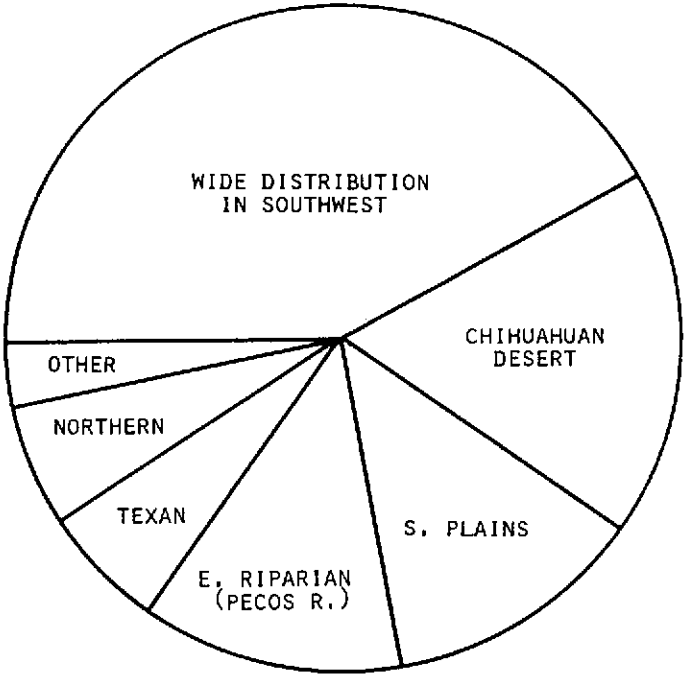


**Fig. 1.** Relative importance of the herpetological faunal elements represented in the Guadalupe Mountains. Refer to text for further explanation.

**Species with Wide Distributions in the Southwest** (28 species, 42.4%).—Forms included here are all of such wide distribution that they cannot be assigned to any particular biotic or physiographic region. The greater number occur in the Chihuahuan Desert, but none have their centers of distribution there. Most are limited to arid or semiarid regions in Mexico and the western United States, but some ( as *Lampropeltis getulus* or *Ambystoma tigrinum*) range widely in more mesic regions.

**Chihuahuan Desert Element** (12 forms, 18.2%).—This category consists of forms that are associated with the Chihuahuan Desert, although they may have limited distributions in adjacent areas. Included are *Cnemidophorus inornatus, C. tigris marmoratus, Coleonyx brevis, Cophosaurus texanus,*

*Phrynosoma modestum, Sceloporus poinsetti, Elaphe subocularis, Gyalopion canum, Lampropeltis mexicana, Tantilla atriceps, Crotalus lepidus*, and *C. scutulatus*. Although *Cnemidophorus tigris* has a much wider distribution, the largely disjunct eastern element of the species (primarily *C. t. marmoratus*) is closely tied to the Chihuahuan Desert and may be used as a biogeographic indicator of that region.

**Plains Element** (8 forms, 12.1%).—This element is composed of forms that have their distributional centers within the Kansan biotic province (southern Great Plains). Included are *Scaphiopus bombifrons, Kinosternon flavescens, Terrapene ornata, Eumeces obsoletus, Elaphe guttata emoryi, Heterodon nasicus, Sonora episcopa*, and *Tantilla nigriceps*.

**Eastern Riparian (Pecos River) Element** (eight species, 12.1%).—This distinctive element consists of the aquatic and semiaquatic species of mostly eastern affinities that have been able to invade (or persist in) the area because of the proximity of the Pecos River. All of the forms are associated with permanent water at lower altitudes on the eastern or northeastern side of the mountains. Included here are *Rana berlandieri, Acris crepitans, Chelydra serpentina, Chrysemys scripta, C. concinna, Trionyx spiniferus, Natrix erythrogaster*, and *Thamnophis proximus*.

**Northern Element** (four species, 6.1%).—This small but heterogeneous group includes forms that approach or attain their southern limits of distribution in western Texas in the Guadalupe Mountains region. Two (*Opheodrys vernalis, Chrysemys picta*) are essentially northern and eastern forms that occur as post-Pleistocene isolates in the Southwest. Populations of the short-horned lizard *Phrynosoma douglassi*, in both the Guadalupe Mountains and the Davis Mountains are disjunct from main elements of the species to the north in New Mexico, and also qualify as relicts. Also included here is the many-lined skink, *Eumeces multivirgatus*. This species is known to occur further to the south in the Chihuahuan Desert, but is primarily associated with the western margin of the Great Plains and the Navahonian biotic province. The subspecies (*E. m. gaigei*) that is found in the Guadalupe Mountains has a distribution that corresponds closely to the Navahonian. The striped phase of this form predominates at higher altitudes, whereas the patternless ("*taylori*") phase is more common at lower altitudes (Mecham 1957).

**"Texan" Element** (four species, 6.1%).—This rather artificial category includes species (*Hylactophryne augusti, Bufo speciosus, Cnemidophorus gularis*, and *Leptotyphlops dulcis*) that are primarily limited to Texas in the United States, although three have extensive ranges in Mexico. New Mexico populations of *Hylactophryne* apparently are isolated from Balconian elements of the species, presumably as a result of a climatic trend toward increased aridity.

**Other species** (two forms, 3.0%).—Two parthenogenetic whiptails, *Cnemidophorus tesselatus* and *C. exanguis*, do not fit any of the foregoing

categories. Both are about equally distributed between parts of the Chihuahuan and Navahonian biotic provinces.

By way of summary of the various faunal elements, it may be said that aside from the large group of species with wide distributions in the Southwest, the most important contribution is made by the Chihuahuan Desert element, with southern Great Plains and eastern riparian elements following in importance. In addition, there is a small but distinctive northern contribution, and a few forms of importance in Texas–Mexico also reach the area. This picture is not inconsistent with that obtained in terms of biotic provinces. The Chihuahuan Desert contribution was found to be of outstanding importance in both cases, and the northern or Navahonian contribution was found to be relatively minor. The low importance of the latter is not unexpected in view of the decreased importance of terrestrial poikilotherms to the north and in the Rocky Mountains, and should not be viewed as indicative of the composition of the biota as a whole. The plains (or Kansan) affinities were identified as important in both analyses, and both indicated some influence from Texas, although the contribution of the Balconian in the biotic province analysis appears to have been exaggerated by failure to exclude either widely distributed forms or Pecos River elements.

The overall picture that emerges is the extreme diversity of the herpetofauna in terms of its origins, and the critical location of the Guadalupe Mountains at the contact zone between various biotic or herpetofaunistic regions. This is emphasized by the rather remarkable fact that at least 23 of the 66 naturally occurring species reported from the Guadalupe Mountain area reach their limits of distribution in or near there. This includes eight forms of the Chihuahuan Desert, four eastern riparian species, two "Texas" species, two northern forms, and seven other southwestern species.

Some correlations can be seen between the various faunal elements and local distributional patterns. This is most obvious, of course, for the Pecos River element, members of which are confined to permanent water which is found mostly at lower altitudes on the eastern side of the escarpment. Most species of the plains element, with the exception of *Eumeces obsoletus* and possibly *Kinosternon flavescens*, are limited to the plains belt and lowermost part of the roughlands belt. The same is essentially true of the Texan element. Of the northern forms, both *Phrynosoma douglassi* and *Opheodrys vernalis* appear to be restricted to higher and more mesic environments. Although *Eumeces multivirgatus* is found at lower altitudes, it is common in the highest parts of the mountains. Local distribution of the Chihuahuan and other species show no consistent patterns. It is interesting to note in this connection that *Crotalus lepidus* and *Sceloporus poinsetti*, two Chihuahuan Desert species that reach their northern limits of distribution in southern New Mexico, together with *Crotalus molossus*, which ranges only slightly further north, all occur at the highest altitudes in the montane belt.

This striking inconsistency between altitudinal range and northern distributional limits may be the result of continual local dispersal of these saxicolous reptiles from lower habitats. Without this replenishment, the high altitude populations might not be able to maintain themselves over a long period of time.

Finally, attention should be drawn to the fact that there are considerable differences between the herpetofaunas at lower altitudes on the eastern and western sides of the mountains. As already emphasized, the eastern riparian elements essentially are limited to the eastern side, primarily because of proximity of the Pecos River and associated drainage patterns, but also because of the scarcity of permanent water on the western face. *Thamnophis marcianus*, although not included in this element, also conforms to this local pattern. On the other hand, extreme desert habitats including sandy or dune situations near the salt flats on the southwestern side support certain species (*Crotalus scutulatus, Crotaphytus wislizeni, Cnemidophorus tigris, Holbrookia maculata*) that apparently are absent on the immediate eastern side. Limited information suggests that local distribution of some other species is consistent with this dichotomy, but more documentation is needed.

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# *Compositional Aspects of Breeding Avifaunas in Selected Woodlands of the Southern Guadalupe Mountains, Texas*

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The Guadalupe Mountains, located in the Trans-Pecos area of west Texas and in the southeast portion of New Mexico, have been the object of numerous geological investigations (e.g., Cys, 1971; Newell et al. 1972). Perhaps this mountain range is best known for its unique Carlsbad Caverns system, situated at the northern end of the mountain mass. At the southern end of the Guadalupe complex, however, are found landmarks which were of great importance to man long before the discovery of the now famous caverns. El Capitan with its uninterrupted cliff facing rising more than 2000 ft (610 m) and Guadalupe Peak, the highest peak in Texas at 8791 ft (2679.5 m), have provided massive landmarks utilized by early explorers and travelers (Levy 1971).

The federal government recognized the scientific, aesthetic, and historical value of the southern Guadalupe Mountains by creating Guadalupe Mountains National Park on 15 October 1966 (Public Law 89-667). This relatively new national park consists of 77,500 acres (31,364.3 ha). Its northern boundary is the New Mexico-Texas state line and the southern boundary encompasses El Capitan and Guadalupe Peak. An assemblage of diverse habitats ranging from Chihuahuan Desert, surrounding the wedge-shaped mountain mass, to coniferous forest at the high mountain elevations characterize this unique area. Rugged canyons penetrate deep into the interior of the mountains, providing environmental conditions which support mesic relict woodland communities (Gehlbach 1967).

Published accounts of bird investigations pertaining to the Guadalupe Mountains date back to 1901 to the work of Mr. and Mrs. Vernon Bailey (Bailey 1905). Burleigh and Lowery (1940) reported on their findings resulting from several collecting excursions to the Guadalupes in 1938 and 1939. At about the same time as Burleigh and Lowery, W. B. Davis, along with

several of his students, made collections and recorded bird observations from the southern Guadalupe Mountains (Biaggi 1960). However, these early accounts provided little quantitative information on breeding birds of the Guadalupes.

Investigations of bird populations of other southwestern mountain ranges have been accomplished by Marshall (1957) in southern Arizona, Hubbard (1965) in the Mogollon Mountains of New Mexico, Tatschl (1967) in the Sandia Mountains of New Mexico, Wauer (1971) in the Chisos Mountains of Texas, Carothers et al. (1973) in the San Francisco and White Mountains of Arizona, and Johnson (1974) in the Grapevine and Potosi mountains of Nevada.

In the summers of 1969, 1970, and 1971, at the invitation of the National Park Service, I began preliminary investigations of the breeding avifaunas of selected woodland communities within Guadalupe Mountains National Park (Newman 1971, 1974a,b). Beginning in 1972 and continuing through

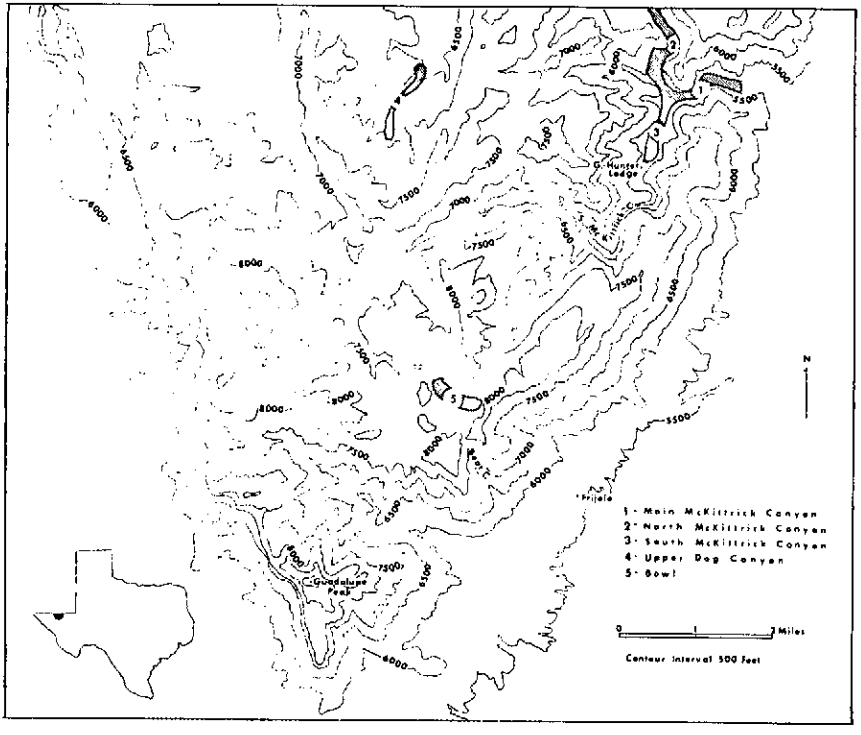


FIG. 1.—Map of southern Guadalupe Mountain region, adapted from the U.S. Geological Survey map of the Guadalupe Peak Quadrangle. Inset shows the relation of the southern Guadalupe Mountains to the remainder of the state of Texas.

the summers of 1973 and 1974, I made intensive surveys of the breeding birds in Main McKittrick Canyon, South McKittrick Canyon, North McKittrick Canyon, Upper Dog Canyon, and The Bowl.

The purposes of this study were: (1) to quantitatively document the breeding avifaunas of relict woodlands of the Southern Guadalupe Mountains; (2) to determine the stability of the breeding avifaunas on a year to year basis; (3) to compare selected breeding avifaunas of the southern Guadalupe Mountains with those previously studied by other scientists in other southwestern mountain ranges.

## METHODS

Five study plots were established in the summer of 1972, one each in the following areas: Main McKittrick Canyon; North McKittrick Canyon; South McKittrick Canyon; Upper Dog Canyon; The Bowl (Fig. 1). In the canyon areas, study plots were established according to the natural terrain and were limited to the canyon floors and lower terraces. The study plot in The Bowl was established in an area showing little disturbance by man. Study plot sizes were constant at 24 acres (9.7 ha) for South McKittrick Canyon, Upper Dog Canyon, and The Bowl. The Main McKittrick and North McKittrick study plots consisted of 30 acres (12.1 ha) and 20 acres (8.1 ha), respectively. The variation in size in the Main McKittrick and North McKittrick plots was due to natural terrain factors which dictated plot boundaries. Plot sizes were determined with the aid of a planimeter and aerial photographs. All boundaries of study plots were identified according to natural features and were constant throughout the 3-year study period.

Expeditions to the Guadalupes lasted from late May through June each summer, 1972 to 1974. Plots were visited in the same rotation each summer—McKittrick Canyon system, then Upper Dog Canyon, and finally The Bowl. All three McKittrick study plots were easily accessible from a camp at Pratt Lodge and time was divided equally among these three areas. Eight to 10 days each summer were spent working Upper Dog Canyon from a camp at the Ranger Station. The Bowl was worked during the latter part of June each summer for a period of 6 to 10 days from a primitive camp.

Vegetation descriptions of the study areas were based on tree data collected by the author, during the summer of 1974, using the Cottam and Curtis (1956) point-quarter method. Only those trees with a minimum circumference of 30 cm were included in the sampling procedure. An analysis of the vegetation of the Guadalupe escarpment has been presented by Gehlbach (1967).

Techniques adapted from Kendeigh (1944) were used to measure the absolute numbers of breeding birds per study plot. A combination of early morning censuses, searches for nests, and limited mist-netting were carried out on each study plot. The steep canyon walls set well-defined limits on canyon plots and so it was possible to determine accurately what birds were truly

breeding within them. Singing-male censuses were taken by slowly walking through the study plots, with periodic pauses to record singing males on specially designed census cards. All singing-male censuses began at sunrise (ca. 06:00 MDST) and lasted about 2 hours (08:00 MDST). Other daylight hours were utilized in searching for nests and in netting activities. The absolute numbers of breeding birds per study area were expanded to the standardized expression, numbers of birds per 100 acres. Observations were augmented by the use of Leitz Trinovid 10 × 40 binoculars.

Of more ecological meaning than numbers of birds per unit area is grams of biomass per unit area. Biomass computations for breeding birds were based on average fresh weights of specimens collected from near the study plots over a 6-year period (1969–1974), except for the weights of the Elf Owl (*Micrathene whitneyi*) and the Blue-throated Hummingbird (*Lampornis clemenciae*) which were taken from specimens in the Texas Cooperative Wildlife Collections of Texas A&M University. Standing crop biomass was computed by multiplying the density of a species by the mean weight of that species.

Consuming biomass, an indication of food consumption, was figured as suggested by Salt (1957). The average weight of each species was raised to the 0.633 power (Karr 1968) and then multiplied by the number of individuals per species present per 100 acres (40.47 ha). The summation of the values thus obtained for each species gives an indication of energy requirement for a given avifauna.

Species were assigned to foraging categories in ways similar to those used by Salt (1953, 1957) and Anderson (1970). Assignment to categories was on the basis of field observations made during the breeding seasons and on the basis of published data on feeding habits of the species under consideration. Where a species fitted into more than one foraging group, it was placed in the group which characterized more than 50 percent of its feeding effort. Categories used in this study were foliage insect, aerial insect, ground insect, timber drilling, timber searching, foliage seed, foliage nectar, ground seed, and ground predator.

Species diversity indices of breeding avifaunas were computed by the Shannon-Weiner index ($H' = -\sum pi \log_e pi$). Coefficients of similarity as described by Beals (1960) were computed and used to compare the avifaunas of each study area.

## RESULTS

### Main McKittrick Canyon

**Habitat Description**—Main McKittrick Canyon cuts deep into the east face of the Guadalupe escarpment. The overall direction of drainage in Main McKittrick is from west to east, though the course of the stream bed varies. From the mouth of Main McKittrick to the junction of North and South McKittrick along the canyon floor is a distance of about 1.8 mi. (2.9 km).

Canyon walls rise abruptly to a height of 2000 ft (610 m) above the canyon floor. The floor of the canyon varies in width but is not much greater than 360 ft (110 m) at its widest sect and gradually narrows towards the west. Elevation of the canyon floor increases from 5000 ft (1524 m) at the mouth of the canyon to 5200 ft (1585 m) at the junction of North and South McKittrick. The vegetational growth form along the canyon floor gradually shifts from shrub and grass domination near the mouth of the canyon to tree domination. Above-ground water exists year-round in Main McKittrick. The stream flow is intermittent in space, alternately flowing above and below ground. This flow is from drainage of precipitation and from active springs in North and South McKittrick canyons.

The east boundary of the Main McKittrick study plot is located about 0.8 mi. (1.3 km) in from the mouth of the canyon and runs a linear distance of about 1.0 mi. (1.6 km).

One hundred and twenty trees were measured on the study plot. A comparison of the relative density, relative dominance, relative frequency, and importance value of trees in Main McKittrick, South McKittrick, North McKittrick, Upper Dog, and The Bowl is shown in Tables 1–4. Wavy-leaf oak (*Quercus undulata*), alligator juniper (*Juniperus deppeana*), and Texas madrone (*Arbutus texana*), were relatively important (Table 4) in Main McKittrick with values of 80.17, 67.81, and 52.52, respectively. Common

TABLE 1. Relative density, obtained by the point-quarter method, of tree species in Main McKittrick (1), North McKittrick (2), South McKittrick (3), Upper Dog (4), and The Bowl (5).

| Species | Relative density | | | | |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 |
| *Quercus undulata* | 32.50 | 16.67 | 11.67 | | |
| *Juniperus deppeana* | 20.00 | 22.50 | 13.33 | 9.00 | 0.83 |
| *Arbutus texana* | 15.83 | 12.50 | 6.11 | 1.00 | |
| *Acer grandidentatum* | 10.00 | 16.67 | 27.22 | 28.50 | |
| *Quercus muhlenbergia* | 7.50 | 20.00 | 25.00 | 38.50 | |
| *Fraxinus velutina* | 5.00 | | 3.89 | | |
| *Pinus ponderosa* | 3.33 | 1.67 | 9.44 | 7.00 | 30.42 |
| *Prunus serotina* | 2.50 | 1.67 | 1.11 | | 0.83 |
| *Juglans microcarpa* | 1.67 | | | | |
| *Juniperus* sp. | 0.83 | | 1.11 | | |
| *Chilopsis linearfolia* | 0.83 | | | | |
| *Ostrya knowltonii* | | 4.17 | | 3.00 | |
| *Juniperus scopulorum* | | 2.50 | | 2.00 | |
| *Pseudotsuga menziesii* | | 1.67 | | 3.50 | 18.33 |
| *Quercus grisea* | | | 1.11 | | |
| *Quercus gambeli* | | | | 7.00 | 17.08 |
| *Juniperus monosperma* | | | | 0.50 | |
| *Pinus flexilis* | | | | | 32.50 |

TABLE 2. Relative dominance, obtained by the point-quarter method, of tree species in Main McKittrick (1), North McKittrick (2), South McKittrick (3), Upper Dog (4), and The Bowl (5).

| Species | Relative dominance | | | | |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 |
| *Quercus undulata* | 23.48 | 10.90 | 7.71 | | |
| *Juniperus deppeana* | 26.15 | 28.36 | 10.98 | 12.45 | 0.40 |
| *Arbutus texana* | 18.64 | 12.80 | 6.43 | 0.78 | |
| *Acer grandidentatum* | 7.08 | 12.25 | 20.97 | 22.20 | |
| *Quercus muhlenbergia* | 8.70 | 25.26 | 31.17 | 36.98 | |
| *Fraxinus velutina* | 5.44 | | 7.21 | | |
| *Pinus ponderosa* | 3.45 | 1.74 | 12.67 | 11.56 | 24.30 |
| *Prunus serotina* | 2.57 | 1.66 | 1.11 | | 0.58 |
| *Juglans microcarpa* | 2.07 | | | | |
| *Juniperus* sp. | 1.64 | | 1.00 | | |
| *Chilopsis linearfolia* | 0.77 | | | | |
| *Ostrya knowltonii* | | 2.37 | | 2.07 | |
| *Juniperus scopulorum* | | 3.13 | | 3.09 | |
| *Pseudotsuga menziesii* | | 1.55 | | 5.01 | 28.89 |
| *Quercus grisea* | | | 0.78 | | |
| *Quercus gambeli* | | | | 5.54 | 11.18 |
| *Juniperus monosperma* | | | | 0.48 | |
| *Pinus flexilis* | | | | | 34.66 |

TABLE 3. Relative frequency, obtained by the point-quarter method, of tree species in Main McKittrick (1), North McKittrick (2), South McKittrick (3), Upper Dog (4), and The Bowl (5).

| Species | Relative frequency | | | | |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 |
| *Quercus undulata* | 24.19 | 15.56 | 11.92 | | |
| *Juniperus deppeana* | 21.66 | 20.62 | 12.69 | 12.12 | 1.28 |
| *Arbutus texana* | 18.05 | 12.84 | 6.92 | 1.52 | |
| *Acer grandidentatum* | 9.75 | 15.56 | 27.31 | 25.76 | |
| *Quercus muhlenbergia* | 8.30 | 19.46 | 23.08 | 32.58 | |
| *Fraxinus velutina* | 6.14 | | 4.23 | | |
| *Pinus ponderosa* | 3.61 | 2.72 | 9.23 | 8.33 | 25.53 |
| *Prunus serotina* | 3.61 | 2.72 | 1.54 | | 1.28 |
| *Juglans microcarpa* | 2.53 | | | | |
| *Juniperus* sp. | 1.08 | | 1.54 | | |
| *Chilopsis linearfolia* | 1.08 | | | | |
| *Ostrya knowltonii* | | 3.89 | | 3.79 | |
| *Juniperus scopulorum* | | 3.89 | | 3.03 | |
| *Pseudotsuga menziesii* | | 2.72 | | 5.30 | 20.43 |
| *Quercus grisea* | | | 1.54 | | |
| *Quercus gambeli* | | | | 6.82 | 20.43 |
| *Juniperus monosperma* | | | | 0.76 | |
| *Pinus flexilis* | | | | | 31.06 |

TABLE 4. Importance value, obtained by the point-quarter method, of tree species in Main McKittrick (1), North McKittrick (2), South McKittrick (3), Upper Dog (4), and The Bowl (5).

| Species | Importance value | | | | |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 |
| *Quercus undulata* | 80.17 | 43.13 | 31.30 | | |
| *Juniperus deppeana* | 67.81 | 71.48 | 37.00 | 33.57 | 2.51 |
| *Arbutus texana* | 52.52 | 38.14 | 19.46 | 3.30 | |
| *Acer grandidentatum* | 26.83 | 44.48 | 75.50 | 76.46 | |
| *Quercus muhlenbergia* | 24.50 | 64.72 | 79.25 | 108.06 | |
| *Fraxinus velutina* | 16.58 | | 15.33 | | |
| *Pinus ponderosa* | 10.39 | 6.13 | 31.34 | 26.89 | 80.25 |
| *Prunus serotina* | 8.68 | 6.05 | 3.76 | | 2.69 |
| *Juglans microcarpa* | 6.27 | | | | |
| *Juniperus* sp. | 3.55 | | 3.65 | | |
| *Chilopsis linearfolia* | 2.68 | | | | |
| *Ostrya knowltonii* | | 10.43 | | 8.86 | |
| *Juniperus scopulorum* | | 9.52 | | 8.12 | |
| *Pseudotsuga menziesii* | | 5.94 | | 13.81 | 67.65 |
| *Quercus grisea* | | | 3.43 | | |
| *Quercus gambeli* | | | | 19.36 | 48.69 |
| *Juniperus monosperma* | | | | 1.74 | |
| *Pinus flexilis* | | | | | 98.22 |

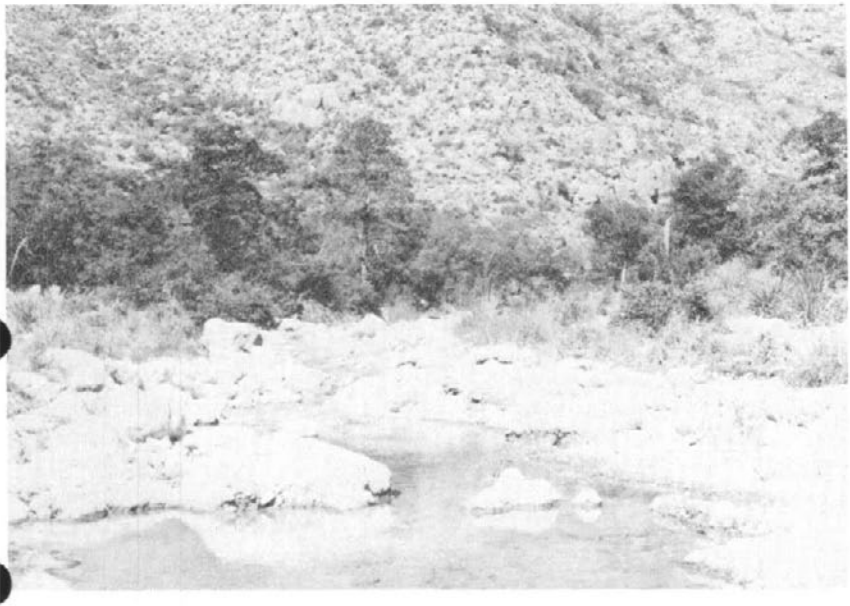

FIG. 2.—Main McKittrick Canyon, Guadalupe Mountains National Park, Texas.

TABLE 5. Density of breeding bird populations in Main McKittrick Canyon for 1972, 1973, and 1974.

| Species | Pairs per 100 acres | | |
|---|---|---|---|
| | 1972 | 1973 | 1974 |
| Blue-gray Gnatcatcher (*Polioptila caerulea*) | 23.3 | 16.7 | 23.3 |
| Bewick's Wren (*Thryomanes bewickii*) | 20.0 | 6.7 | 16.7 |
| Rufous-crowned Sparrow (*Aimophila ruficeps*) | 20.0 | 20.0 | 13.3 |
| Solitary Vireo (*Vireo solitarius*) | 16.7 | 20.0 | 16.7 |
| Black-chinned Sparrow (*Spizella atrogularis*) | 16.7 | 10.0 | 23.3 |
| Canyon Wren (*Catherpes mexicanus*) | 16.7 | 6.7 | 13.3 |
| Black-chinned Hummingbird (*Archilochus alexandri*) | 13.3 | 13.3 | 10.0 |
| Ash-throated Flycatcher (*Myiarchus cinerascens*) | 13.3 | 10.0 | 13.3 |
| Western Tanager (*Piranga ludoviciana*) | 13.3 | 13.3 | 10.0 |
| Cassin's Kingbird (*Tyrannus vociferans*) | 10.0 | 10.0 | 6.7 |
| Western Wood Pewee (*Contopus sordidulus*) | 10.0 | 10.0 | 10.0 |
| Violet-green Swallow (*Tachycineta thalassina*) | 10.0 | 3.3 | 6.7 |
| Bushtit (*Psaltriparus minimus*) | 10.0 | 6.7 | 10.0 |
| Lesser Goldfinch (*Spinus psaltria*) | 10.0 | 6.7 | 3.3 |
| Scott's Oriole (*Icterus parisorum*) | 6.7 | 3.3 | 6.7 |
| Brown-headed Cowbird (*Molothrus ater*) | 6.7 | 6.7 | 6.7 |
| Black-headed Grosbeak (*Pheucticus melanocephalus*) | 6.7 | 10.0 | 13.3 |
| Broad-tailed Hummingbird (*Selaphorus platycercus*) | 3.3 | 0.0 | 6.7 |
| Ladder-backed Woodpecker (*Dendrocopos scalaris*) | 3.3 | 6.7 | 0.0 |
| Scrub Jay (*Aphelocoma coerulescens*) | 3.3 | 3.3 | 0.0 |
| House Wren (*Troglodytes aedon*) | 3.3 | 0.0 | 6.7 |
| Gray Vireo (*Vireo vicinior*) | 3.3 | 0.0 | 0.0 |
| Hepatic Tanager (*Piranga flava*) | 3.3 | 3.3 | 3.3 |
| Blue Grosbeak (*Guiraca caerulea*) | 3.3 | 0.0 | 3.3 |
| House Finch (*Carpodacus mexicanus*) | 3.3 | 0.0 | 0.0 |
| Rufous-sided Towhee (*Pipilo erythrophthalmus*) | 3.3 | 6.7 | 10.0 |
| Virginia's Warbler (*Vermivora virginiae*) | 0.0 | 3.3 | 6.7 |
| Olive-sided Flycatcher[a] (*Nuttallornis borealis*) | 0.0 | 3.3 | 3.3 |
| Elf Owl (*Micrathene whitneyi*) | 0.0 | 3.3 | 0.0 |
| Brown Towhee (*Pipilo fuscus*) | 0.0 | 3.3 | 0.0 |
| Western Flycatcher (*Empidonax difficilis*) | 0.0 | 0.0 | 3.3 |
| Rock Wren (*Salpinctes obsoletus*) | 0.0 | 0.0 | 3.3 |
| Hermit Thrush (*Catharus guttatus*) | 0.0 | 0.0 | 3.3 |
| Warbling Vireo (*Vireo gilvus*) | 0.0 | 0.0 | 3.3 |
| Total | 253.1 | 206.6 | 256.5 |

[a]Breeding status not certain.

shrubs and grasses contributing to the understory in Main McKittrick were *Quercus undulata, Juniperus, deppeana, Acer grandidentatum, Dasylirion leiophyllum, Juglans microcarpa, Agave neomexicana, Yucca elata, Cladium jamaicensis, Bouteloua curtipendula*, and *Tridens muticus*.

Physiognomic aspects of Main McKittrick Canyon are shown in Fig. 2.

**Avifaunal Aspects.**—Densities of the breeding avifaunas of Main McKittrick Canyon for 1972, 1973, and 1974 are presented in Table 5. Thirty-four

TABLE 6. Standing crop biomass (SCB) and consuming biomass (CB) in relation to foraging behavior of breeding bird populations in Main McKittrick Canyon for 1972, 1973, and 1974.

| Species | Mean weight (g) | 1972 SCB 100 acres | 1972 CB 100 acres | 1973 SCB 100 acres | 1973 CB 100 acres | 1974 SCB 100 acres | 1974 CB 100 acres |
|---|---|---|---|---|---|---|---|
| | | | Foliage Insect | | | | |
| Western Tanager | 29.5 | 784.7 | 226.6 | 784.7 | 226.6 | 590.0 | 170.4 |
| Solitary Vireo | 17.6 | 587.8 | 205.2 | 704.0 | 245.7 | 587.8 | 205.2 |
| Black-headed Grosbeak | 43.2 | 578.9 | 145.3 | 864.0 | 216.9 | 1149.1 | 288.5 |
| Scott's Oriole | 38.3 | 513.2 | 134.7 | 252.8 | 66.3 | 513.2 | 134.7 |
| Blue-gray Gnatcatcher | 6.1 | 284.3 | 146.4 | 203.7 | 104.9 | 284.3 | 146.4 |
| Hepatic Tanager | 36.3 | 239.6 | 64.1 | 239.6 | 64.1 | 239.6 | 64.1 |
| Blue Grosbeak | 27.6 | 182.2 | 53.9 | 0.0 | 0.0 | 182.2 | 53.9 |
| Bushtit | 5.7 | 114.0 | 60.2 | 76.4 | 40.3 | 114.0 | 60.2 |
| Gray Vireo | 12.8 | 84.5 | 33.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| Virginia's Warbler | 7.8 | 0.0 | 0.0 | 51.5 | 24.2 | 104.5 | 49.2 |
| Warbling Vireo | 12.9 | 0.0 | 0.0 | 0.0 | 0.0 | 85.1 | 33.3 |
| Subtotal | | 3369.2 | 1069.5 | 3176.7 | 989.0 | 3849.8 | 1205.9 |
| | | | Aerial Insect | | | | |
| Cassin's Kingbird | 47.8 | 956.0 | 231.3 | 956.0 | 231.3 | 640.5 | 154.9 |
| Ash-throated Flycatcher | 31.8 | 845.9 | 237.6 | 636.0 | 178.7 | 845.9 | 237.6 |
| Violet-green Swallow | 14.8 | 296.0 | 110.1 | 97.7 | 36.3 | 198.3 | 73.8 |
| Western Wood Pewee | 12.5 | 250.0 | 98.9 | 250.0 | 98.9 | 250.0 | 98.9 |
| Olive-sided Flycatcher | 30.7 | 0.0 | 0.0 | 202.6 | 57.7 | 202.6 | 57.7 |
| Western Flycatcher | 11.9 | 0.0 | 0.0 | 0.0 | 0.0 | 78.5 | 31.6 |
| Subtotal | | 2347.9 | 677.9 | 2142.3 | 602.9 | 2215.8 | 654.5 |

TABLE 6. (continued)

| Species | Mean weight (g) | 1972 SCB 100 acres | 1972 CB 100 acres | 1973 SCB 100 acres | 1973 CB 100 acres | 1974 SCB 100 acres | 1974 CB 100 acres |
|---|---|---|---|---|---|---|---|
| | | | Ground Seed | | | | |
| Rufous-crowned Sparrow | 19.7 | 788.0 | 263.9 | 788.0 | 263.9 | 524.0 | 175.5 |
| Brown-headed Cowbird | 37.9 | 507.9 | 133.8 | 507.9 | 133.8 | 507.9 | 133.8 |
| Black-chinned Sparrow | 13.3 | 444.2 | 171.8 | 266.0 | 102.9 | 619.8 | 239.8 |
| Rufous-sided Towhee | 36.3 | 239.6 | 64.1 | 486.4 | 130.2 | 726.0 | 194.3 |
| Lesser Goldfinch | 9.2 | 184.0 | 81.5 | 123.3 | 54.6 | 60.7 | 26.9 |
| House Finch | 20.3 | 134.0 | 44.4 | 0.0 | 0.0 | 0.0 | 0.0 |
| Brown Towhee | 46.8 | 0.0 | 0.0 | 308.9 | 75.3 | 0.0 | 0.0 |
| Subtotal | | 2297.7 | 759.5 | 2480.5 | 760.7 | 2438.4 | 770.3 |
| | | | Ground Insect | | | | |
| Bewick's Wren | 9.6 | 384.0 | 167.4 | 128.6 | 56.1 | 320.6 | 139.8 |
| Canyon Wren | 11.3 | 377.4 | 155.0 | 151.4 | 62.2 | 300.6 | 123.4 |
| House Wren | 11.4 | 75.2 | 30.8 | 0.0 | 0.0 | 152.8 | 62.5 |
| Elf Owl | 35.1 | 0.0 | 0.0 | 231.7 | 62.8 | 0.0 | 0.0 |
| Hermit Thrush | 25.8 | 0.0 | 0.0 | 0.0 | 0.0 | 170.3 | 51.7 |
| Rock Wren | 14.9 | 0.0 | 0.0 | 0.0 | 0.0 | 98.3 | 36.5 |
| Subtotal | | 836.6 | 353.2 | 511.7 | 181.1 | 1042.6 | 413.9 |
| | | | Foliage Seed | | | | |
| Scrub Jay | 75.2 | 496.3 | 101.7 | 496.3 | 101.7 | 0.0 | 0.0 |
| Subtotal | | 496.3 | 101.7 | 496.3 | 101.7 | 0.0 | 0.0 |

TABLE 6. (continued)

| Species | Mean weight (g) | 1972 SCB 100 acres | 1972 CB 100 acres | 1973 SCB 100 acres | 1973 CB 100 acres | 1974 SCB 100 acres | 1974 CB 100 acres |
|---|---|---|---|---|---|---|---|
| | | | Timber Drilling | | | | |
| Ladder-backed Woodpecker | 35.1 | 231.7 | 62.8 | 470.3 | 127.4 | 0.0 | 0.0 |
| Subtotal | | 231.7 | 62.8 | 470.3 | 127.4 | 0.0 | 0.0 |
| | | | Foliage Nectar | | | | |
| Black-chinned Hummingbird | 3.3 | 87.8 | 56.6 | 87.8 | 56.6 | 66.0 | 42.6 |
| Broad-tailed Hummingbird | 3.6 | 23.8 | 14.8 | 0.0 | 0.0 | 48.2 | 30.1 |
| Subtotal | | 111.6 | 71.4 | 87.8 | 56.6 | 114.2 | 72.7 |
| Total | | 9691.0 | 3096.0 | 9365.6 | 2819.4 | 9660.8 | 3117.3 |

species were recorded as breeding on the study plot over the 3-year period. Nineteen (56%) of the 34 species were represented as breeding birds in all three of the summers. Fifteen species (44%) were present as breeders in 1 or 2 of the 3 years. The greatest number of breeding species for season was 28 in 1974, followed by 26 in 1972, and 25 in 1973. The highest density of birds occurred in 1974 with 256.5 pairs per 100 acres, followed by 253.1 pairs in 1972, and 206.6 pairs in 1973.

Standing crop biomass and consuming biomass of breeding avifaunas, expanded to reflect grams per 100 acres, are presented in Table 6. The years 1972 and 1974 were similar in total avifaunal biomass. In 1973 standing crop biomass was about 3% lower than it was in 1972 and 1974. Consuming biomass in 1973 showed a decrease of about 9% from 1972 and 1974.

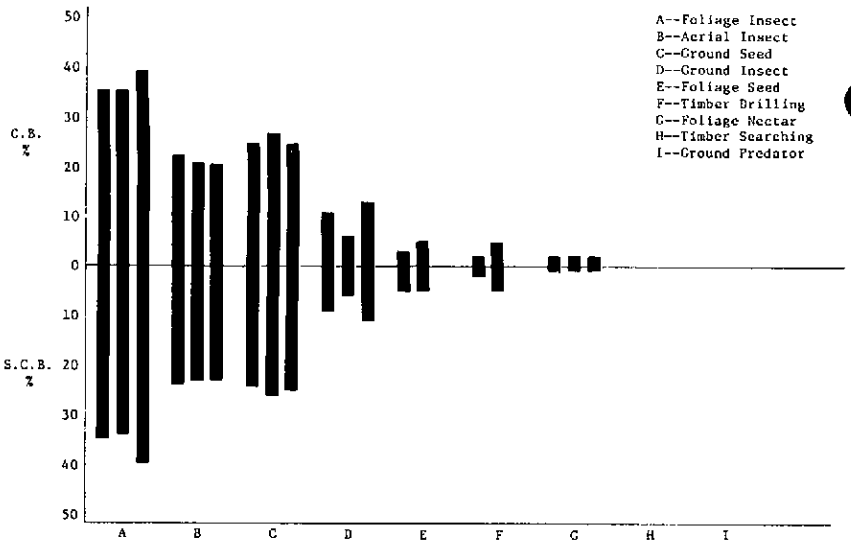


FIG. 3.—Percentage contribution of foraging classes to standing crop biomass (SCB) and consuming biomass (CB) for Main McKittrick Canyon. Bars represent 1972, 1973, and 1974, respectively.

Percentage contributions of each foraging category to standing crop biomass and consuming biomass are shown in Fig. 3. Bird species of the foliage insect category accounted for the greatest percentage of biomass each of the 3 years.

Species diversity for the breeding avifaunas of Main McKittrick Canyon was 3.05 for 1972, 3.04 for 1973, and 3.16 for 1974.

## North McKittrick Canyon

**Habitat Description.**—At the west end of Main McKittrick there is a bifurcation of the canyon into north and south branches. North McKittrick Canyon meanders to the north for a linear distance of about 1.5 mi. (2.4 km) to the New Mexico–Texas state boundary. The canyon floor is narrower than that of Main McKittrick. Above-ground water is limited, except for flash flood conditions, to the northern few hundred yards of my study plot. This plot extends from near the junction of the 3 canyons to the first crossing of the state boundary. Elevation of the canyon floor along the North McKittrick plot gradually increases from 5200 ft (1585 m) at the south end to 5400 ft (1646 m) at the north end. Steep canyon walls rise abruptly from the canyon floor.

Data were collected from a total of 120 trees on this plot. Of the 10 species represented in North McKittrick, alligator juniper and chinquapin oak (*Quercus muhlenbergia*) dominated the landscape (Tables 1–4). Importance values of 71.48 and 64.72, respectively, were recorded (Table 4). Common shrubs contributing to the understory in North McKittrick were *Quercus undulata, Juniperus deppeana, Acer grandidentatum, Dasylirion leiophyllum,* and *Agave neomexicana*. Grass cover is quite limited on the North McKittrick plot.

Figure 4 shows the physiognomy of the vegetation in this canyon.

FIG. 4.—North McKittrick Canyon, Guadalupe Mountains National Park, Texas.

TABLE 7. Density of breeding bird populations in North McKittrick Canyon for 1972, 1973, and 1974.

| Species | Pairs per 100 acres | | |
|---|---|---|---|
| | 1972 | 1973 | 1974 |
| Rufous-sided Towhee (*Pipilo erythrophthalmus*) | 40.0 | 20.0 | 25.0 |
| Solitary Vireo (*Vireo solitarius*) | 35.0 | 20.0 | 45.0 |
| Rufous-crowned Sparrow (*Aimophila ruficeps*) | 30.0 | 30.0 | 35.0 |
| Canyon Wren (*Catherpes mexicanus*) | 30.0 | 25.0 | 30.0 |
| Bewick's Wren (*Thryomanes bewickii*) | 30.0 | 20.0 | 35.0 |
| Blue-gray Gnatcatcher (*Polioptila caerulea*) | 30.0 | 15.0 | 35.0 |
| Black-chinned Hummingbird (*Archilochus alexandri*) | 25.0 | 20.0 | 20.0 |
| Western Wood Pewee (*Contopus sordidulus*) | 25.0 | 10.0 | 20.0 |
| Black-chinned Sparrow (*Spizella atrogularis*) | 20.0 | 20.0 | 35.0 |
| Ash-throated Flycatcher (*Myiarchus cinerascens*) | 20.0 | 20.0 | 25.0 |
| Western Tanager (*Piranga ludoviciana*) | 20.0 | 15.0 | 20.0 |
| Black-headed Grosbeak (*Pheucticus melanocephalus*) | 20.0 | 15.0 | 15.0 |
| Brown-headed Cowbird (*Molothrus ater*) | 15.0 | 5.0 | 10.0 |
| Broad-tailed Hummingbird (*Selasphorus platycercus*) | 10.0 | 10.0 | 25.0 |
| Bushtit (*Psaltriparus minimus*) | 10.0 | 5.0 | 10.0 |
| Scott's Oriole (*Icterus parisorum*) | 10.0 | 5.0 | 10.0 |
| Ladder-backed Woodpecker (*Dendrocopos scalaris*) | 10.0 | 5.0 | 5.0 |
| Lesser Goldfinch (*Spinus psaltria*) | 10.0 | 0.0 | 5.0 |
| Warbling Vireo (*Vireo gilvus*) | 10.0 | 0.0 | 0.0 |
| Violet-green Swallow (*Tachycineta thalassina*) | 10.0 | 0.0 | 0.0 |
| Hermit Thrush (*Catharus guttatus*) | 5.0 | 0.0 | 5.0 |
| Western Flycatcher (*Empidonax difficilis*) | 5.0 | 0.0 | 5.0 |
| Elf Owl (*Micrathene whitneyi*) | 5.0 | 5.0 | 0.0 |
| Cassin's Kingbird (*Tyrannus vociferans*) | 0.0 | 5.0 | 10.0 |
| Rivoli's Hummingbird (*Eugenes fulgens*) | 0.0 | 5.0 | 5.0 |
| Virginia's Warbler (*Vermivora virginiae*) | 0.0 | 0.0 | 5.0 |
| Hepatic Tanager (*Piranga flava*) | 0.0 | 0.0 | 5.0 |
| Total | 425.0 | 275.0 | 440.0 |

**Avifaunal Aspects.**—Twenty-seven breeding species were recorded in North McKittrick Canyon over the 3-year study period (Table 7). Seventeen (63%) of the 27 species were present as breeding birds each summer of the study. Ten species (37%) nested on the study plot only 1 or 2 of the 3 years. Twenty-three, 20, and 24 species were represented for 1972, 1973, and 1974 respectively. Density values ranged from a low of 275.0 pairs per 100 acres in 1973 to a high of 440.0 pairs per 100 acres in 1974. In 1972 there were 425.0 pairs per 100 acres.

Biomass figures differed only slightly for the seasons 1972 and 1974 (Table 8). Corresponding to the marked decrease in density of individuals in 1973, the standing crop biomass was 34% less in 1973 than it was in 1972 and 1974. Consuming biomass showed a decrease of 35% in 1973 compared to 1972 and 1974.

TABLE 8. Standing crop biomass (SCB) and consuming biomass (CB) in relation to foraging behavior of breeding bird populations in North McKittrick Canyon for 1972, 1973, and 1974.

| Species | Mean weight (g) | 1972 SCB 100 acres | 1972 CB 100 acres | 1973 SCB 100 acres | 1973 CB 100 acres | 1974 SCB 100 acres | 1974 CB 100 acres |
|---|---|---|---|---|---|---|---|
| | | | Ground Seed | | | | |
| Rufous-sided Towhee | 36.3 | 2904.0 | 777.2 | 1452.0 | 388.6 | 1815.0 | 485.7 |
| Rufous-crowned Sparrow | 19.7 | 1182.0 | 395.9 | 1182.0 | 395.9 | 1379.0 | 461.8 |
| Brown-headed Cowbird | 37.9 | 1137.0 | 299.5 | 379.0 | 99.8 | 758.0 | 199.7 |
| Black-chinned Sparrow | 13.3 | 532.0 | 205.8 | 532.0 | 205.8 | 931.0 | 360.2 |
| Lesser Goldfinch | 9.2 | 184.0 | 81.5 | 0.0 | 0.0 | 92.0 | 40.7 |
| Subtotal | | 5939.0 | 1759.9 | 3545.0 | 1090.1 | 4975.0 | 1548.1 |
| | | | Foliage Insect | | | | |
| Black-headed Grosbeak | 43.2 | 1728.0 | 433.8 | 1296.0 | 325.4 | 1296.0 | 325.4 |
| Solitary Vireo | 17.6 | 1232.0 | 430.0 | 704.0 | 245.7 | 1584.0 | 552.9 |
| Western Tanager | 29.5 | 1180.0 | 340.8 | 885.0 | 255.6 | 1180.0 | 340.8 |
| Scott's Oriole | 38.3 | 766.0 | 201.0 | 383.0 | 100.5 | 766.0 | 201.0 |
| Blue-gray Gnatcatcher | 6.1 | 366.0 | 188.5 | 183.0 | 94.2 | 427.0 | 219.9 |
| Warbling Vireo | 12.9 | 258.0 | 100.9 | 0.0 | 0.0 | 0.0 | 0.0 |
| Bushtit | 5.7 | 114.0 | 60.2 | 57.0 | 30.1 | 114.0 | 60.2 |
| Hepatic Tanager | 36.3 | 0.0 | 0.0 | 0.0 | 0.0 | 363.0 | 97.1 |
| Virginia's Warbler | 7.8 | 0.0 | 0.0 | 0.0 | 0.0 | 78.0 | 36.7 |
| Subtotal | | 5644.0 | 1755.2 | 3508.0 | 1051.5 | 5808.0 | 1834.0 |

TABLE 8. (continued)

| Species | Mean weight (g) | 1972 SCB 100 acres | 1972 CB 100 acres | 1973 SCB 100 acres | 1973 CB 100 acres | 1974 SCB 100 acres | 1974 CB 100 acres |
|---|---|---|---|---|---|---|---|
| | | | Aerial Insect | | | | |
| Ash-throated Flycatcher | 31.8 | 1272.0 | 357.4 | 1272.0 | 357.4 | 1590.0 | 446.7 |
| Western Wood Pewee | 12.5 | 625.0 | 247.4 | 250.0 | 98.9 | 500.0 | 197.9 |
| Violet-green Swallow | 14.8 | 296.0 | 110.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| Western Flycatcher | 11.9 | 119.0 | 48.0 | 0.0 | 0.0 | 119.0 | 48.0 |
| Cassin's Kingbird | 47.8 | 0.0 | 0.0 | 478.0 | 115.6 | 956.0 | 231.3 |
| Subtotal | | 2312.0 | 762.9 | 2000.0 | 571.9 | 3165.0 | 923.9 |
| | | | Ground Insect | | | | |
| Canyon Wren | 11.3 | 678.0 | 278.5 | 565.0 | 232.0 | 678.0 | 278.5 |
| Bewick's Wren | 9.6 | 576.0 | 251.1 | 384.0 | 167.4 | 672.0 | 293.0 |
| Elf Owl | 35.1 | 351.0 | 95.1 | 351.0 | 95.1 | 351.0 | 95.1 |
| Hermit Thrush | 25.8 | 258.0 | 78.3 | 0.0 | 0.0 | 258.0 | 78.3 |
| Subtotal | | 1863.0 | 703.0 | 1300.0 | 494.5 | 1959.0 | 744.9 |
| | | | Timber Drilling | | | | |
| Ladder-backed Woodpecker | 35.1 | 702.0 | 190.2 | 351.0 | 95.1 | 351.0 | 95.1 |
| Subtotal | | 702.0 | 190.2 | 351.0 | 95.1 | 351.0 | 95.1 |

TABLE 8. (continued)

| Species | Mean weight (g) | 1972 SCB 100 acres | 1972 CB 100 acres | 1973 SCB 100 acres | 1973 CB 100 acres | 1974 SCB 100 acres | 1974 CB 100 acres |
|---|---|---|---|---|---|---|---|
| | | | Foliage Nectar | | | | |
| Black-chinned Hummingbird | 3.3 | 165.0 | 106.5 | 132.0 | 85.2 | 132.0 | 85.2 |
| Broad-tailed Hummingbird | 3.6 | 72.0 | 45.0 | 72.0 | 45.0 | 180.0 | 112.5 |
| Rivoli's Hummingbird | 7.3 | 0.0 | 0.0 | 73.0 | 35.2 | 73.0 | 35.2 |
| Subtotal | | 237.0 | 151.5 | 277.0 | 165.4 | 385.0 | 232.9 |
| Total | | 16697.0 | 5322.7 | 10981.0 | 3468.5 | 16643.0 | 5378.9 |

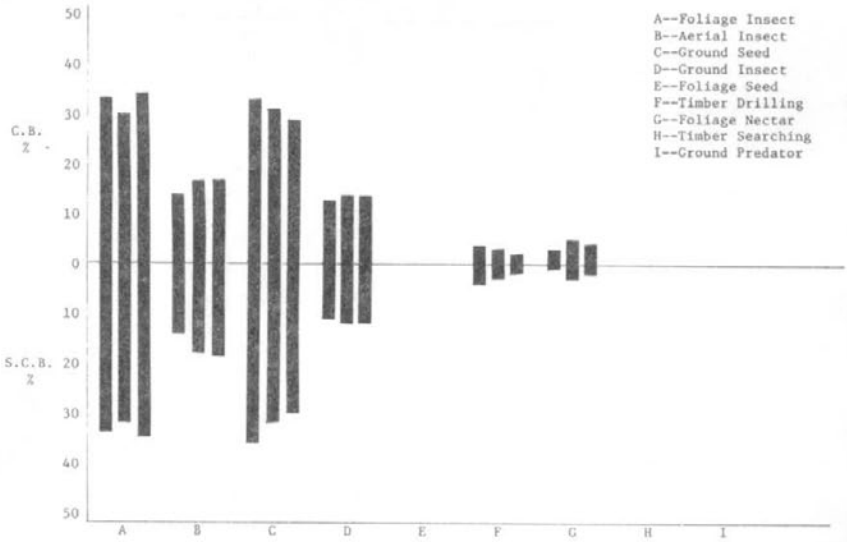


**FIG. 5.**—Percentage contribution of foraging classes to standing crop biomass (SCB) and consuming biomass (CB) for North McKittrick Canyon. Bars represent 1972, 1973, and 1974, respectively.

**FIG. 6.**—South McKittrick Canyon, Guadalupe Mountains National Park, Texas.

Six foraging categories were represented in North McKittrick (Fig. 5). The foliage insect and ground seed foragers were of major importance each year in this area.

Species diversity was 3.00 in 1972, 2.83 in 1973, and 2.95 in 1974.

## South McKittrick Canyon

**Habitat Description.**—The study plot in South McKittrick begins a couple of hundred yards south of the juncture with Main McKittrick and runs linearly about 1.0 mi. (1.6 km) to the site of the old Grisham-Hunter Lodge.

TABLE 9. Density of breeding-bird populations in South McKittrick Canyon for 1972, 1973, and 1974.

| Species | Pairs per 100 acres | | |
|---|---|---|---|
| | 1972 | 1973 | 1974 |
| Solitary Vireo (*Vireo solitarius*) | 33.3 | 25.0 | 25.0 |
| Black-chinned Hummingbird (*Archilochus alexandri*) | 25.0 | 37.5 | 20.8 |
| Bewick's Wren (*Thryomanes bewickii*) | 25.0 | 12.5 | 20.8 |
| Broad-tailed Hummingbird (*Selasphorus platycercus*) | 20.8 | 8.3 | 25.0 |
| Western Wood Pewee (*Contopus sordidulus*) | 16.7 | 29.2 | 29.2 |
| Western Tanager (*Piranga ludoviciana*) | 16.7 | 20.8 | 16.7 |
| Black-headed Grosbeak (*Pheucticus melanocephalus*) | 16.7 | 20.8 | 16.7 |
| Rufous-crowned Sparrow (*Aimophila ruficeps*) | 16.7 | 16.7 | 16.7 |
| Ash-throated Flycatcher (*Myiarchus cinerascens*) | 16.7 | 12.5 | 12.5 |
| Canyon Wren (*Catherpes mexicanus*) | 16.7 | 0.0 | 4.2 |
| Warbling Vireo (*Vireo gilvus*) | 12.5 | 20.8 | 25.0 |
| Black-chinned Sparrow (*Spizella atrogularis*) | 12.5 | 16.7 | 8.3 |
| Violet-green Swallow (*Tachycineta thalassina*) | 12.5 | 8.3 | 12.5 |
| Lesser Goldfinch (*Spinus psaltria*) | 12.5 | 4.2 | 16.7 |
| Blue-gray Gnatcatcher (*Polioptila caerulea*) | 8.3 | 16.7 | 16.7 |
| Rufous-sided Towhee (*Pipilo erythrophthalmus*) | 8.3 | 12.5 | 16.7 |
| Western Flycatcher (*Empidonax difficilis*) | 8.3 | 8.3 | 12.5 |
| Brown-headed Cowbird (*Molothrus ater*) | 8.3 | 4.2 | 12.5 |
| White-breasted Nuthatch (*Sitta carolinensis*) | 8.3 | 0.0 | 4.2 |
| Scott's Oriole (*Icterus parisorum*) | 4.2 | 8.3 | 16.7 |
| Bushtit (*Psaltriparus minimus*) | 4.2 | 8.3 | 12.5 |
| Hepatic Tanager (*Piranga flava*) | 4.2 | 8.3 | 12.5 |
| Mountain Chickadee (*Parus gambeli*) | 4.2 | 8.3 | 8.3 |
| Hairy Woodpecker (*Dendrocopos villosus*) | 4.2 | 8.3 | 8.3 |
| Virginia's Warbler (*Vermivora virginiae*) | 4.2 | 4.2 | 12.5 |
| Grace's Warbler (*Dendroica graciae*) | 4.2 | 4.2 | 12.5 |
| Rivoli's Hummingbird (*Eugenes fulgens*) | 4.2 | 0.0 | 4.2 |
| Ladder-backed Woodpecker (*Dendrocopos scalaris*) | 4.2 | 0.0 | 0.0 |
| Elf Owl (*Micrathene whitneyi*) | 0.0 | 4.2 | 0.0 |
| Blue-throated Hummingbird (*Lampornis clemenciae*) | 0.0 | 4.2 | 0.0 |
| Cassin's Kingbird (*Tyrannus vociferans*) | 0.0 | 4.2 | 0.0 |
| Hermit Thrush (*Catharus guttatus*) | 0.0 | 4.2 | 0.0 |
| Total | 333.6 | 341.7 | 400.2 |

TABLE 10. Standing crop biomass (SCB) and consuming biomass (CB) in relation to foraging behavior of breeding bird populations in South McKittrick Canyon for 1972, 1973, and 1974.

| Species | Mean weight (g) | 1972 | | 1973 | | 1974 | |
|---|---|---|---|---|---|---|---|
| | | SCB 100 acres | CB 100 acres | SCB 100 acres | CB 100 acres | SCB 100 acres | CB 100 acres |
| | | | Foliage Insect | | | | |
| Black-headed Grosbeak | 43.2 | 1442.9 | 362.2 | 1797.1 | 451.2 | 1442.9 | 362.2 |
| Solitary Vireo | 17.6 | 1172.2 | 409.2 | 880.0 | 307.2 | 880.0 | 307.2 |
| Western Tanager | 29.5 | 985.3 | 284.5 | 1227.2 | 354.4 | 985.3 | 284.5 |
| Warbling Vireo | 12.9 | 322.5 | 126.2 | 536.6 | 209.9 | 645.0 | 252.3 |
| Scott's Oriole | 38.3 | 321.7 | 84.4 | 635.8 | 166.8 | 1279.2 | 335.7 |
| Hepatic Tanager | 36.3 | 304.9 | 81.6 | 602.6 | 161.3 | 907.5 | 352.6 |
| Blue-gray Gnatcatcher | 6.1 | 101.3 | 52.1 | 203.7 | 104.9 | 203.7 | 104.9 |
| Mountain Chickadee | 11.4 | 95.3 | 39.1 | 188.4 | 77.3 | 188.4 | 77.3 |
| Grace's Warbler | 8.4 | 70.6 | 32.3 | 70.6 | 32.3 | 210.0 | 96.2 |
| Virginia's Warbler | 7.8 | 65.5 | 30.8 | 65.5 | 30.8 | 195.0 | 91.8 |
| Bushtit | 5.7 | 47.9 | 25.3 | 94.6 | 50.0 | 142.5 | 75.2 |
| Subtotal | | 4930.1 | 1527.7 | 6302.1 | 1946.1 | 7079.5 | 2339.9 |
| | | | Ground Seed | | | | |
| Rufous-crowned Sparrow | 19.7 | 658.0 | 220.4 | 658.0 | 220.4 | 658.0 | 220.4 |
| Brown-headed Cowbird | 37.9 | 629.1 | 165.7 | 318.4 | 83.9 | 947.5 | 249.6 |
| Rufous-sided Towhee | 36.3 | 602.6 | 161.3 | 907.5 | 242.9 | 1212.4 | 324.5 |
| Black-chinned Sparrow | 13.3 | 332.5 | 128.6 | 444.2 | 171.8 | 220.8 | 85.4 |
| Lesser Goldfinch | 9.2 | 230.0 | 101.9 | 77.3 | 34.2 | 307.3 | 136.1 |
| Subtotal | | 2452.2 | 777.9 | 2405.4 | 753.2 | 3346.0 | 1016.0 |

TABLE 10. (continued)

| Species | Mean weight (g) | 1972 SCB 100 acres | 1972 CB 100 acres | 1973 SCB 100 acres | 1973 CB 100 acres | 1974 SCB 100 acres | 1974 CB 100 acres |
|---|---|---|---|---|---|---|---|
| | | | Aerial Insect | | | | |
| Ash-throated Flycatcher | 31.8 | 1062.1 | 298.4 | 795.0 | 223.3 | 795.0 | 223.3 |
| Western Wood Pewee | 12.5 | 417.5 | 165.2 | 730.0 | 288.9 | 730.0 | 288.9 |
| Violet-green Swallow | 14.8 | 370.0 | 137.6 | 245.7 | 91.4 | 370.0 | 137.6 |
| Western Flycatcher | 11.9 | 197.5 | 79.6 | 197.5 | 79.6 | 297.5 | 119.9 |
| Cassin's Kingbird | 47.8 | 0.0 | 0.0 | 401.5 | 97.1 | 0.0 | 0.0 |
| Subtotal | | 2047.1 | 680.8 | 2369.7 | 780.3 | 2192.5 | 769.7 |
| | | | Ground Insect | | | | |
| Bewick's Wren | 9.6 | 480.0 | 209.3 | 240.0 | 104.6 | 399.4 | 174.1 |
| Canyon Wren | 11.3 | 377.4 | 155.0 | 0.0 | 0.0 | 94.9 | 39.0 |
| Elf Owl | 35.1 | 0.0 | 0.0 | 294.8 | 79.9 | 0.0 | 0.0 |
| Hermit Thrush | 25.8 | 0.0 | 0.0 | 216.7 | 65.7 | 0.0 | 0.0 |
| Subtotal | | 857.4 | 364.3 | 751.2 | 250.2 | 494.3 | 213.1 |
| | | | Timber Drilling | | | | |
| Hairy Woodpecker | 60.4 | 506.9 | 112.6 | 1001.8 | 222.5 | 1001.8 | 222.5 |
| Ladder-backed Woodpecker | 35.1 | 294.8 | 79.9 | 0.0 | 0.0 | 0.0 | 0.0 |
| Subtotal | | 801.7 | 192.5 | 1001.8 | 222.5 | 1001.8 | 222.5 |

TABLE 10. (continued)

| Species | Mean weight (g) | 1972 SCB 100 acres | 1972 CB 100 acres | 1973 SCB 100 acres | 1973 CB 100 acres | 1974 SCB 100 acres | 1974 CB 100 acres |
|---|---|---|---|---|---|---|---|
| | | | Foliage Nectar | | | | |
| Black-chinned Hummingbird | 3.3 | 165.0 | 106.5 | 247.5 | 159.7 | 137.3 | 88.6 |
| Broad-tailed Hummingbird | 3.6 | 149.8 | 93.6 | 59.8 | 37.3 | 180.0 | 112.5 |
| Rivoli's Hummingbird | 7.3 | 61.3 | 29.6 | 0.0 | 0.0 | 61.3 | 29.6 |
| Blue-throated Hummingbird | 7.7 | 0.0 | 0.0 | 64.7 | 30.6 | 0.0 | 0.0 |
| Subtotal | | 376.1 | 229.7 | 372.0 | 227.6 | 378.6 | 230.7 |
| | | | Timber Searching | | | | |
| White-breasted Nuthatch | 17.9 | 297.1 | 103.1 | 0.0 | 0.0 | 150.4 | 52.2 |
| Subtotal | | 297.1 | 103.1 | 0.0 | 0.0 | 150.4 | 52.2 |
| Total | | 11761.7 | 3876.0 | 13202.2 | 4179.9 | 14643.1 | 4844.1 |

The stream in this canyon flows above ground in segments and provides a fairly constant water source for wildlife. Elevation at the north end is 5200 ft (1585 m), increasing to 5300 ft (1615 m) at the south end of the plot. As in the other two McKittrick plots, steep canyon walls rise abruptly 2000 ft (610 m) above the canyon floor.

The vegetation in South McKittrick Canyon is dominated by chinquapin oak and big-toothed maple (*Acer grandidentatum*); importance values were 79.25 and 75.50, respectively (Tables 1–4). Ten species were represented among 180 trees sampled. Common shrubs and grasses contributing to the understory in South McKittrick were *Acer grandidentatum, Juniperus deppeana, Quercus undulata, Agave neomexicana, Cladium jamaicensis, Bouteloua curtipendula*, and *Muhlenbergia* sp.

Figure 6 is a view of this study plot.

**Avifaunal Aspects.**—The breeding avifaunas in South McKittrick Canyon were represented by 32 species over the 3-year study period (Table 9). Twenty-four (75%) of these species were present each summer. The total number of species was 28 in 1972, 28 in 1973, and 27 in 1974. Density values ranged from a low of 333.6 pairs per 100 acres in 1972 to 400.2 pairs per 100 acres in 1974. In the summer of 1973, 341.7 pairs per 100 acres were recorded.

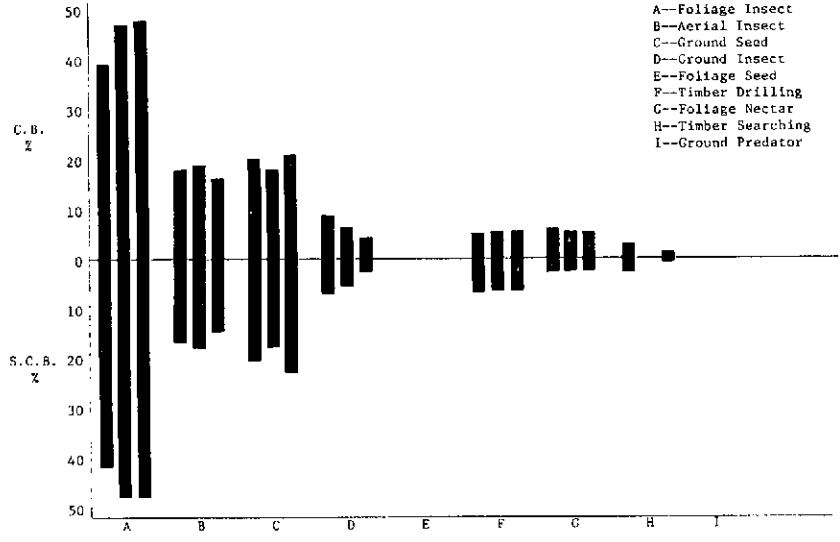


FIG. 7.—Percentage contribution of foraging classes to standing crop biomass (SCB) and consuming biomass (CB) for South McKittrick Canyon. Bars represent 1972, 1973, and 1974, respectively.

Standing crop biomass increased by 12% in 1973 compared to 1972, and by 11% in 1974 compared to 1973 (Table 10). Consuming biomass increased by 8% in 1973 compared to 1972, and by 16% in 1974 compared to 1973.

Figure 7 shows the percentage contribution of each foraging category to total standing crop and consuming biomass for South McKittrick. The foliage insect feeders contribute by far the greatest biomass of the seven categories represented.

Species diversity values were 3.15 in 1972, 3.11 in 1973, and 3.20 in 1974.

## Upper Dog Canyon

**Habitat Description.**—Upper Dog Canyon lies about 3.0 mi. (4.8 km) due west of the McKittrick Canyon system and is separated from that complex by mountainous terrain reaching 7700 ft (2347 m) in elevation. Drainage in Upper Dog Canyon is in a northerly direction. This canyon is dissected by the Texas-New Mexico state boundary. The study plot here runs from about 600 ft (183 m) south of the Dog Canyon Ranger Station along the canyon floor a linear distance of about 1.0 mi. (1.6 km). At the south end of the study area is a spring seepage, the only constant supply of above ground water on this plot. Elevation ranges from 6300 ft (1920 m) to 6700 ft (2042 m).

Tables 1–4 summarize quantitative data respecting trees in Upper Dog Canyon. Two hundred trees belonging to 10 species were sampled. Chinquapin oak dominated the canyon woodland (importance value, IV 108.06) followed in importance by big-toothed maple (IV 76.46). Common shrubs and grasses contributing to the understory in Upper Dog were *Acer grandidentatum, Juniperus deppeana, Agave neomexicana, Opuntia imbricata, Muhlenbergia* sp., and *Stipa tenuissima.*

The physiognomy of this study plot is shown in Fig. 8.

**FIG. 8.**—Upper Dog Canyon, Guadalupe Mountains National Park, Texas.

TABLE 11. Density of breeding bird populations in Upper Dog Canyon for 1972, 1973, and 1974.

| Species | Pairs per 100 acres | | |
|---|---|---|---|
| | 1972 | 1973 | 1974 |
| Western Wood Pewee (*Contopus sordidulus*) | 37.5 | 33.3 | 41.7 |
| Solitary Vireo (*Vireo solitarius*) | 25.0 | 29.2 | 29.2 |
| Black-chinned Hummingbird (*Archilochus alexandri*) | 25.0 | 16.7 | 16.7 |
| Chipping Sparrow (*Spizella passerina*) | 20.8 | 16.7 | 25.0 |
| Warbling Vireo (*Vireo gilvus*) | 20.8 | 16.7 | 25.0 |
| Lesser Goldfinch (*Spinus psaltria*) | 20.8 | 16.7 | 20.8 |
| Blue-gray Gnatcatcher (*Polioptila caerulea*) | 16.7 | 20.8 | 12.5 |
| Western Tanager (*Piranga ludoviciana*) | 16.7 | 16.7 | 16.7 |
| Ash-throated Flycatcher (*Myiarchus cinerascens*) | 16.7 | 16.7 | 16.7 |
| White-breasted Nuthatch (*Sitta carolinensis*) | 16.7 | 16.7 | 12.5 |
| Mountain Chickadee (*Parus gambeli*) | 16.7 | 12.5 | 8.3 |
| House Finch (*Carpodacus mexicanus*) | 16.7 | 16.7 | 4.2 |
| Virginia's Warbler (*Vermivora virginiae*) | 12.5 | 16.7 | 16.7 |
| Grace's Warbler (*Dendroica graciae*) | 12.5 | 12.5 | 16.7 |
| Black-headed Grosbeak (*Pheucticus melanocephalus*) | 12.5 | 12.5 | 12.5 |
| Western Bluebird (*Sialia mexicana*) | 12.5 | 8.3 | 8.3 |
| Rufous-sided Towhee (*Pipilo erythrophthalmus*) | 12.5 | 12.5 | 4.2 |
| Violet-green Swallow (*Tachycineta thalassina*) | 12.5 | 8.3 | 0.0 |
| Pygmy Nuthatch (*Sitta pygmaea*) | 12.5 | 0.0 | 0.0 |
| Canyon Wren (*Catherpes mexicanus*) | 8.3 | 12.5 | 12.5 |
| Brown-headed Cowbird (*Molothrus ater*) | 8.3 | 12.5 | 8.3 |
| Rufous-crowned Sparrow (*Aimophila ruficeps*) | 8.3 | 12.5 | 8.3 |
| Rock Wren (*Salpinctes obsoletus*) | 8.3 | 4.2 | 4.2 |
| Black-chinned Sparrow (*Spizella atrogularis*) | 8.3 | 8.3 | 8.3 |
| Western Flycatcher (*Empidonax difficilis*) | 8.3 | 16.7 | 20.8 |
| Acorn Woodpecker (*Melanerpes formicivorus*) | 8.3 | 4.2 | 4.2 |
| Bewick's Wren (*Thryomanes bewickii*) | 4.2 | 8.3 | 12.5 |
| Broad-tailed Hummingbird (*Selasphorus platycercus*) | 4.2 | 16.7 | 8.3 |
| Hairy Woodpecker (*Dendrocopos villosus*) | 4.2 | 4.2 | 8.3 |
| Hepatic Tanager (*Piranga flava*) | 4.2 | 4.2 | 4.2 |
| Common Flicker (*Colaptes auratus*) | 4.2 | 4.2 | 4.2 |
| Hermit Thrush (*Catharus guttatus*) | 4.2 | 0.0 | 8.3 |
| Scrub Jay (*Aphelocoma coerulescens*) | 4.2 | 0.0 | 4.2 |
| Steller's Jay (*Cyanocitta stelleri*) | 4.2 | 0.0 | 0.0 |
| Cassin's Kingbird (*Tyrannus vociferans*) | 4.2 | 0.0 | 4.2 |
| Cooper's Hawk (*Accipiter cooperii*) | 1.0 | 1.0 | 0.0 |
| Great Horned Owl (*Bubo virginianus*) | 1.0 | 1.0 | 1.0 |
| Bushtit (*Psaltriparus minimus*) | 0.0 | 12.5 | 20.8 |
| Scott's Oriole (*Icterus parisorum*) | 0.0 | 0.0 | 8.3 |
| Yellow-rumped Warbler (*Dendroica coronata*) | 0.0 | 0.0 | 8.3 |
| Rivoli's Hummingbird (*Eugenes fulgens*) | 0.0 | 0.0 | 8.3 |
| House Wren (*Troglodytes aedon*) | 0.0 | 0.0 | 4.2 |
| Total | 435.5 | 423.2 | 459.4 |

TABLE 12. Standing crop biomass (SCB) and consuming biomass (CB) in relation to foraging behavior of breeding bird populations in Upper Dog Canyon for 1972, 1973, and 1974.

| Species | Mean weight (g) | 1972 SCB 100 acres | 1972 CB 100 acres | 1973 SCB 100 acres | 1973 CB 100 acres | 1974 SCB 100 acres | 1974 CB 100 acres |
|---|---|---|---|---|---|---|---|
| | | | Foliage Insect | | | | |
| Black-headed Grosbeak | 43.2 | 1080.0 | 271.1 | 1080.0 | 271.1 | 1080.0 | 271.1 |
| Western Tanager | 29.5 | 985.3 | 284.5 | 985.3 | 284.5 | 985.3 | 284.5 |
| Solitary Vireo | 17.6 | 880.0 | 307.2 | 1027.8 | 358.8 | 1027.8 | 358.8 |
| Warbling Vireo | 12.9 | 536.6 | 209.9 | 430.9 | 168.6 | 645.0 | 252.3 |
| Mountain Chickadee | 11.4 | 380.8 | 155.9 | 285.0 | 116.7 | 189.2 | 77.5 |
| Hepatic Tanager | 36.3 | 304.9 | 81.6 | 304.9 | 81.6 | 304.9 | 81.6 |
| Pygmy Nuthatch | 10.2 | 255.0 | 123.7 | 0.0 | 0.0 | 0.0 | 0.0 |
| Grace's Warbler | 8.4 | 210.0 | 96.2 | 210.0 | 96.2 | 280.6 | 128.5 |
| Blue-gray Gnatcatcher | 6.1 | 203.7 | 104.9 | 253.8 | 130.7 | 152.5 | 78.5 |
| Virginia's Warbler | 7.8 | 195.0 | 91.8 | 260.5 | 122.6 | 260.5 | 122.6 |
| Bushtit | 5.7 | 0.0 | 0.0 | 142.5 | 75.2 | 237.1 | 125.2 |
| Yellow-rumped Warbler | 12.9 | 0.0 | 0.0 | 0.0 | 0.0 | 214.1 | 83.8 |
| Scott's Oriole | 38.3 | 0.0 | 0.0 | 0.0 | 0.0 | 635.8 | 166.8 |
| Subtotal | | 5031.3 | 1726.8 | 4980.7 | 1706.0 | 6012.8 | 2031.2 |

TABLE 12. (continued)

| Species | Mean weight (g) | 1972 SCB 100 acres | 1972 CB 100 acres | 1973 SCB 100 acres | 1973 CB 100 acres | 1974 SCB 100 acres | 1974 CB 100 acres |
|---|---|---|---|---|---|---|---|
| | | | Ground Seed | | | | |
| Rufous-sided Towhee | 36.3 | 907.5 | 242.9 | 907.5 | 242.9 | 304.9 | 81.6 |
| House Finch | 20.3 | 678.0 | 224.6 | 678.0 | 224.6 | 170.5 | 56.5 |
| Brown-headed Cowbird | 37.9 | 629.1 | 165.7 | 947.5 | 249.6 | 629.1 | 165.7 |
| Lesser Goldfinch | 9.2 | 382.7 | 169.5 | 307.3 | 136.1 | 382.7 | 169.5 |
| Rufous-crowned Sparrow | 19.7 | 327.0 | 109.5 | 492.5 | 164.9 | 327.0 | 109.5 |
| Black-chinned Sparrow | 13.3 | 220.8 | 85.4 | 220.8 | 85.4 | 220.8 | 85.4 |
| Subtotal | | 3145.1 | 997.6 | 3553.6 | 1103.5 | 2035.0 | 668.2 |
| | | | Ground Insect | | | | |
| Common Flicker | 137.4 | 1154.2 | 189.5 | 1154.2 | 189.5 | 1154.2 | 189.5 |
| Western Bluebird | 28.0 | 700.0 | 206.1 | 464.8 | 136.8 | 464.8 | 136.8 |
| Chipping Sparrow | 11.6 | 482.6 | 196.3 | 387.4 | 157.6 | 580.0 | 235.9 |
| Rock Wren | 14.9 | 247.3 | 91.8 | 125.2 | 46.4 | 125.2 | 46.4 |
| Hermit Thrush | 25.8 | 216.7 | 65.7 | 0.0 | 0.0 | 428.3 | 129.9 |
| Canyon Wren | 11.3 | 187.6 | 77.0 | 282.5 | 116.0 | 282.5 | 116.0 |
| Bewick's Wren | 9.6 | 80.6 | 35.2 | 159.4 | 69.5 | 240.0 | 104.6 |
| House Wren | 11.4 | 0.0 | 0.0 | 0.0 | 0.0 | 95.8 | 39.2 |
| Subtotal | | 3069.0 | 861.6 | 2573.5 | 715.8 | 3370.8 | 998.3 |

TABLE 12. (continued)

| Species | Mean weight (g) | 1972 SCB 100 acres | 1972 CB 100 acres | 1973 SCB 100 acres | 1973 CB 100 acres | 1974 SCB 100 acres | 1974 CB 100 acres |
|---|---|---|---|---|---|---|---|
| | | | Aerial Insect | | | | |
| Ash-throated Flycatcher | 31.8 | 1062.1 | 298.4 | 1062.1 | 298.4 | 1062.1 | 298.4 |
| Western Wood Pewee | 12.5 | 937.5 | 371.0 | 832.5 | 329.5 | 1042.5 | 412.6 |
| Cassin's Kingbird | 47.8 | 401.5 | 97.1 | 0.0 | 0.0 | 401.5 | 97.1 |
| Violet-green Swallow | 14.8 | 370.0 | 137.6 | 245.7 | 91.4 | 0.0 | 0.0 |
| Western Flycatcher | 11.9 | 197.5 | 79.6 | 397.5 | 160.2 | 495.0 | 199.5 |
| Subtotal | | 2968.6 | 983.7 | 2537.8 | 879.5 | 3001.1 | 1007.6 |
| | | | Foliage Seed | | | | |
| Acorn Woodpecker | 68.1 | 1130.5 | 240.2 | 572.0 | 121.5 | 572.0 | 121.5 |
| Steller's Jay | 100.8 | 846.7 | 155.8 | 0.0 | 0.0 | 0.0 | 0.0 |
| Scrub Jay | 75.2 | 631.7 | 129.4 | 0.0 | 0.0 | 631.7 | 129.4 |
| Subtotal | | 2608.9 | 525.4 | 572.0 | 121.5 | 1203.7 | 250.9 |
| | | | Timber Searching | | | | |
| White-breasted Nuthatch | 17.9 | 597.9 | 207.4 | 597.9 | 207.4 | 447.5 | 155.2 |
| Subtotal | | 597.9 | 207.4 | 597.9 | 207.4 | 447.5 | 155.2 |
| | | | Timber Drilling | | | | |
| Hairy Woodpecker | 60.4 | 507.4 | 112.6 | 507.4 | 112.6 | 1002.6 | 222.6 |
| Subtotal | | 507.4 | 112.6 | 507.4 | 112.6 | 1002.6 | 222.6 |

TABLE 12. (continued)

| Species | Mean weight (g) | 1972 SCB 100 acres | 1972 CB 100 acres | 1973 SCB 100 acres | 1973 CB 100 acres | 1974 SCB 100 acres | 1974 CB 100 acres |
|---|---|---|---|---|---|---|---|
| | | | Foliage Nectar | | | | |
| Black-chinned Hummingbird | 3.3 | 165.0 | 106.5 | 110.2 | 71.1 | 110.2 | 71.1 |
| Broad-tailed Hummingbird | 3.6 | 30.2 | 18.9 | 120.2 | 75.1 | 59.8 | 37.3 |
| Rivoli's Hummingbird | 7.3 | 0.0 | 0.0 | 0.0 | 0.0 | 121.2 | 58.4 |
| Subtotal | | 195.2 | 125.4 | 230.4 | 146.2 | 291.2 | 166.8 |
| Total | | 18123.4 | 5540.5 | 15553.3 | 4992.5 | 17364.7 | 5500.8 |

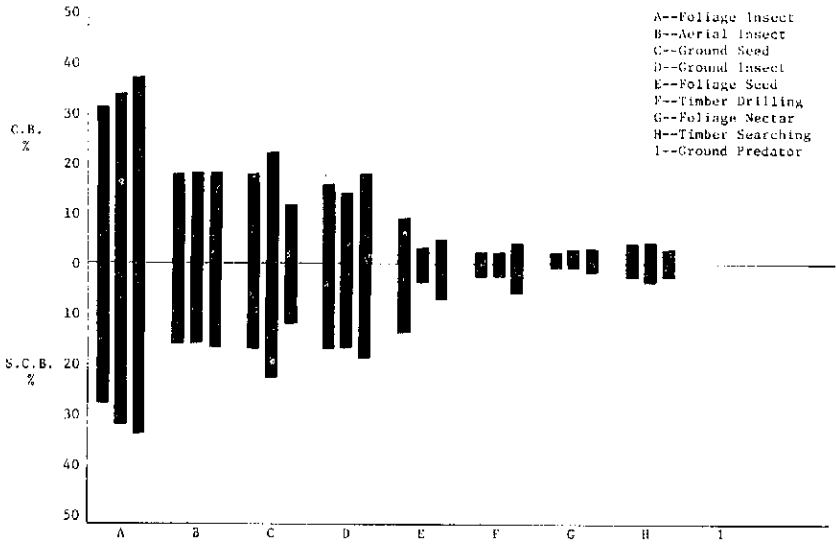


FIG. 9.—Percentage contribution of foraging classes to standing crop biomass (SCB) and consuming biomass (CB) for Upper Dog Canyon. Bars represent 1972, 1973, and 1974, respectively.

**Avifaunal Aspects.**—A total of 42 species utilized the Upper Dog Canyon plot for breeding over the 3-year period (Table 11). Thirty of these species (71%) were represented each summer of the study. Total number of breeding species present each summer was 37 in 1972, 33 in 1973, and 38 in 1974. Density values fluctuated from a low of 423.2 pairs per 100 acres in 1973 to a high of 459.4 pairs per 100 acres in 1974. In 1972 there were 435.5 pairs per 100 acres.

Standing crop biomass and consuming biomass were lowest in 1973 (Table 12). Standing crop biomass was 17% greater in 1972 than in 1973, and 12% greater in 1974 than in 1973. Consuming biomass was 11% greater in 1972 than in 1973, and 10% greater in 1974 than in 1973.

Of the eight foraging classes represented in Upper Dog Canyon, the foliage insect category contributed the highest biomass (standing crop and consuming) percentage (Fig. 9).

Species diversity values were 3.40 in 1972, 3.37 in 1973, 3.43 in 1974.

## The Bowl

**Habitat Description.**—The Bowl contains a conifer-dominated community (Fig. 10) of about 300 acres (121.4 ha) located at the top of Pine Top Mountain. It lacks the weather-moderating influence exerted on the other study areas by steep canyon walls. Gentle slopes lead up to the rims of The Bowl from a low elevation of 7750 ft (2362 m) to 8000 ft (2438 m). Situated in The Bowl is a man-made impoundment created when the land was in pri-

vate ownership. This tank is usually dry during the months of June and July, depending on precipitation. When it is dry, wildlife must obtain drinking water from one of the spring-fed streams of a nearby canyon. The study plot in The Bowl consisted of 24 acres (9.7 ha) situated away from major disturbance areas (e.g., log cabin, surface tank, meadow). This plot was rectangular in shape and ran in an approximately east-west direction along the gentle slope of the south side of The Bowl.

Tables 1–4 summarize data descriptive of the forest on this plot. Limber pine (*Pinus flexilis*), ponderosa pine (*Pinus ponderosa*), and Douglas fir (*Pseudotsuga menziesii*) all show high importance values (98.22, 80.25, and 67.65, respectively). Six species were represented among the 240 trees sampled. The understory in The Bowl consists primarily of young conifers (*Pinus flexilis, Pinus ponderosa, Pseudotsuga menziesii*) with some *Quercus gambeli* and a grass cover of *Muhlenbergia* sp.

**Avifaunal Aspects.**—Total number of breeding species represented in The Bowl study plot over the 3-year period was 32 (Table 13). Of this total, 21 (66%) were present each summer. Numbers of breeding species per year were 25 in 1972, 26 in 1973, and 26 in 1974. Density values were relatively constant—237.5 pairs per 100 acres in 1972, 244.8 pairs per 100 acres in 1973, and 236.3 pairs per 100 acres in 1974.

Standing crop biomass and consuming biomass fluctuated slightly from year to year over the 3-year period (Table 14). The lowest standing crop bio-

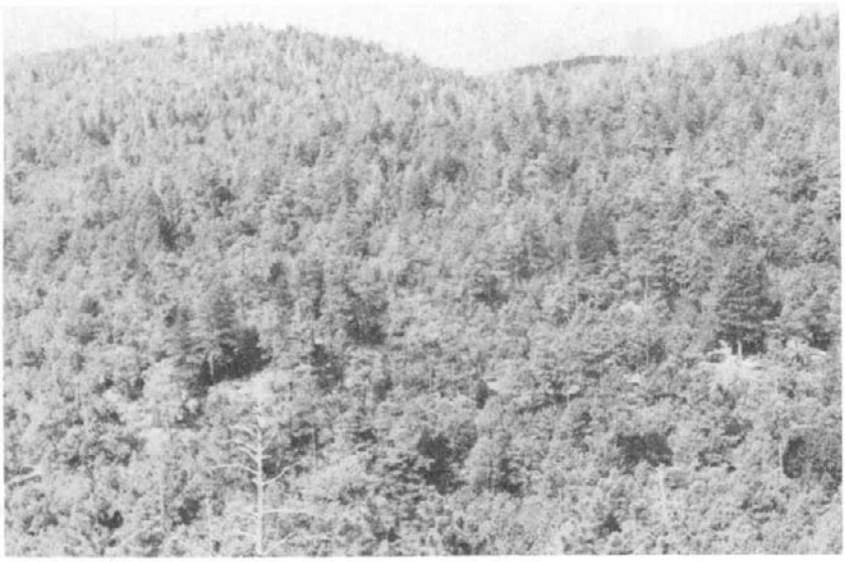

**Fig. 10.**—The Bowl, Guadalupe Mountains National Park, Texas.

mass was in 1973. In 1972 standing crop biomass was 9% greater than in 1973 and in 1974 it was 15% greater than in 1973. There was a 4% greater consuming biomass in 1972 than in 1973, and in 1974 it was 5% greater than in 1973.

Nine foraging categories were represented in The Bowl study plot (Fig. 11). The foliage insect category contributed the highest biomass (standing crop and consuming) percentage. The aerial insect category was greatly reduced in importance in The Bowl as compared to its contribution in the other study areas.

TABLE 13. Density of breeding bird populations in The Bowl for 1972, 1973, and 1974.

| Species | Pairs per 100 acres | | |
|---|---|---|---|
| | 1972 | 1973 | 1974 |
| Gray-headed Junco (*Junco caniceps*) | 33.3 | 25.0 | 20.8 |
| Mountain Chickadee (*Parus gambeli*) | 25.0 | 25.0 | 20.8 |
| Pygmy Nuthatch (*Sitta pygmaea*) | 16.7 | 16.7 | 16.7 |
| Yellow-rumped Warbler (*Dendroica coronata*) | 12.5 | 20.8 | 20.8 |
| White-breasted Nuthatch (*Sitta carolinensis*) | 12.5 | 8.3 | 8.3 |
| Solitary Vireo (*Vireo solitarius*) | 12.5 | 8.3 | 8.3 |
| Red Crossbill (*Loxia curvirostra*) | 12.5 | 0.0 | 0.0 |
| Orange-crowned Warbler (*Vermivora celata*) | 8.3 | 16.7 | 12.5 |
| Rufous-sided Towhee (*Pipilo erythrophthalmus*) | 8.3 | 16.7 | 12.5 |
| Black-headed Grosbeak (*Pheucticus melanocephalus*) | 8.3 | 8.3 | 16.7 |
| Western Flycatcher (*Empidonax difficilis*) | 8.3 | 16.7 | 4.2 |
| Steller's Jay (*Cyanocitta stelleri*) | 8.3 | 8.3 | 8.3 |
| Hermit Thrush (*Catharus guttatus*) | 8.3 | 8.3 | 8.3 |
| Warbling Vireo (*Vireo gilvus*) | 8.3 | 4.2 | 12.5 |
| Hairy Woodpecker (*Dendrocopos villosus*) | 8.3 | 4.2 | 8.3 |
| Common Flicker (*Colaptes auratus*) | 8.3 | 4.2 | 8.3 |
| Western Tanager (*Piranga ludoviciana*) | 4.2 | 8.3 | 8.3 |
| Grace's Warbler (*Dendroica graciae*) | 4.2 | 4.2 | 12.5 |
| Broad-tailed Hummingbird (*Selasphorus platycercus*) | 4.2 | 8.3 | 4.2 |
| Violet-green Swallow (*Tachycineta thalassina*) | 4.2 | 12.5 | 4.2 |
| Brown Creeper (*Certhia familiaris*) | 4.2 | 4.2 | 4.2 |
| Western Bluebird (*Sialia mexicanus*) | 4.2 | 4.2 | 4.2 |
| House Wren (*Troglodytes aedon*) | 4.2 | 4.2 | 0.0 |
| Western Wood Pewee (*Contopus sordidulus*) | 4.2 | 0.0 | 0.0 |
| Blue-throated Hummingbird (*Lampornis clemenciae*) | 4.2 | 0.0 | 0.0 |
| Acorn Woodpecker (*Melanerpes formicivorus*) | 0.0 | 0.0 | 4.2 |
| Whip-poor-will (*Caprimulgus vociferus*) | 0.0 | 4.2 | 4.2 |
| Flammulated Owl (*Otus flammeolus*) | 0.0 | 1.0 | 1.0 |
| Saw-whet Owl (*Aegolius acadicus*) | 0.0 | 1.0 | 0.0 |
| Great Horned Owl (*Bubo virginianus*) | 0.0 | 0.0 | 1.0 |
| Cooper's Hawk (*Accipiter cooperii*) | 0.0 | 1.0 | 0.0 |
| Red-tailed Hawk (*Buteo jamaicensis*) | 0.0 | 0.0 | 1.0 |
| Total | 237.5 | 244.8 | 236.3 |

TABLE 14. Standing crop biomass (SCB) and consuming biomass (CB) in relation to foraging behavior of breeding bird populations in The Bowl for 1972, 1973, and 1974.

| Species | Mean weight (g) | 1972 SCB 100 acres | 1972 CB 100 acres | 1973 SCB 100 acres | 1973 CB 100 acres | 1974 SCB 100 acres | 1974 CB 100 acres |
|---|---|---|---|---|---|---|---|
| | | | Foliage Insect | | | | |
| Black-headed Grosbeak | 43.2 | 717.1 | 180.0 | 717.1 | 180.0 | 1442.9 | 362.2 |
| Mountain Chickadee | 11.4 | 570.0 | 233.3 | 570.0 | 233.3 | 474.2 | 194.1 |
| Solitary Vireo | 17.6 | 440.0 | 153.6 | 292.2 | 102.0 | 292.2 | 102.0 |
| Pygmy Nuthatch | 10.2 | 340.7 | 145.3 | 340.7 | 145.3 | 340.7 | 145.3 |
| Yellow-rumped Warbler | 12.9 | 322.5 | 126.2 | 536.6 | 209.9 | 536.6 | 209.9 |
| Western Tanager | 29.5 | 247.8 | 71.6 | 489.7 | 141.4 | 489.7 | 141.4 |
| Warbling Vireo | 12.9 | 214.1 | 83.8 | 108.4 | 42.4 | 322.5 | 65.1 |
| Orange-crowned Warbler | 8.7 | 144.4 | 65.3 | 290.6 | 131.4 | 217.5 | 98.3 |
| Violet-green Swallow | 14.8 | 124.3 | 46.2 | 370.0 | 137.6 | 124.3 | 46.2 |
| Grace's Warbler | 8.4 | 70.6 | 32.3 | 70.6 | 32.3 | 210.0 | 96.2 |
| Subtotal | | 3191.5 | 1137.6 | 3785.9 | 1355.6 | 4450.6 | 1460.7 |
| | | | Ground Insect | | | | |
| Common Flicker | 137.4 | 2280.8 | 374.5 | 1154.2 | 189.5 | 2280.8 | 374.5 |
| Hermit Thrush | 25.8 | 428.3 | 129.9 | 428.3 | 129.9 | 428.3 | 129.9 |
| Western Bluebird | 28.0 | 235.2 | 69.2 | 235.2 | 69.2 | 235.2 | 69.2 |
| House Wren | 11.4 | 95.8 | 39.2 | 95.8 | 39.2 | 0.0 | 0.0 |
| Flammulated Owl | 48.0 | 0.0 | 0.0 | 96.0 | 23.2 | 96.0 | 23.2 |
| Subtotal | | 3040.1 | 612.8 | 2009.5 | 451.0 | 3040.3 | 596.8 |

TABLE 14. (continued)

| Species | Mean weight (g) | 1972 SCB 100 acres | 1972 CB 100 acres | 1973 SCB 100 acres | 1973 CB 100 acres | 1974 SCB 100 acres | 1974 CB 100 acres |
|---|---|---|---|---|---|---|---|
| | | | Foliage Seed | | | | |
| Steller's Jay | 100.8 | 1673.3 | 307.8 | 1673.3 | 307.8 | 1673.3 | 307.8 |
| Red Crossbill | 33.5 | 837.5 | 230.8 | 0.0 | 0.0 | 0.0 | 0.0 |
| Acorn Woodpecker | 68.1 | 0.0 | 0.0 | 0.0 | 0.0 | 572.0 | 121.5 |
| Subtotal | | 2510.8 | 538.6 | 1673.3 | 307.8 | 2245.3 | 429.3 |
| | | | Ground Seed | | | | |
| Gray-headed Junco | 21.4 | 1425.2 | 463.0 | 1070.0 | 347.6 | 890.2 | 289.2 |
| Rufous-sided Towhee | 36.3 | 602.6 | 161.3 | 1212.4 | 324.5 | 907.5 | 242.9 |
| Subtotal | | 2027.8 | 624.3 | 2282.4 | 672.1 | 1797.7 | 532.1 |
| | | | Timber Drilling | | | | |
| Hairy Woodpecker | 60.4 | 1002.6 | 222.6 | 507.4 | 112.6 | 1002.6 | 222.6 |
| Subtotal | | 1002.6 | 222.6 | 507.4 | 112.6 | 1002.6 | 222.6 |
| | | | Timber Searching | | | | |
| White-breasted Nuthatch | 17.9 | 447.5 | 155.2 | 297.1 | 103.1 | 297.1 | 103.1 |
| Brown Creeper | 8.4 | 70.6 | 32.3 | 70.6 | 32.3 | 70.6 | 32.3 |
| Subtotal | | 518.1 | 187.5 | 367.7 | 135.4 | 367.7 | 135.4 |

TABLE 14. (continued)

| Species | Mean weight (g) | 1972 SCB 100 acres | 1972 CB 100 acres | 1973 SCB 100 acres | 1973 CB 100 acres | 1974 SCB 100 acres | 1974 CB 100 acres |
|---|---|---|---|---|---|---|---|
| | | | Aerial Insect | | | | |
| Western Flycatcher | 11.9 | 197.5 | 79.6 | 397.5 | 160.2 | 100.0 | 40.3 |
| Western Wood Pewee | 12.5 | 105.0 | 41.6 | 0.0 | 0.0 | 0.0 | 0.0 |
| Whip-poor-will | 47.8 | 0.0 | 0.0 | 401.5 | 97.1 | 401.5 | 97.1 |
| Subtotal | | 302.5 | 121.2 | 799.0 | 257.3 | 501.5 | 137.4 |
| | | | Foliage Nectar | | | | |
| Blue-throated Hummingbird | 7.7 | 64.7 | 30.6 | 0.0 | 0.0 | 0.0 | 0.0 |
| Broad-tailed Hummingbird | 3.6 | 30.2 | 18.9 | 59.8 | 37.3 | 30.2 | 18.9 |
| Subtotal | | 94.9 | 49.5 | 59.8 | 37.3 | 30.2 | 18.9 |
| | | | Ground Predator | | | | |
| Saw-whet Owl | 89.0 | 0.0 | 0.0 | 178.0 | 34.3 | 0.0 | 0.0 |
| Subtotal | | 0.0 | 0.0 | 178.0 | 34.3 | 0.0 | 0.0 |
| Total | | 12688.3 | 3494.1 | 11663.0 | 3363.4 | 13435.9 | 3533.2 |

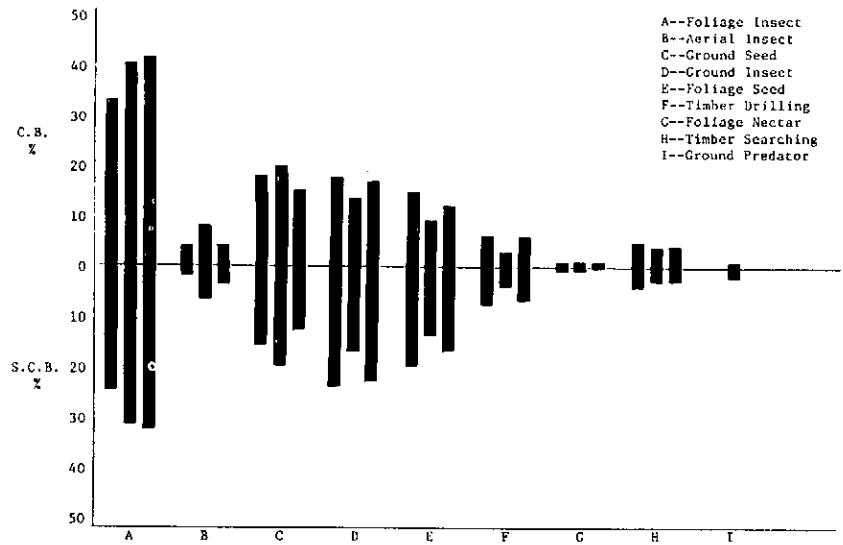


Fig. 11.—Percentage contribution of foraging classes to standing crop biomass (SCB) and consuming biomass (CB) for The Bowl. Bars represent 1972, 1973, and 1974, respectively.

Species diversity values were fairly constant for each of the 3 years—3.02 in 1972, 2.98 in 1973, 3.03 in 1974.

**Avifaunal Comparisons**

Table 15 compares all breeding bird species recorded during 1972, 1973, and 1974, for each of the woodland habitats under consideration in this study. Of the 57 species represented, four (Solitary Vireo, Western Tanager, Black-headed Grosbeak, Rufous-sided Towhee) were successful in meeting their needs each year in all of the study areas. Six other species (Western Wood Pewee, Violet-green Swallow, Broad-tailed Hummingbird, Western Flycatcher, Hermit Thrush, Warbling Vireo) were recorded in all habitats under consideration, but did not occur each year in all areas. The Western Wood Pewee was a marginal breeding species in the conifer-dominated Bowl, being found there only in 1972. The preferred habitat of this species in the Guadalupes was that of the deciduous woodlands which provided more desirable nesting sites and more open canopy better suited to its feeding behavior. Violet-green Swallows were recorded nesting only 1 year in North McKittrick Canyon and 2 years in Upper Dog Canyon. A small number of suitable nesting sites and therfore increased competition by other hole-nesters for available sites may account for the fluctuations of this species. Broad-tailed Hummingbirds nested in all habitats studied but were present only in 1972 and 1974 in Main McKittrick Canyon. This species is probably

TABLE 15. Breeding bird species of Guadalupe woodlands, 1972, 1973, and 1974. Species presence noted by X.

| | Study Areas | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Main McKittrick | | | North McKittrick | | | South McKittrick | | | Upper Dog | | | The Bowl | | |
| Species | 1972 | 1973 | 1974 | 1972 | 1973 | 1974 | 1972 | 1973 | 1974 | 1972 | 1973 | 1974 | 1972 | 1973 | 1974 |
| Gray Vireo | X | | | | | | | | | | | | | | |
| Brown Towhee | | X | | | | | | | | | | | | | |
| Olive-Sided Flycatcher | | X | X | | | | | | | | | | | | |
| Blue Grosbeak | X | | X | | | | | | | | | | | | |
| Elf Owl | | X | | X | X | | | X | | | | | | | |
| Ladder-backed Woodpecker | X | X | | X | X | X | X | | | | | | | | |
| House Finch | X | | | | | | | | | X | X | X | | | |
| Rock Wren | | | X | | | | | | | X | X | X | | | |
| Scrub Jay | X | X | | | | | | | | X | | X | | | |
| Cassin's Kingbird | X | X | X | | X | X | | X | | X | | X | | | |
| Scott's Oriole | X | X | X | X | X | X | X | X | X | | | X | | | |
| Bushtit | X | X | X | X | X | X | X | X | X | | X | X | | | |
| Virginia's Warbler | | X | X | | | X | X | X | X | X | X | X | | | |
| Canyon Wren | X | X | X | X | X | X | X | | X | X | X | X | | | |
| Lesser Goldfinch | X | X | X | X | | X | X | X | X | X | X | X | | | |
| Hepatic Tanager | X | X | X | | | X | X | X | X | X | X | X | | | |
| Blue-gray Gnatcatcher | X | X | X | X | X | X | X | X | X | X | X | X | | | |
| Bewick's Wren | X | X | X | X | X | X | X | X | X | X | X | X | | | |
| Rufous-crowned Sparrow | X | X | X | X | X | X | X | X | X | X | X | X | | | |
| Black-chinned Sparrow | X | X | X | X | X | X | X | X | X | X | X | X | | | |
| Black-chinned Hummingbird | X | X | X | X | X | X | X | X | X | X | X | X | | | |
| Ash-throated Flycatcher | X | X | X | X | X | X | X | X | X | X | X | X | | | |
| Brown-headed Cowbird | X | X | X | X | X | X | X | X | X | X | X | X | | | |
| Western Wood Pewee | X | X | X | X | X | X | X | X | X | X | X | X | X | | |
| Solitary Vireo | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| Western Tanager | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |

TABLE 15. (continued).

| Species | Study Areas | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Main McKittrick | | | North McKittrick | | | South McKittrick | | | Upper Dog | | | The Bowl | | |
| | 1972 | 1973 | 1974 | 1972 | 1973 | 1974 | 1972 | 1973 | 1974 | 1972 | 1973 | 1974 | 1972 | 1973 | 1974 |
| Black-headed Grosbeak | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| Rufous-sided Towhee | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| Violet-green Swallow | X | X | X | X | | | X | X | X | X | X | | X | X | X |
| Broad-tailed Hummingbird | X | | X | X | X | X | X | X | X | X | X | X | X | X | X |
| Western Flycatcher | | | X | X | | X | X | X | X | X | X | X | X | X | X |
| Hermit Thrush | | | X | X | | X | | X | | X | | X | X | X | X |
| Warbling Vireo | | | X | X | | | X | X | X | X | X | X | X | X | X |
| House wren | X | | X | | | | | | | | | X | X | X | |
| Mountain Chickadee | | | | | | | X | X | X | X | X | X | X | X | X |
| Rivoli's Hummingbird | | | | | X | X | X | | X | | | X | | | |
| Chipping Sparrow | | | | | | | | | | X | X | X | | | |
| Hairy Woodpecker | | | | | | | X | X | X | X | X | X | X | X | X |
| Grace's Warbler | | | | | | | X | X | X | X | X | X | X | X | X |
| White-breasted Nuthatch | | | | | | | X | | X | X | X | X | X | X | X |
| Blue-throated Hummingbird | | | | | | | | X | | | | | X | | |
| Western Bluebird | | | | | | | | | | X | X | X | X | X | X |
| Common Flicker | | | | | | | | | | X | X | X | X | X | X |
| Acorn Woodpecker | | | | | | | | | | X | X | X | | | X |
| Great Horned Owl | | | | | | | | | | X | X | X | | | X |
| Cooper's Hawk | | | | | | | | | | X | X | | | X | |
| Pygmy Nuthatch | | | | | | | | | | X | | | X | X | X |
| Yellow-rumped Warbler | | | | | | | | | | | | X | X | X | X |
| Steller's Jay | | | | | | | | | | X | | | X | X | X |
| Gray-headed Junco | | | | | | | | | | | | | X | X | X |

TABLE 15. (continued)

| Species | Study Areas | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Main McKittrick | | | North McKittrick | | | South McKittrick | | | Upper Dog | | | The Bowl | | |
| | 1972 | 1973 | 1974 | 1972 | 1973 | 1974 | 1972 | 1973 | 1974 | 1972 | 1973 | 1974 | 1972 | 1973 | 1974 |
| Orange-crowned Warbler | | | | | | | | | | | | | X | X | X |
| Brown Creeper | | | | | | | | | | | | | X | X | X |
| Whip-poor-will | | | | | | | | | | | | | | X | X |
| Flammulated Owl | | | | | | | | | | | | | | X | X |
| Red Crossbill | | | | | | | | | | | | | X | | |
| Saw-whet Owl | | | | | | | | | | | | | | X | |
| Red-tailed Hawk | | | | | | | | | | | | | | | X |

dependent on a food source provided by more mesically adapted flowering vegetation than is consistently found in Main McKittrick. The Western Flycatcher, Hermit Thrush, and Warbling Vireo found the lower canyon systems suitable only as marginal habitats. These species were consistent breeders in the more mesic communities of the higher elevation.

Four species (Blue Grosbeak, Olive-sided Flycatcher, Gray Vireo, Brown Towhee) were found only in Main McKittrick. Three of these species (Blue Grosbeak, Gray Vireo, Brown Towhee) were found more commonly near the mouth of Main McKittrick than on the census plot. As environmental factors fluctuate from year to year these more xerically adapted species may move, during the drier years, further into Main McKittrick. Olive-sided Flycatchers were recorded consistently, during the breeding season in 1973 and 1974, only in Main McKittrick. I list this species as a potential nesting species as I have no definite proof that it successfully nested.

There were no species found only in North McKittrick or only in South McKittrick. One species (Chipping Sparrow) was unique to Upper Dog Canyon. There were several species which were found only in the coniferous forest community of The Bowl. These species were Gray-headed Junco, Orange-crowned Warbler, Brown Creeper, Whip-poor-will, Flammulated Owl, Red Crossbill, Saw-whet Owl, and Red-tailed Hawk. Eight species (Western Bluebird, Acorn Woodpecker, Common Flicker, Great Horned Owl, Cooper's Hawk, Pygmy Nuthatch, Yellow-rumped Warbler, and Steller's Jay) were found in both Upper Dog Canyon and The Bowl. The inconsistency shown in the data for owls may be due to difficulty in gathering owl data rather than a true indication of presence or absence.

## DISCUSSION

The greatest avifaunal species diversity (total number of species and Shannon–Weiner index), density, standing crop biomass, and consuming biomass occurred consistently throughout the 3-year study period in Upper Dog Canyon (Table 16). The elevation and terrain of Upper Dog Canyon, being intermediate between that of The Bowl and the McKittrick Canyon system, allows for mixing of tree species creating a transitional zone between the two extremes. The greater structural diversity of the vegetation in Upper Dog thereby presents conditions allowing a greater avifaunal complexity.

Stability of breeding avifaunas from year to year as judged by biomass computations, number of species, and species diversity was best maintained in The Bowl and Upper Dog Canyon communities. Due to terrain features, the vegetational aspects of these two communities are less likely to suffer flash flooding disturbances than are vegetational communities of the McKittrick system. The greater vegetational stability of The Bowl and Upper Dog Canyon communities accounts for the greater stability in breeding avifaunas of these two areas. Flash flooding in the McKittrick system creates dynamic vegetational communities along the canyon floors

TABLE 16. A comparison of total numbers of species, Shannon–Weiner Index, density (pairs per 100 acres), standing crop biomass (SCB), and consuming biomass (CB), for breeding avifaunas of selected woodlands of the southern Guadalupe Mountains.

| Study area and year | Total species | Shannon–Weiner index | Pairs per 100 acres | SCB (g per 100 acres) | CB (g per 100 acres) |
|---|---|---|---|---|---|
| Main McKittrick | | | | | |
| 1972 | 26 | 3.05 | 253.1 | 9691.0 | 3096.0 |
| 1973 | 25 | 3.04 | 206.6 | 9365.6 | 2819.4 |
| 1974 | 28 | 3.16 | 256.5 | 9660.8 | 3117.3 |
| North McKittrick | | | | | |
| 1972 | 23 | 3.00 | 425.0 | 16697.0 | 5322.7 |
| 1973 | 20 | 2.83 | 275.0 | 10981.0 | 3468.5 |
| 1974 | 24 | 2.95 | 440.0 | 16643.0 | 5378.9 |
| South McKittrick | | | | | |
| 1972 | 28 | 3.15 | 333.6 | 11761.7 | 3876.0 |
| 1973 | 28 | 3.11 | 341.7 | 13202.2 | 4179.9 |
| 1974 | 27 | 3.20 | 400.2 | 14643.1 | 4844.1 |
| Upper Dog | | | | | |
| 1972 | 37 | 3.40 | 435.5 | 18123.4 | 5540.5 |
| 1973 | 33 | 3.37 | 423.2 | 15553.3 | 4992.5 |
| 1974 | 38 | 3.43 | 459.4 | 17364.7 | 5500.8 |
| The Bowl | | | | | |
| 1972 | 25 | 3.02 | 237.5 | 12688.3 | 3494.1 |
| 1973 | 26 | 2.98 | 244.8 | 11663.0 | 3363.4 |
| 1974 | 26 | 3.03 | 236.3 | 13435.9 | 3533.2 |

This disturbance is reflected in the relatively unstable breeding avifaunas of Main, North, and South McKittrick canyons. North McKittrick is more susceptible to severe flooding than is South McKittrick. The breeding avifauna of North McKittrick was the least stable of all.

Percentage contributions by foraging categories of total biomass varied only slightly from year to year in each of the communities studied. Foliage insect and ground seed (including fruit) foragers contributed heavily to the avifaunal composition of all five communities. The more open vegetative canopy of the canyon systems favored more utilization by aerial insect feeders than did the more closed canopy of The Bowl.

Seven foraging classes were represented in Main McKittrick Canyon (Fig. 3). The increase shown in the foliage insect class for 1974 was due primarily to an increase in the breeding population of Black-headed Grosbeaks. Yearly fluctuations in the ground insect class resulted from a decrease in Bewick's Wrens and House Wrens in 1973 and the utilization of this habitat by Hermit Thrushes and Rock Wrens in 1974. The percentage contribution

of the foliage seed class was reduced to zero in 1974 because of the absence of Scrub Jays. The Ladder-backed Woodpecker did not utilize the Main McKittrick study area in 1974, thereby reducing the percentage contribution of the timber drilling class to zero for that year. The foraging categories timber searching and ground predator were not represented on the study plot in Main McKittrick Canyon.

Six foraging classes were represented in North McKittrick Canyon (Fig. 5). The foliage seed category, represented by Scrub Jays in Main McKittrick Canyon, was absent in this community. Percentage contributions by foraging classes remained fairly constant throughout the 3-year study period, even though there was a reduced gross avifaunal biomass in North McKittrick Canyon in 1973 (Table 8). The reduced total biomass could therefore be attributed to a reduction during 1973 in several food sources, both vegetative and insect.

Seven foraging classes are represented in South McKittrick Canyon (Fig. 7). The timber-searching category, absent in Main and North McKittrick, was represented by White-breasted Nuthatches in this community. Foliage insects remain the most important source of food supporting the avifauna in this area. The percentage contribution of this category to consuming biomass increased from 39 percent in 1972 to 47 percent in 1973. Nearly all bird populations belonging to this foraging category increased in 1973 with the exception of Solitary Vireos (Table 10). The percentage contribution of the ground-insect class dropped in consuming biomass from 9 percent in 1972 to a low of 4 percent in 1974. This change was due primarily to a decreased utilization of the study area by Canyon Wrens. White-breasted Nuthatches did not nest on the study plot in 1973, thereby reducing the percentage contribution of the timber-searching category to zero for that year.

Eight foraging classes were represented each year in Upper Dog Canyon (Fig. 9). The increase in percentage contribution from 1972 to 1973 shown in the foliage-insect category was influenced by increases in Solitary Vireos, Blue-gray Gnatcatchers, and Virginia's Warblers (Table 12). A further increase in 1974 can be attributed to population increases in Warbling Vireos, Grace's Warblers, Bushtits, Yellow-rumped Warblers, and Scott's Orioles. An increase in the percentage contribution of the ground-seed category in 1973 resulted from increases in Brown-headed Cowbirds and Rufous-crowned Sparrows. The drop in percentage contribution in the foliage-seed category from 1972 to 1973 is the result of reduced utilization by Acorn Woodpeckers and an absence of Steller's and Scrub Jays in 1973. Scrub Jays once again utilized this study area in 1974.

Nine foraging classes were represented in The Bowl (Fig. 11). The ground-predator category was represented by Saw-whet Owls which utilized this study area in 1973. Aerial insects as an avifaunal food source contributed considerably less to total consuming biomass in The Bowl than they did in the other study areas. The increase shown in this category from 1972 to 1973 resulted in part from increases in populations of Yellow-rumped Warblers, Western Tanagers, Orange-crowned Warblers, and

TABLE 17. Coefficients of similarity of breeding avifaunas between Main McKittrick, North McKittrick, South McKittrick, Upper Dog, and The Bowl for 1972, 1973, and 1974.

| Study area | Main McKittrick | North McKittrick | South McKittrick | Upper Dog | The Bowl |
|---|---|---|---|---|---|
| | | 1972 | | | |
| Main McKittrick | 1.00 | 0.66 | 0.67 | 0.50 | 0.17 |
| North McKittrick | 0.66 | 1.00 | 0.73 | 0.54 | 0.19 |
| South McKittrick | 0.67 | 0.73 | 1.00 | 0.64 | 0.29 |
| Upper Dog | 0.50 | 0.54 | 0.64 | 1.00 | 0.39 |
| The Bowl | 0.17 | 0.19 | 0.29 | 0.39 | 1.00 |
| | | 1973 | | | |
| Main McKittrick | 1.00 | 0.71 | 0.62 | 0.52 | 0.16 |
| North McKittrick | 0.71 | 1.00 | 0.66 | 0.52 | 0.19 |
| South McKittrick | 0.62 | 0.66 | 1.00 | 0.69 | 0.30 |
| Upper Dog | 0.52 | 0.52 | 0.69 | 1.00 | 0.34 |
| The Bowl | 0.16 | 0.19 | 0.30 | 0.34 | 1.00 |
| | | 1974 | | | |
| Main McKittrick | 1.00 | 0.66 | 0.60 | 0.55 | 0.24 |
| North McKittrick | 0.66 | 1.00 | 0.65 | 0.53 | 0.17 |
| South McKittrick | 0.60 | 0.65 | 1.00 | 0.72 | 0.33 |
| Upper Dog | 0.55 | 0.53 | 0.72 | 1.00 | 0.35 |
| The Bowl | 0.24 | 0.17 | 0.33 | 0.35 | 1.00 |

Violet-green Swallows. A reduction in the Common Flicker population was in part responsible for the decrease in percentage contribution shown for the ground–insect category in 1973. Red Crossbills accounted for the higher percentage shown in the foliage–seed category for 1972, and the addition of Acorn Woodpeckers in 1974 accounted for the increase of that year. Fluctuations in the timber–drilling category were caused by reduced numbers of Hairy Woodpeckers, the only member of this category, in 1973.

A comparison of the avifaunal communities using the coefficient of similarity as described by Beals (1960) shows, as would be expected, that the canyon systems were much more similar to each other than they were to The Bowl (Table 17). Coefficient of similarity values ranged from zero, for those avifaunal communities least alike, to 1.00 for identical communities. The most avifaunally distinct communities were those at the elevation extremes (Main McKittrick as compared to The Bowl). Upper Dog Canyon and South McKittrick Canyon had relatively similar avifaunas, as did the contiguous canyons of the McKittrick system.

Comparable data to that collected for The Bowl were provided for coniferous forest regions of Arizona by Carothers et al. (1973). They found in a ponderosa pine community of the San Francisco Mountains a breeding avifauna consisting of 23 species, 232 pairs per 100 acres, 15,993 g per 100

acres standing crop biomass, 3835.9 g per 100 acres consuming biomass, and species diversity (Shannon–Weiner index) equal to 2.83. The Arizona study also included a fir, pine, aspen community and gave the following results: 27 species; 253 pairs per 100 acres; 16,011 g per 100 acres standing crop biomass; 3936.5 g per 100 acres consuming biomass; species diversity equal to 2.92. The Guadalupe Bowl has 18 and 19 breeding species, respectively, in common with the ponderosa pine and fir, pine, aspen communities of the San Francisco Mountains. Species diversity in The Bowl was slightly higher than that shown for either community of the Arizona study. In pairs per 100 acres The Bowl was intermediate between the two Arizona sites. Standing crop biomass and consuming biomass were less in The Bowl than in either Arizona community. The size and sources of the statistical samples used to determine bird weights may account for discrepancies in biomass computations between the two geographical locations.

Snyder (1950) reported on the breeding avifaunas of three different coniferous plant communities in the mountains of Colorado. Population densities per 100 acres were 102 pairs in Douglas fir–ponderosa pine, 94 pairs in Engelmann spruce–subalpine fir, and 59 pairs in lodgepole pine. More than twice as many breeding pairs per 100 acres occurred in the coniferous forest region of The Bowl than in the Douglas fir–ponderosa pine community of Colorado.

Wauer (1971) reported 42 breeding species in the deciduous woodland communities of the Chisos Mountains. The combined number of breeding species for comparable deciduous woodland associations (McKittrick Canyon system and Upper Dog Canyon) of the Guadalupe Mountains was 45.

Tatschl (1967) found 31 breeding species with a density of 425 breeding pairs per 100 acres in the ponderosa pine community of the Sandia Mountains of New Mexico. This compares to 32 breeding species and 245 breeding pairs per 100 acres in the Guadalupe Bowl.

Salt (1957) stated that the efficiency of an avifauna in terms of energy use is indicated by the ratio of consuming biomass to standing crop biomass. The smaller the value of the ratio, the more efficient is the avifauna. Salt's premise is based on the fact that large birds require less food per gram of body weight than do small birds. Of the Guadalupe communities studied, The Bowl had the lowest consuming biomass to standing crop biomass (CB/SCB) ratio (0.28 in 1972, 0.29 in 1973, 0.26 in 1974). The CB/SCB ratio of the canyon woodlands ranged from 0.30 to 0.33. Carothers et al. (1971) found CB/SCB ratios of 0.25 and 0.24, respectively, in the fir, pine, aspen community and in the ponderosa pine community of the San Francisco Mountains in Arizona.

The work of Burleigh and Lowery (1940) provides a document of interest for comparison to the present study. Though their paper does not present quantitative data on the breeding avifaunas of the Guadalupes, indications of abundance are alluded to in the narratives of their species list. Direct comparison on a species basis to their work is presented in the appendix to this paper.

# APPENDIX I

## Annotated List of Bird Specimens Collected by George A. Newman from the Guadalupe Mountains, Texas

Listed in this appendix are all of the bird specimens collected from the Guadalupe Mountains by George A. Newman from 1969 to 1974. The nomenclature used follows that of *The A.O.U. Checklist of North American Birds* (1957), and published supplements to that work.

Where there has been a significant change in status of a species when compared to earlier ornithological investigations of the Guadalupe Mountains, notation of such change is made. References to Burleigh and Lowery refer to their 1940 publication as given in the Literature Cited section of the main text. Detailed information on density and biomass of bird species which breed in the woodland areas of the southern Guadalupe Mountains may be found in the text of this report and is not repeated here.

There are 302 specimens representing 99 species and 26 families making up this collection. The numbers given after the initials GAN are the field numbers of the author. Deposition of the skins is indicated by AMNH (American Museum of Natural History, New York), A&M (Texas Cooperative Wildlife Collection—Texas A&M University, College Station, Texas), H-SU (Hardin-Simmons University, Abilene, Texas).

**Accipiter cooperii** (Bonaparte), Cooper's Hawk

1972.—1 adult female, Upper Dog Canyon, 19 June, GAN #302, A&M.

1973.—1 adult female, The Bowl, 26 June, GAN #439, H-SU.

This species appears to be more common now than when Burleigh and Lowery did their research. I found active nests in Upper Dog Canyon and in Smith Canyon.

**Buteo jamaicensis calurus** (Cassin), Red-tailed Hawk

1974.—1 imm. male, The Bowl, 16 June, GAN #499, A&M.

The specimen collected was acquiring its first adult plumage; it shows one almost full length red rectrix along with the typically barred rectrices of immature plumage.

This species regularly breeds in the region of The Bowl and along the high cliffs of Upper Dog Canyon.

**Actitis macularia** (Linnaeus), Spotted Sandpiper

1972.—1 adult male, Main McKittrick Canyon, 31 May, GAN #272, A&M.

This species was seen only rarely along the stream in McKittrick Canyon.

**Columba fasciata fasciata** (Say), Band-tailed Pigeon

1970.—1 adult female, South McKittrick Canyon, 21 May, GAN #185, H-SU.

This species was found to be fairly common as a regular breeding bird along the wooded canyon slopes of upper South McKittrick. It was also seen regularly during the early summer in Upper Dog Canyon and in The Bowl. Burleigh and Lowery found this species to be fairly rare.

**Otus flammeolus flammeolus** (Kaup), Flammulated Owl

1973.—1 adult male, The Bowl, 25 June, GAN #435, H-SU.

This secretive species was found regularly in The Bowl, but in very few numbers.

**Bubo virginianus pallescens** (Stone), Great Horned Owl

1973.—1 adult female, Upper Dog Canyon, 11 June, GAN #408, A&M.

This species is a regular breeding bird in the Upper Dog Canyon area. I have also heard it calling and have seen it in McKittrick Canyon and The Bowl in early summer.

**Strix occidentalis lucida** (Nelson), Spotted Owl

1972.—1 adult female, Smith Canyon, 30 December, GAN #364, H-SU.

This species was also recorded in Upper Dog Canyon during early summer 1974. It is of rare occurrence as a breeding species in the Guadalupes.

**Aegolius acadicus acadicus** (Gmelin), Saw-whet Owl

1973.—1 imm. male, The Bowl, 23 June, GAN #433, A&M; 1 imm. female, The Bowl, 23 June, GAN #434, H-SU.

This species was not recorded by Burleigh and Lowery. My only sighting was of five immature birds which responded to my call during the early evening of 23 June 1973, while I was camped in The Bowl.

**Caprimulgus vociferus arizonae** (Brewster), Whip-poor-will

1969.—1 adult male, The Bowl, 3 June, GAN #149, AMNH.

1973.—1 adult male, The Bowl, 26 June, GAN #440, H-SU.

I found this species to be fairly common as a breeding bird in The Bowl; recorded by Burleigh and Lowery as "rather scarce."

**Phalaenoptilus nuttallii nuttallii** (Audubon), Poor-will

1974.—1 adult female, The Bowl, 17 June, GAN #500, H-SU.

This species was found to be common in the breeding season along the mountain slopes of the major canyon systems and in The Bowl.

**Chordeiles minor howellii** (Oberholser), Common Nighthawk

1969.—1 adult female, The Bowl, 4 June, GAN #150, AMNH.

1973.—1 adult female, The Bowl, 25 June, GAN #438, A&M.

This species was seen commonly each summer (1972, 1973, 1974) feeding at dusk over the meadow in The Bowl. Verification of subspecific identification was made by John Hubbard.

**Aeronautes saxatalis saxatalis** (Woodhouse), White-throated Swift

1970.—1 adult female, South McKittrick Canyon, 22 May, GAN #204, H-SU.

**Archilochus alexandri** (Bourcier and Mulsant), Black-chinned Hummingbird

1970.—1 adult male, North McKittrick Canyon, 22 May, GAN #207, H-SU; 1 adult female, South McKittrick Canyon, 21 May, GAN #208, AMNH.

1973.—1 adult male, South McKittrick Canyon, 30 May, GAN #397, A&M; 1 adult female, South McKittrick Canyon, 29 May, GAN #395, H-SU; 1 adult female, Upper Dog Canyon, 12 June, GAN #411, H-SU.

1974.—1 adult female, South McKittrick Canyon, 28 May, GAN #475, H-SU.

This species was found by Burleigh and Lowery to "breed rather sparingly" and was recorded by them only in Pine Springs Canyon and Guadalupe Canyon. I found this species to be common as a breeding bird in the McKittrick Canyon system and in Upper Dog Canyon.

**Selasphorus platycercus platycercus** (Swainson), Broad-tailed Hummingbird

1971.—1 adult male, Smith Canyon, 24 May, GAN #231, AMNH.

1974.—1 adult male, South McKittrick Canyon, 28 May, GAN #476, H-SU.

This species regularly breeds in the McKittrick Canyon system, Upper Dog Canyon, and The Bowl.

**Eugenes fulgens aureoviridis** (van Rossem), Rivoli's Hummingbird

1972.—1 adult female, South McKittrick Canyon, 6 June, GAN #280, H-SU.

1974.—1 adult female, North McKittrick Canyon, 2 June, GAN #480, A&M.

This species was not recorded by Burleigh and Lowery. Though rare, this species was seen fairly regularly in the McKittrick Canyon system and/or Upper Dog Canyon in the summers of 1972, 1973, 1974.

**Colaptes auratus cafer** (Gmelin), Common Flicker

1969.—1 adult male, The Bowl, 6 June, GAN #151, H-SU; 1 adult female, The Bowl, 6 June, GAN #153, H-SU.

1970.—1 adult male, The Bowl, 2 June, GAN #216, AMNH.

1972.—1 adult female, Upper Dog Canyon, 21 June, GAN #316, H-SU; 1 adult male, the Bowl, 8 July, GAN #340, A&M.

1973.—1 adult female, Frijole, 4 January, GAN #383, A&M.

**Colaptes auratus cafer × auratus**, Common Flicker

1969.—1 adult female, The Bowl, 4 June, GAN #154, H-SU; 1 adult male, The Bowl, 5 June, GAN #152, A&M.

**Melanerpes formicivorus formicivorus** (Swainson), Acorn Woodpecker

1969.—1 adult female, The Bowl, 7 June, GAN #155, H-SU.

1973.—1 adult male, Upper Dog Canyon, 13 June, GAN #415, A&M.

Burleigh and Lowery recorded this species only in The Bowl. I found it to be fairly common as a breeding bird in Upper Dog Canyon and of rather spasmodic occurrence in The Bowl.

**Sphyrapicus varius nuchalis** (Baird), Yellow-bellied Sapsucker

1971.—1 adult female, The Bowl, 3 June, GAN #240, AMNH.

1973.—1 adult female, South McKittrick Canyon, 12 October, GAN #445, A&M.

This species was found only in October by Burleigh and Lowery. The June specimen was probably a late transient rather than a breeding bird. The October 1973 specimen was identified by John Hubbard as *S. v. nuchalis*, but as showing some affinity for *S. v. varius*.

**Sphyrapicus varius varius** (Linnaeus), Yellow-bellied Sapsucker

1973.—1 adult female, South McKittrick Canyon, 5 January, GAN #385, H-SU.

Verification of subspecific identification was made by John Hubbard.

**Dendrocopos villosus leucothorectis** (Oberholser), Hairy Woodpecker

1970.—1 adult male, The Bowl, 2 June, GAN #215, AMNH.

1972.—1 adult female, Upper Dog Canyon, 22 June, GAN #318, A&M; 1 adult male, The Bowl, 10 July, GAN #342, H-SU.

Verification of subspecific identification was made by John Hubbard.

**Dendrocopos scalaris symplectus** (Oberholser), Ladder-backed Woodpecker

1971.—1 adult male, South McKittrick Canyon, 28 May, GAN #234, AMNH.

1973.—1 adult female, Frijole, 4 January, GAN #378, H-SU.

Both of these specimens were identified as *D. s. symplectus* by John Hubbard, who states that they do show some overlap with *D. s. cactophilus*.

**Dendrocopos scalaris** ssp., Ladder-backed Woodpecker

1972.—1 adult male, Smith Canyon, 14 June, GAN #290, H-SU.

1973.—1 adult male, Upper Dog Canyon, 14 June, GAN #420, A&M.

Subspecific identification uncertain at this time.

**Tyrannus vociferans vociferans** (Swainson), Cassin's Kingbird

1971.—1 adult male, Main McKittrick Canyon, 27 May, GAN #238, H-SU; 1 adult female, Main McKittrick Canyon, 27 May, GAN #239, H-SU.

1972.—1 adult male, Upper Dog Canyon, 23 June, GAN #324, A&M.

1973.—1 adult female, Frijole, 6 June, GAN #404, H-SU.

**Myiarchus cinerascens cinerascens** (Lawrence), Ash-throated Flycatcher

1970.—1 adult male, South McKittrick Canyon, 21 May, GAN #194, AMNH; 1 adult male, North McKittrick Canyon, 22 May, GAN #195, H-SU.

1971.—1 adult male, North McKittrick Canyon, 26 May, GAN #236, H-SU.

1972.—1 adult female, Upper Dog Canyon, 19 June, GAN #305, A&M.

**Sayornis nigricans semiatra** (Vigors), Black Phoebe

1972.—1 imm., The Bowl, 9 July, GAN #341, H-SU.

My only sighting of this species in the Guadalupe Mountains was of the immature individual which I collected. Burleigh and Lowery did not record this species.

**Sayornis saya saya** (Bonaparte), Say's Phoebe

1972.—1 adult male, Upper Dog Canyon, 23 June, GAN #323, H-SU.

1973.—1 adult female, Upper Dog Canyon, 15 June, GAN #421, H-SU.

1974.—1 adult male, Upper Dog Canyon, 6 June, GAN #482, A&M.

**Empidonax oberholseri** (Phillips), Dusky Flycatcher

1972.—1 adult female, Upper Dog Canyon, 20 June, GAN #308, H-SU; 1 adult female, Upper Dog Canyon, 24 June, GAN #327, H-SU.

1974.—1 adult female, Main McKittrick Canyon, 25 May, GAN #470, A&M; 1 adult female, Upper Dog Canyon, 7 June, GAN #483, A&M.

The breeding status of this species is yet uncertain in the Guadalupe Mountains. Verification of species identification was made by John Hubbard.

**Empidonax difficilis difficilis** (Baird), Western Flycatcher

1969.—1 adult female, The Bowl, 28 May, GAN #159, H-SU.

1970.—1 adult male, South McKittrick Canyon, 27 May, GAN #192, AMNH.

Verification of subspecific identification was made by John Hubbard.

**Empidonax difficilis hellmayri** (Brodkorb), Western Flycatcher

1969.—1 adult male, The Bowl, 29 May, GAN #158, H-SU.

1970.—1 adult male, South McKittrick Canyon, 28 May, GAN #193, AMNH.

1972.—1 adult male, The Bowl, 10 July, GAN #344, H-SU.

1973.—1 adult male, South McKittrick Canyon, 30 May, GAN #398, H-SU; 1 adult male, Upper Dog Canyon, 18 June, GAN #429, A&M.

1974.—1 adult male, Upper Dog Canyon, 22 May, GAN #461, H-SU.

**Contopus sordidulus veliei** (Coues), Western Wood Pewee

1969.—1 adult female, The Bowl, 3 June, GAN #157, H-SU.

1970.—2 adult males, South McKittrick Canyon, 21 May, GAN #190, #189, AMNH; 1 adult male, North McKittrick Canyon, 22 May, GAN #191, H-SU.

1971.—1 adult female, North McKittrick Canyon, 26 May, GAN #230, H-SU.

1972.—1 adult female, Guadalupe Spring, 16 June, GAN #294, H-SU; 1 adult male, Upper Dog Canyon, 23 June, GAN #325, H-SU.

1973.—1 adult male, Upper Dog Canyon, 18 June, GAN #428, A&M.

**Nuttallornis borealis** (Swainson), Olive-sided Flycatcher

1971.—1 adult female, Smith Canyon, 24 May, GAN #235, AMNH.

1973.—1 adult female, Main McKittrick Canyon, 31 May, GAN #399, H-SU.

1974.—1 adult female, Main McKittrick Canyon, 25 May, GAN #467, A&M.

This species was recorded as a breeding bird in the Bowl by Burleigh and Lowery. I did not find it in The Bowl, but I did record it as a possible breeding species in Main McKittrick Canyon.

**Tachycineta thalassina lepida** (Mearns), Violet-green Swallow

1969.—1 adult female, The Bowl, 7 June, GAN #156, H-SU.

1970.—1 adult female, 1 adult male, The Bowl, 2 June, GAN #206, #205, AMNH.

1971.—1 adult male, Main McKittrick Canyon, 27 May, GAN #232, A&M.

1972.—1 adult male, Upper Dog Canyon, 22 June, GAN #320, H-SU.

Listed by Burleigh and Lowery as occurring in summer at an altitude above 7000 ft. I found this species to be fairly common during the summer in the wooded canyons and at Manzanita Spring at elevations down to 5200 ft.

**Cyanocitta stelleri macrolopha** (Baird), Steller's Jay

1969.—1 adult male, The Bowl, 27 May, GAN #160, H-SU.

1970.—1 adult male, The Bowl, 1 June, GAN #184, AMNH.

1972.—1 imm., Upper Dog Canyon, 25 June, GAN #330, H-SU.

1973.—1 adult female, Frijole, 1 January, GAN #367, A&M.

**Aphelocoma coerulescens woodhouseii** (Baird), Scrub Jay

1972.—1 imm. female, Upper Dog Canyon, 20 June, GAN #312, H-SU; 1 imm. male, Upper Dog Canyon, 26 June, GAN #331, A&M.

1973.—1 adult female, Frijole, 3 January, GAN #376, H-SU.

1974.—1 adult male, Upper Dog Canyon, 10 June, GAN #496, H-SU.

Placement of these specimens in this subspecific category is tentative at this time.

**Nucifraga columbiana** (Wilson), Clark's Nutcracker

1969.—1 adult male, The Bowl, 1 June, GAN #162, H-SU; 1 adult female, The Bowl, 1 June, GAN #161, A&M.

This species was not recorded by Burleigh and Lowery. A flock of seven nutcrackers, two of which were collected, were seen regularly from 31 May to 7 June 1969, while I was camped in The Bowl.

**Parus gambeli gambeli** (Ridgway), Mountain Chickadee

1969.—1 adult male, The Bowl, 28 May, GAN #163, H-SU.

1970.—1 adult male, The Bowl, 2 June, GAN #210, AMNH.

1972.—1 adult male, Upper Dog Canyon, 20 June, GAN #310, A&M.

1973.—1 adult male, South McKittrick Canyon, 28 May, GAN #393, H-SU; 1 adult female, Main McKittrick Canyon, 5 January, GAN #384, H-SU.

This species breeds sparingly in wooded canyons down to an elevation of about 5200 ft; this is a common nesting bird of The Bowl at 8000 ft elevation.

**Parus inornatus ridgwayi** (Richmond), Plain Titmouse

1972.—1 adult female, Frijole, 29 December, GAN #355, H-SU.

1973.—1 adult female, Frijole, 6 June, GAN #405, A&M.

This species puzzled Burleigh and Lowery because it seemed to be absent during the breeding season. I found a pair, with young, that were using a dead pear tree as a nesting site near the Frijole Ranger Station in the summer of 1973. Verification of subspecific identification was made by John Hubbard.

**Psaltriparus minimus plumbeous** (Baird), Bushtit

1970.—1 adult male, South McKittrick Canyon, 28 May, GAN #211, AMNH.

1971.—1 adult male, South McKittrick Canyon, 25 May, GAN #267, H-SU.

1972.—1 adult (sex undetermined), Main McKittrick Canyon, 8 June, GAN #283, H-SU.

1973.—1 adult male, Upper Dog Canyon, 15 June, GAN #423, A&M; 1 imm., Upper Dog Canyon, 15 June, GAN #422, A&M.

**Sitta carolinensis nelsoni** (Mearns), White-breasted Nuthatch

1969.—1 adult female, The Bowl, 5 June, GAN #164, H-SU.

1972.—1 adult male, South McKittrick Canyon, 31 May, GAN #274, H-SU; 1 adult male, Upper Dog Canyon, 21 June, GAN #317, A&M.

I found this species, as did Burleigh and Lowery, to be a common breeding bird in The Bowl. It is also commonly found breeding in Upper Dog Canyon.

**Sitta canadensis** (Linnaeus), Red-breasted Nuthatch

1973.—1 adult (sex undetermined), The Bowl, 13 October, GAN #446, A&M.

**Sitta pygmaea melanotis** (van Rossem), Pygmy Nuthatch

1969.—1 adult male, The Bowl, 3 June, GAN #165, H-SU.

1970.—1 adult male, The Bowl, 1 June, GAN #196, AMNH.

1972.—1 imm., Upper Dog Canyon, 20 June, GAN #315, A&M.

1974.—1 imm. male, The Bowl, 18 June, GAN #501, H-SU.

Breeds commonly in The Bowl and is a sporadic breeder in Upper Dog Canyon.

**Certhia familiaris montana** (Ridgway), Brown Creeper

1969.—1 adult female, The Bowl, 29 May, GAN #166, H-SU.

1972.—1 imm., The Bowl, 8 July, GAN #339, A&M.

1973.—1 adult male, Main McKittrick Canyon, 5 January, GAN #386, H-SU.

Subspecific identification was verified by John Hubbard.

**Troglodytes aedon parkmanii** (Audubon), House Wren

1969.—1 adult female, The Bowl, 29 May, GAN #168, H-SU.

1972.—1 imm., The Bowl, 8 July, GAN #338, A&M.

Appears to have decreased in abundance since Burleigh and Lowery researched the Guadalupes.

**Thryomanes bewickii eremophilus** (Oberholser), Bewick's Wren

1970.—1 adult female, North McKittrick Canyon, 22 May, GAN #212, AMNH.

1972.—1 adult male, Upper Dog Canyon, 27 June, GAN #333, H-SU.

1973.—1 adult male, South McKittrick Canyon, 2 June, GAN #401, A&M.

**Campylorhynchus brunneicapillus couesi** (Sharpe), Cactus Wren

1973.—1 adult male, Frijole, 2 January, GAN #374, H-SU.

1974.—1 imm., PX Flat, 9 June, GAN #491, A&M.

This species was thought by Burleigh and Lowery not to breed at an elevation higher than

5600 ft in the Guadalupes. I have found it to be a fairly common nesting species in PX Flat at an elevation of about 6500 ft.

**Catherpes mexicanus conspersus** (Ridgway), Canyon Wren

1970.—1 adult male, South McKittrick Canyon, 28 May, GAN #213, AMNH.
1972.—1 imm., Upper Dog Canyon, 24 June, GAN #329, A&M.
1973.—1 adult female, Frijole, 3 January, GAN #375, H-SU.

**Salpinctes obsoletus obsoletus** (Say), Rock Wren

1969.—1 adult male, Frijole, 4 April, GAN #167, H-SU.
1972.—1 imm. male, Upper Guadalupe Spring, 16 June, GAN #295, H-SU.
1973.—1 imm. male, Upper Dog Canyon, 13 June, GAN #413, A&M; 1 adult female, Upper Dog Canyon, 13 June, GAN #414, H-SU.

**Mimus polyglottos leucopterus** (Vigors), Mockingbird

1972.—1 adult male, Lower Guadalupe Spring, 16 June, GAN #296, H-SU.
1974.—1 adult male, Upper Dog Canyon, 8 June, GAN #490, A&M.

**Toxostoma curvirostre celsum** (Moore), Curve-billed Thrasher

1972.—1 adult female, Upper Dog Canyon, 28 June, GAN #334, A&M.
1973.—1 adult female, Frijole, 2 January, GAN #372, H-SU; 1 adult female, Upper Dog Canyon, 14 June, GAN #419, H-SU.

**Oreoscoptes montanus** (Townsend), Sage Thrasher

1973.—1 adult male, Frijole, 4 January, GAN #379, A&M.

**Turdus migratorius propinquus** (Ridgway), Robin

1972.—1 adult male, Frijole, 17 June, GAN #298, A&M; 1 adult female, Smith Canyon, 30 December, GAN #359, H-SU.

The status of this species in the Guadalupe Mountains has changed considerably since the work of Burleigh and Lowery. They recorded it as a common nesting species of the high country. The only Robin I found during the breeding season from 1969 to 1974 was the one collected at Frijole. There seems to have been a great decline in the breeding population of this species in the Guadalupes.

**Catharus guttatus guttatus** (Pallas), Hermit Thrush

1973.—1 adult male, Pine Springs Canyon, 1 January, GAN #366, A&M.

**Catharus guttatus slevini** (Grinnell), Hermit Thrush

1973.—1 adult (sex undetermined), The Bowl, 13 October, GAN #448, H-SU.
1974.—1 adult male, Main McKittrick Canyon, 19 March, GAN #455, A&M; 2 adult females, Main McKittrick Canyon, 19 March, GAN #456, #457, H-SU.

**Catharus guttatus auduboni** (Baird), Hermit Thrush

1972.—1 adult female, Upper Dog Canyon, 24 June, GAN #328, H-SU; 1 imm. male, The Bowl, 10 July, GAN #343, A&M.
1974.—1 adult female, Upper Dog Canyon, 22 May, GAN #459, H-SU.

Burleigh and Lowery did not find this species occurring as a breeding bird below 8000 ft elevation. I found it to occur fairly commonly in Upper Dog Canyon at 6200 ft, as well as in The Bowl. Subspecific identification was verified by John Hubbard.

**Catharus ustulatus ustulatus** (Nuttall), Swainson's Thrush

1971.—1 adult male, South McKittrick Canyon, 25 May, GAN #237, A&M.

This species was not recorded by Burleigh and Lowery. Though rare, I found it to be fairly regular in late spring in the McKittrick Canyon system. Subspecific identification was verified by John Hubbard.

**Catharus ustulatus swainsoni** (Tschudi), Swainson's Thrush

1973.—1 adult male, South McKittrick Canyon, 28 May, GAN #392, H-SU.
1974.—1 adult male, Main McKittrick Canyon, 25 May, GAN #471, A&M.

Subspecific identification was verified by John Hubbard.

**Sialia mexicana bairdi** (Ridgway), Western Bluebird

1969.—1 adult male, The Bowl, 6 June, GAN #169, H-SU.
1970.—1 adult male, The Bowl, 1 June, GAN #226, AMNH.

1972.—1 adult male, Upper Dog Canyon, 18 June, GAN #299, A&M; 1 adult male, Frijole, 29 December, GAN #354, H-SU.

This species breeds sparingly in The Bowl, but is fairly common during the breeding season in Upper Dog Canyon.

**Myadestes townsendi townsendi** (Audubon), Townsend's Solitaire

1972.—1 adult female, Smith Canyon, 30 December, GAN #361, A&M.

**Polioptila caerulea amoenissima** (Grinnell), Blue-gray Gnatcatcher

1970.—1 adult male, North McKittrick Canyon, 22 May, GAN #209, AMNH.

1972.—1 adult female, North McKittrick Canyon, 3 June, GAN #279, H-SU; 1 imm. male, Main McKittrick Canyon, 9 June, GAN #285, H-SU; 1 adult male, Upper Dog Canyon, 24 June, GAN #326, H-SU.

1973.—1 adult male, Upper Dog Canyon, 16 June, GAN #427, A&M.

**Regulus calendula calendula** (Linnaeus), Ruby-crowned Kinglet

1973.—1 adult female, Main McKittrick Canyon, 12 October, GAN #443, H-SU.

**Anthus spinoletta** ssp., Water Pipit

1974.—1 adult female, North McKittrick Canyon, 2 June, GAN #481, A&M.

**Bombycilla cedrorum** (Vieillot), Cedar Waxwing

1973.—1 adult female, Frijole, 4 January, GAN #381, H-SU.

**Vireo vicinior** (Coues), Gray Vireo

1972.—1 adult male, Main McKittrick Canyon, 31 May, GAN #276, A&M.

1973.—1 adult male, Main McKittrick Canyon, 29 June, GAN #441, H-SU.

**Vireo solitarius plumbeus** (Coues), Solitary Vireo

1969.—1 adult female, The Bowl, 3 June, GAN #170, H-SU.

1970.—1 adult female, South McKittrick Canyon, 27 May, GAN #203, H-SU; 1 adult male, The Bowl, 1 June, GAN #202, AMNH.

1972.—1 adult male, South McKittrick Canyon, 31 May, GAN #277, H-SU; 1 adult female, North McKittrick Canyon, 7 June, GAN #282, H-SU; 1 adult male, Upper Dog Canyon, 20 June, GAN #307, A&M.

**Vireo olivaceus** (Linnaeus), Red-eyed Vireo

1970.—1 adult male, South McKittrick Canyon, 21 May, GAN #214, AMNH.

1972.—1 adult male, South McKittrick Canyon, 31 May, GAN #275, H-SU.

This species was not recorded by Burleigh and Lowery. I found it to occur sporadically in the Guadalupes in late spring.

**Vireo gilvus swainsonii** (Baird), Warbling Vireo

1969.—1 adult female, The Bowl, 3 June, GAN #171, H-SU.

1970.—1 adult male, South McKittrick Canyon, 20 May, GAN #201, H-SU; 1 adult male, South McKittrick Canyon, 21 May, GAN #200, AMNH.

1972.—1 adult female, Upper Dog Canyon, 19 June, GAN #300, A&M.

**Helmitheros vermivorus** (Gmelin), Worm-eating Warbler

1973.—1 adult male, South McKittrick Canyon, 28 May, GAN #394, A&M.

This species was not recorded by Burleigh and Lowery. The collected specimen was taken from a mist net and is the only record that I have for this species in the Guadalupes.

**Vermivora celata orestera** (Oberholser), Orange-crowned Warbler

1969.—1 adult male, The Bowl, 30 May, GAN #172, H-SU.

1970.—1 adult male, The Bowl, 1 June, GAN #199, AMNH.

1973.—1 adult female, The Bowl, 25 June, GAN #436, H-SU.

1974.—1 adult female, Upper Dog Canyon, 21 May, GAN #458, A&M.

Subspecific identification verified by John Hubbard.

**Vermivora virginiae** (Baird), Virginia's Warbler

1972.—1 adult female, Upper Dog Canyon, 20 June, GAN #314, A&M; 1 imm., Upper Dog Canyon, 22 June, GAN #319, A&M.

1973.—1 adult male, Upper Dog Canyon, 12 June, GAN #410, H-SU.

1974.—1 adult male, Upper Dog Canyon, 10 June, GAN #494, H-SU.

This species was not recorded as a breeding bird by Burleigh and Lowery. I found it to breed fairly commonly in Upper Dog Canyon and to breed sporadically in South McKittrick Canyon.

**Dendroica coronata auduboni** (Townsend), Yellow-rumped Warbler

1969.—1 adult female, The Bowl, 5 June, GAN #173, H-SU.

1970.—1 adult male, The Bowl, 1 June, GAN #198, AMNH.

1973.—1 adult male, The Bowl, 25 June, GAN #437, A&M; 1 adult female, The Bowl, 13 October, GAN #447, H-SU.

1974.—1 adult female, Upper Dog Canyon, 7 June, GAN #487, H-SU.

This species was found most commonly in The Bowl, but it also was a sporadic breeding bird in Upper Dog Canyon.

**Dendroica nigrescens** (Townsend), Black-throated Gray Warbler

1974.—1 adult female, Upper Dog Canyon, 7 June, GAN #485, A&M.

The collected specimen was not in breeding condition. This species recorded only in October by Burleigh and Lowery.

**Dendroica graciae graciae** (Baird), Grace's Warbler

1970.—1 adult male, The Bowl, 2 June, GAN #197, AMNH.

1972.—1 adult female, South McKittrick Canyon, 11 June, GAN #286, H-SU; 1 imm., South McKittrick Canyon, 11 June, GAN #287, H-SU; 1 adult female, Upper Dog Canyon, 20 June, GAN #311, H-SU.

1973.—1 adult male, Upper Dog Canyon, 11 June, GAN #409, A&M.

**Dendroica pensylvanica** (Linnaeus), Chestnut-sided Warbler

1971.—1 adult female, Frijole, 24 May, GAN #229, A&M.

The specimen collected is my only record of this species in the Guadalupes. It was not recorded by Burleigh and Lowery.

**Oporornis tolmiei tolmiei** (Townsend), MacGillivrays Warbler

1974.—1 adult female, Upper Dog Canyon, 22 May, GAN #462, A&M.

Subspecific identification was verified by John Hubbard.

**Wilsonia pusilla pileolata** (Pallas), Wilson's Warbler

1971.—1 adult male, South McKittrick Canyon, 25 May, GAN #228, AMNH.

1974.—1 adult female, Upper Dog Canyon, 22 May, GAN #460, A&M.

**Wilsonia pusilla pusilla** (Wilson), Wilson's Warbler

1974.—1 adult female, South McKittrick Canyon, 24 May, GAN #463, H-SU; 1 adult female, Upper Dog Canyon, 7 June, GAN #484, H-SU; 1 adult male, Upper Dog Canyon, 10 June, GAN #495, A&M.

Subspecific identification was verified by John Hubbard.

**Setophaga ruticilla ruticilla** (Linnaeus), American Redstart

1974.—1 adult male, Main McKittrick Canyon, 25 May, GAN #469, A&M.

I recorded this species only in the late spring of 1974 in McKittrick Canyon. It was not recorded by Burleigh and Lowery.

**Passer domesticus domesticus** (Linnaeus), House Sparrow

1973.—2 adult females, Frijole, 7 June, GAN #406, #407, A&M.

This species is common locally at Frijole and occurs sparingly around the Upper Dog Canyon Ranger Station. It was not found away from human habitation.

**Icterus cucullatus nelsoni** (Ridgway), Hooded Oriole

1972.—1 adult male, Frijole, 14 June, GAN #289, A&M.

1974.—1 adult male, Frijole, 15 June, GAN #498, H-SU.

This species occurs sparingly around Frijole during the breeding season. It was not recorded by Burleigh and Lowery.

**Icterus parisorum** (Bonaparte), Scott's Oriole

1970.—1 adult male, Main McKittrick Canyon, 29 May, GAN #221, H-SU; 1 adult female, Main McKittrick Canyon, 29 May, GAN #220, AMNH.

1972.—1 adult male, Upper Guadalupe Spring, 16 June, GAN #297, A&M.

**Molothrus ater obscurus** (Gmelin), Brown-headed Cowbird

1972.—1 adult male, Main McKittrick Canyon, 31 May, GAN #273, H-SU; 1 adult male, Upper Dog Canyon, 26 June, GAN #332, A&M.

1973.—1 adult male, Upper Dog Canyon, 14 June, GAN #417, H-SU; 1 adult male, Upper Dog Canyon, 16 June, GAN #426, H-SU.
1974.—1 adult female, Frijole, 15 June, GAN #497, H-SU.

This species occurred fairly commonly in the canyons and was quite common around Frijole. John Hubbard identified the male specimens as *M. ater obscurus* > *artemisiae*..

**Piranga ludoviciana** (Wilson), Western Tanager

1969.—1 adult male, The Bowl, 3 June, GAN #174, A&M.
1970.—1 adult male, Main McKittrick Canyon, 22 May, GAN #222, AMNH; 1 adult female, North McKittrick Canyon, 22 May, GAN #223, H-SU.
1971.—1 adult female, Main McKittrick Canyon, 27 May, GAN #233, AMNH.
1972.—1 adult female, Upper Dog Canyon, 19 June, GAN #303, H-SU.

Burleigh and Lowery recorded this species as being limited during the breeding season to an elevation of 8000 ft and above. I found this species to breed regularly in the canyons of the Guadalupes down to an elevation of 5200 ft.

**Piranga olivacea** (Gmelin), Scarlet Tanager

1974.—1 adult male, Main McKittrick Canyon, 25 May, GAN #468, A&M.

My only record of this species is that of the specimen collected. It was not recorded by Burleigh and Lowery.

**Piranga flava hepatica** (Swainson), Hepatic Tanager

1970.—1 adult male, Main McKittrick Canyon, 23 May, GAN #225, AMNH; 1 adult female, South McKittrick Canyon, 28 May, GAN #224, AMNH.
1971.—1 adult female, Main McKittrick Canyon, 27 May, GAN #242, H-SU.
1972.—1 adult male, Upper Dog Canyon, 22 June, GAN #322, A&M.
1974.—1 adult male, South McKittrick Canyon, 24 May, GAN #466, H-SU.

**Piranga rubra cooperi** (Ridgway), Summer Tanager

1972.—1 adult male, Frijole, 15 June, GAN #292, A&M.

Subspecific identification was verified by John Hubbard.

**Piranga rubra rubra** (Linnaeus), Summer Tanager

1974.—1 adult male, South McKittrick Canyon, 24 May, GAN #465, H-SU.

Subspecific identification was verified by John Hubbard.

**Pyrrhuloxia sinuata sinuata** (Bonaparte), Pyrrhuloxia

1973.—1 adult female, Frijole, 3 January, GAN #377, H-SU.

**Pheucticus melanocephalus melanocephalus** (Swainson), Black-headed Grosbeak

1969.—1 adult male, The Bowl, 6 June, GAN #175, H-SU.
1970.—1 adult male, North McKittrick Canyon, 22 May, GAN #219, AMNH; 1 adult female, Main McKittrick Canyon, 28 May, GAN #218, AMNH.
1972.—1 adult male, Upper Dog Canyon, 20 June, GAN #313, A&M.

I found this to be a fairly common breeding species in the canyons and high country of the Guadalupes. It was considered uncommon by Burleigh and Lowery.

**Guiraca caerulea interfusa** (Dwight and Griscom), Blue Grosbeak

1972.—1 adult female, Main McKittrick Canyon, 1 June, GAN #278, A&M.
1974.—1 adult female, Main McKittrick Canyon, 25 May, GAN #473, H-SU.

I found this species to occur regularly at the mouth of McKittrick Canyon.

**Passerina cyanea** (Linnaeus), Indigo Bunting

1974.—1 adult male, South McKittrick Canyon, 27 May, GAN #474, A&M; 1 adult male, Main McKittrick Canyon, 29 May, GAN #477, H-SU.

Several Indigo Buntings were seen near the water in Main and South McKittrick canyons in late May 1974. These were my only sightings of this species in the Guadalupes. This species was not recorded in the Guadalupes by Burleigh and Lowery.

**Carpodacus mexicanus frontalis** (Say), House Finch

1972.—1 adult female, Main McKittrick Canyon, 13 June, GAN #288, H-SU; 1 adult male, Upper Dog Canyon, 20 June, GAN #309, A&M.
1973.—1 adult male, Main McKittrick Canyon, 4 June, GAN #402, H-SU; 1 adult male, Upper Dog Canyon, 12 June, GAN #412, H-SU.

1974.—1 adult female, Upper Dog Canyon, 8 June, GAN #489, H-SU.

**Spinus pinus pinus** (Wilson), Pine Siskin

1970.—1 adult male, The Bowl, 2 June, GAN #186, AMNH.

1973.—1 adult female, Frijole, 4 January, GAN #382, H-SU; 1 adult male, South McKittrick Canyon, 29 May, GAN #396, A&M.

1974.—1 adult female, South McKittrick Canyon, 24 May, GAN #464, H-SU.

**Spinus psaltria psaltria** (Say), Lesser Goldfinch

1971.—1 adult male, South McKittrick Canyon, 25 May, GAN #227, AMNH.

1972.—1 adult female, Main McKittrick Canyon, 8 June, GAN #284, H-SU; 1 adult male, Upper Dog Canyon, 19 June, GAN #306, A&M.

1973.—1 adult male, Upper Dog Canyon, 13 June, GAN #416, H-SU; 1 adult male, Upper Dog Canyon, 14 June, GAN #418, H-SU; 2 adult males, Upper Dog Canyon, 18 June, GAN #430, #431, H-SU.

1974.—1 adult male, Upper Dog Canyon, 8 June, GAN #488, H-SU.

This species appears to be much more common than it was when Burleigh and Lowery did their work. Subspecific identification was verified by John Hubbard.

**Loxia curvirostra bendirei** (Ridgway), Red Crossbill

1972.—1 adult male, The Bowl, 7 July, GAN #336, H-SU; 1 adult female, The Bowl, 7 July, GAN #337, A&M.

1974.—1 adult male, The Bowl, 17 March, GAN #454, H-SU.

The female specimen of this subspecies was carrying a well-developed egg (19 mm × 13 mm) in the oviduct. Identification of subspecies was made by Alan R. Phillips.

**Loxia curvirostra benti** (Griscom), Red Crossbill

1972.—1 adult female, The Bowl, 7 July, GAN #335, H-SU.

Subspecific identification by Alan R. Phillips.

**Chlorura chlorura** (Audubon), Green-tailed Towhee

1974.—1 adult female, South McKittrick Canyon, 30 May, GAN #478, A&M.

**Pipilo erythropthalmus gaigei** (Van Tyne and Sutton), Rufous-sided Towhee

1969.—1 adult female, The Bowl, 3 June, GAN #177, H-SU.

1970.—1 adult male, South McKittrick Canyon, 21 May, GAN #217, AMNH.

1972.—1 adult male, North McKittrick Canyon, 7 June, GAN #281, H-SU; 1 imm., Upper Dog Canyon, 22 June, GAN #321, A&M.

Subspecific identification was verified by John Hubbard.

**Pipilo fuscus mesoleucus** (Baird), Brown Towhee

1969.—1 adult female, Frijole, 4 April, GAN #176, H-SU.

1972.—1 adult male, Upper Dog Canyon, 19 June, GAN #304, H-SU; 1 adult male, Frijole, 29 December, GAN #358, A&M.

1973.—1 adult female, Main McKittrick Canyon, 4 June, GAN #403, H-SU.

**Aimophila ruficeps scottii × eremoeca**, Rufous-crowned Sparrow

1971.—1 adult female, Main McKittrick Canyon, 27 May, GAN #241, AMNH.

1972.—1 adult female, Upper Guadalupe Spring, 16 June, GAN #293, H-SU.

1974.—1 adult female, Upper Dog Canyon, 7 June, GAN #486, H-SU; 1 adult male, PX Flat, 9 June, GAN #492, A&M.

Subspecific identification was made by John Hubbard.

**Amphispiza bilineata opuntia** (Burleigh and Lowery), Black-throated Sparrow

1972.—1 adult male, Smith Canyon, 14 June, GAN #291, H-SU.

1974.—1 adult female, PX Flat, 9 June, GAN #493, A&M.

Subspecific identification was verified by John Hubbard.

**Junco hyemalis montanus**, Dark-eyed Junco

1972.—1 adult female, Frijole, 29 December, GAN #357, H-SU.

1973.—1 adult female, Frijole, 2 January, GAN #370, H-SU; 1 adult (sex undetermined), 2 January, GAN #371, H-SU.

Subspecific identification was made by John Hubbard.

**Junco hyemalis hyemalis** (Linnaeus), Dark-eyed Junco

1973.—1 adult male, Frijole, 1 January, GAN #368, H-SU.
Subspecific identification was made by John Hubbard.

**Junco caniceps caniceps** (Woodhouse), Gray-headed Junco

1972.—1 adult male, Frijole, 30 December, GAN #363, A&M.
1973.—1 adult (sex undetermined), Frijole, 2 January, GAN #369, H-SU.
1974.—1 adult female, Main McKittrick Canyon, 31 May, GAN #479, H-SU.
Subspecific identification was made by John Hubbard.

**Junco caniceps dorsalis** (Henry), Gray-headed Junco

1969.—2 adult females, The Bowl, 28 May, GAN #178, A&M, GAN #179, H-SU.
1972.—1 imm. female, The Bowl, 11 July, GAN #345, H-SU.
Subspecific identification of adult specimens was made by John Hubbard.

**Spizella passerina arizonae** (Coues), Chipping Sparrow

1969.—1 adult male, The Bowl, 3 June, GAN #180, H-SU.
1972.—1 imm., Upper Dog Canyon, 19 June, GAN #301, H-SU; 1 adult male, Frijole, 29 December, GAN #356, H-SU; 1 adult male, Frijole, 30 December, GAN #360, H-SU.
1973.—1 adult male, Upper Dog Canyon, 16 June, GAN #425, H-SU; 1 adult female, Upper Dog Canyon, 16 June, GAN #424, A&M; 1 adult male, South McKittrick Canyon, 12 October, GAN #444, H-SU.

**Spizella atrogularis evura** (Coues), Black-chinned Sparrow

1970.—1 adult male, Main McKittrick Canyon, 23 May, GAN #188, H-SU; 1 adult male, Main McKittrick Canyon, 28 May, GAN #187, A&M.
1973.—1 adult male, Frijole, 2 January, GAN #373, H-SU; 1 adult male, Main McKittrick Canyon, 1 June, GAN #400, H-SU.

**Zonotrichia leucophrys gambellii** (Nuttall), White-crowned Sparrow

1973.—1 adult female, Frijole, 4 January, GAN #380, A&M.
1974.—1 adult female, Main McKittrick Canyon, 25 May, GAN #472, H-SU.
Subspecific identification verified by John Hubbard.

**Zonotrichia albicollis** (Gmelin), White-throated Sparrow

1972.—1 adult male, Frijole, 30 December, GAN #362, H-SU.

**Melospiza lincolnii lincolnii** (Audubon), Lincoln's Sparrow

1972.—1 adult (sex undetermined), Smith Canyon, 30 December, GAN #365, H-SU.

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# *Post-Pleistocene Mammals from Pratt Cave and Their Environmental Significance*

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This report is one of several resulting from a multidisciplinary study of Pratt Cave, its deposits, and the archeological and paleontological materials derived from it. Only a brief description of the cave, its location, and the character of its deposits will be given here, as these subjects will be dealt with in more detail elsewhere. The major subject of this paper is the description and analysis of the mammal bones found in the cave.

Pratt Cave is located in the southwest wall of the mouth of McKittrick Canyon near the northwest corner of Sec. 12, Block 65, Twp. 1, T and T Survey, in the southern Guadalupe Mountains, Culberson County, Texas. It is at the base of a 130-ft (39 m) cliff and at the top of a steep talus slope that extends to the bottom of the canyon 300 ft (90 m) below. The approximate elevation of the cave is 5300 ft (1590 m).

The cave was formed by solution near the base of the Lamar member of the Bell Canyon Formation of Guadalupian (Upper Middle Permian) age. The cave probably formed before or during the early stages of the deposition of the Ogallala Formation of Pliocene age (Bretz 1949; Horberg 1949).

The cave is an elongate tunnel oriented N41° E, S41° W (Fig. 1). Its entrance is oval with a horizontal diameter of 8 ft (240 cm) and a vertical diameter of about 5 ft (150 cm). The cave widens to approximately 9 ft (270 cm) within 6 ft (180 cm) of the entrance and then narrows rapidly to a passage 3 to 4 ft (90 to 120 cm) in width. The roof of the cave rises rapidly 5 ft (150 cm) from the entrance to form a chimney more than 10 ft (300 cm) in height, centered over the widest part of the cave. Beyond the chimney, the roof height varies from 3 to 4 ft (90 to 120 cm).

The cave fill consists of fine sand and silt, with a concentration of platy limestone chips in the lowest part. There is a general gradation upward from this zone into subangular to subround grains of limestone. Quartz and calcite grains and abundant pebble to cobble-sized rock fragments are found throughout the deposit. The latter are plate-like fragments that have spalled off the roof and walls. The finer-grained material probably had an aeolian

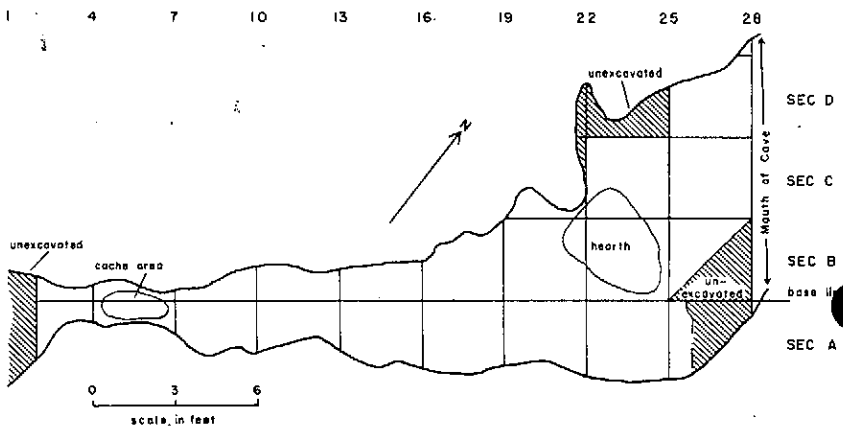


**Fig. 1.** Plan view of Pratt Cave showing horizontal grid and location of the hearth and cache.

origin. There is no apparent internal stratigraphy, and correlation of different parts of the cave is difficult.

The deposits are thin, ranging from 2.5 ft (75 cm) in the front part of the cave to nothing toward the back where bedrock is exposed at the surface (Fig. 2). Two holes in the center of the cave are evidence of disturbance by vandals. In addition to these, an earlier disturbance was found—a hole filled with burned rocks and bone fragments, remnants of a hearth.

Mammal bones from Pratt Cave provide an opportunity to investigate postglacial faunal changes in a mountainous region of the southwestern United States. Previous work has shown that the regional Pleistocene fauna contained, in addition to the extinct species, extant forms such as *Marmota*

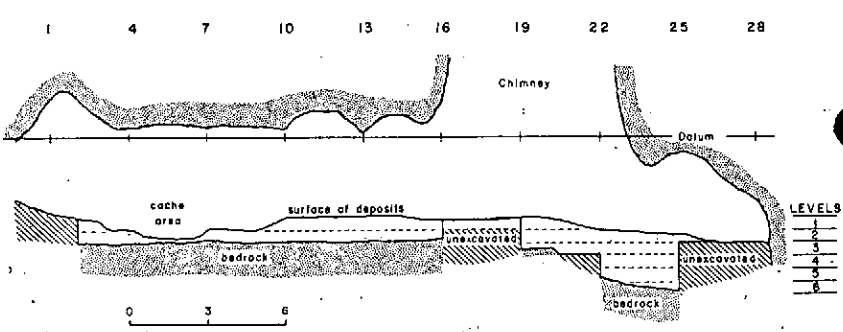


**Fig. 2.** Longitudinal section of Pratt Cave along the base line.

*flaviventris, Neotoma cinerea, Sorex cinereus, Lagurus curtatus*, and *Microtus ochrogaster* that are now found farther north and east and at generally higher altitudes or in more humid areas (Stearns 1942; Schultz and Howard 1935; Murray 1957; Harris 1970). Very little is known about the faunal transition from Late Wisconsin to the present, although Murray (1957) outlines a post-Wisconsin warming and drying trend. Studies of amphibian and reptile remains from Pratt Cave (Gehlbach and Holman 1974) and of the pollen (Schoenwetter, unpublished; Bryant, unpublished) show a minor change toward more arid conditions through the time represented by these deposits.

## METHODS

The excavations were done according to standard archeological techniques. A base line (compass orientation N41° E, S41° W) was established along the long axis of the cave 36 in. (90 cm) above the highest point of the cave deposits. A grid of 3-ft$^2$ (234 cm$^2$) blocks was used for the excavations, and material was removed in 6-in. (15 cm) levels. Level data within the deposits were recorded with reference to the base line.

Mammal bones were identified to the lowest possible taxon. For most mandibles and maxillae with teeth, specific identifications were possible. Most post-cranial material could not be identified below the generic level. Environmental interpretations are based on modern distributions and habitat preferences of the species represented in the cave deposits.

The mammalian remains are cataloged in the collection of the Texas Memorial Museum, the University of Texas at Austin, under the locality number TMM 41172. Abbreviations used in the text and tables are as follows: TMM, Texas Memorial Museum; M, Texas Memorial Museum Recent Collection; UNM, University of New Mexico; TNHC, Texas Natural History Collection (housed at the Texas Memorial Museum).

## PRESERVATION OF BONES

Mammal bones from Pratt Cave are, in general, well preserved. Except for bones of large animals, there is little breakage. There is a small amount of articulated material, some of which (e.g., the foot of a small mammal) is held together by dried ligaments. Most bones are of animals no larger than a jackrabbit, and the low degree of breakage in this size range suggests an owl pellet accumulation, although some species (e.g., wood rats) certainly lived in and around the cave.

There are some burned human bones which are the remains of an aboriginal cremation. The bones of the larger animals such as deer, antelope, and horse were probably brought into the cave by mammalian carnivores, for the scarcity of artifacts in the cave rules out any significant occupation by humans.

## AGE

The age of the deposits in Pratt Cave is only partially known. Four C–14 dates are available: TX–1021 wood from a cache in the back of the cave 1420 ±60 years BP; TX–1022 basketry from the cache at the back of the cave 1840 ±60 years BP; TX–2191 bone from level 2 of blocks 10-15 apatite carbonate 2560 ± 340 years BP, collagen 2820 ± 180 years BP; TX–2192 bone from level 2 of blocks 2–9 apatite carbonate 2090 ± 420 years BP, collagen 2320 ± 70 years BP.

Both dates based on the basketry and wood from the cache are younger than those based on bone from level 2. This is consistent with the higher stratigraphic position of the cache.

The C–14 dates from the two areas of level 2 differ by approximately 500 years. The dates based on the apatite carbonate fraction overlap extensively at 1 standard deviation. Those based on the collagen fraction do not overlap at 2 standard deviations. It is doubtful that a significant age difference exists for level 2 in blocks 2 through 15.

These dates are all from the back part of the cave where the deposits are relatively thin. The correlation of these dated units with the sequence near the opening is tentative. A lithologic correlation indicates that the tan silty layer found in level 2 in blocks 5–7, 13–15 is equivalent to a similar silt found in level 6 in blocks 22–24. In all these areas this silt rests on the bedrock and appears to represent the beginning of the accumulation of sediment in the cave.

## ENVIRONMENTAL INTERPRETATION

The Pratt Cave mammalian fauna has no extinct taxa. Three species, *Marmota flaviventris*, *Neotoma cinerea*, and *Geomys bursarius*, are not known to live today in the southern Guadalupe Mountains. The first two species are potential indicators of climatic change.

Both *Marmota flaviventris* and *Neotoma cinerea* now live well to the north of Pratt Cave and at higher altitudes. Harris (1963a, 1963b, 1970) showed that the limit of the southern and lower altitudinal distribution of *Marmota flaviventris* is controlled by the availability of green fodder during the spring, which is, in turn, controlled by winter precipitation.

The factors that control the distribution of *N. cinerea* are less well known and more complex than in the case of *Marmota* because they apparently involve competing species of *Neotoma*. The situation is further confused by the fact that the *N. cinerea* material from Pratt Cave (and also from Dark Canyon Cave—a late Pleistocene assemblage near Carlsbad, New Mexico) is closer in size to living populations in Wyoming than to living populations in New Mexico (Table 1). Moreover, there are evidently four species of *Neotoma* in the Pratt Cave Fauna. Finley (1958) found no area in Colorado where the same four species occurred together and only small areas where three were found together. The lack of stratification in Pratt Cave and the presence of an intrusive burial make demonstration of contemporaneity of

TABLE 1. Numerical data on occlusal length of $M_1$ in various samples of *Neotoma*.

| Species and locality | No. of specimens | Mean | Observed range |
|---|---|---|---|
| *N. cinerea* (Pratt Cave) | 3 | 3.72 | 3.63–3.81 |
| *N. cinerea* (Recent-New Mexico) | 4 | 3.24 | 3.08–3.43 |
| *N. cinerea* (Recent-Wyoming) | 10 | 3.75 | 3.52–3.96 |
| *N. cinerea* (Pleistocene-Dark Canyon Cave) | 14 | 3.63 | 3.38–3.86 |
| *N. mexicana* (Recent-New Mexico) | 2 | 3.20 | 3.16–3.24 |

all four species difficult if not impossible. *N. cinerea* specimens were recovered from blocks 13–15, level 1, along with *N. albigula* and *N. mexicana*, from blocks 10–12, level 2, with *N. albigula, N. micropus*, and *N. mexicana*; and from level 1 in the hearth with *N. mexicana* and *N. albigula*. The material in part of blocks 13–15 had been disturbed, and the association of the remains of the three species might be the result of this disturbance. However, the material in blocks 10–12 showed no evidence of disturbance, and the association may be more meaningful. In addition, three species of *Neotoma* (*N. mexicana, N. albigula*, and *N. micropus*) are found together in many blocks at many levels, and it is unlikely that this represents post-depositional mixing.

The presence of *Marmota flaviventris* and *Neotoma cinerea* in the Pratt Cave deposits indicates more mesic conditions at some time in the past. The four species of *Neotoma* indicate a greater diversity of niches in the past. This is similar to the situation found in Pleistocene faunas in many areas of North America (Hibbard 1960; Guilday et al. 1964; Lundelius 1967; Dalquest et al. 1969). In the absence of a more complete post-Pleistocene sequence, it is difficult to ascertain whether this diversity is a Pleistocene relict or whether it represents a short-lived situation in the transition from Pleistocene to present conditions. The distribution of *Neotoma* in the Pratt Cave deposits contributes little information on this question because of the absence of well-defined stratigraphy and sufficient C-14 dates to permit reliable correlations. The specimens of *N. cinerea* are either associated with the C-14 date of 2560 years BP or are stratigraphically above it. The failure to find all four species of *Neotoma* together in any late Pleistocene fauna so far reported elsewhere in the southwest might be taken as evidence of such a transition. A careful restudy of the *Neotoma* material from all faunas in this region is needed.

McKittrick Canyon today is much more mesic than the surrounding area. It seems likely that this has been the case for all of post-Pleistocene time and perhaps earlier. Conditions in the canyon remained favorable for the maintenance of both *Marmota flaviventris* and *Neotoma cinerea* after they had disappeared in the surrounding area. Eventually, this regional climatic change affected McKittrick Canyon fauna.

*Geomys bursarius* is no longer found in the region of the Guadalupe Mountains or in the area to the south. This is the area that separates *G. bursarius* from its close relative *G. arenarius* in the El Paso region. The presence of *G. bursarius* in level 1 of blocks 10–12 of the Pratt Cave deposits indicates a recent disappearance from this locality (post 2000 years). The reason for its disappearance is not known. Semken (1961) postulated soil erosion resulting from overgrazing during the last century as the cause of this animal's recent disappearance from the Edward's Plateau of central Texas.

## SYSTEMATIC DESCRIPTIONS

CLASS Mammalia

Order Insectivora
- Family Soricidae
  - *Notiosorex crawfordi* (Coues)

Order Carnivora
- Family Mustelidae
  - *Mephitis mephitis* (Schreber)
  - *Mustela frenata* Lichtenstein
- Family Canidae
  - *Urocyon cinereoargenteus* (Schreber)
- Family Procyonidae
  - *Bassariscus astutus* (Lichtenstein)
  - *Procyon lotor* (Linnaeus)

Order Perissodactyla
- Family Equidae
  - *Equus* sp.

Order Artiodactyla
- Family Cervidae
  - *Odocoileus* sp.
- Family Antilocapridae
  - gen. and sp. indet.

Order Rodentia
- Family Sciuridae
  - *Spermophilus variegatus* (Erxleben)
  - *Cynomys ludovicianus* (Ord)
  - *Eutamias canipes* Bailey
  - *Marmota flaviventris* (Audubon and Bachman)
  - gen. and sp. indet.
- Family Erethizontidae
  - *Erethizon dorsatum* (Linnaeus)
- Family Cricetidae
  - *Microtus mexicanus* (Saussure)
  - *Neotoma albigula* Hartley
  - *N. cinerea* (Ord)
  - *N. mexicana* Baird
  - *N. micropus* Baird
  - *Onychomys leucogaster* (Wied-Neuwied)
  - *O. torridus* (Coues)
  - *Peromyscus difficilis* (Allen)
  - *Peromyscus* sp.

*Reithrodontomys megalotis* (Baird)
*Sigmodon hispidus* Say and Ord
Family Geomyidae
*Pappogeomys castanops* (Baird)
*Geomys bursarius* (Shaw)
*Thomomys bottae* (Eydoux and Gervais)
Family Heteromyidae
*Dipodomys ordii* Woodhouse
*D. spectabilis* Merriam
*Perognathus hispidus* Baird
*P. merriami* Allen
Order Lagomorpha
Family Leporidae
*Lepus californicus* Gray
*Sylvilagus audubonii* (Baird)
*Sylvilagus* sp.

CLASS Mammalia

ORDER Insectivora
Family Soricidae
*Notiosorex crawfordi* (Coues), Desert Shrew

**Material.**—Nine right and three left mandibles (TMM 41172-63, -373, -400, -659, -762, -763, -765, -766, -768 and TMM 41172-42, -761, -767); two palates (TMM 41172-759, -764); one right maxillary (TMM 41172-760) from levels 1 through 5.
**Description and Discussion.**—This material is readily recognized as *N. crawfordi* by the presence of the deep, rounded notch in the condyle of the mandible (Hibbard and Taylor 1960) and the presence of only three unicuspid teeth in the upper dentition. In addition, the teeth are only lightly pigmented, and the coronoid process lacks a posterointernal ramal fossa (Gaughran 1954).

The desert shrew is known from widely scattered localities in the southwestern desert, grassland, and woodland communities.

ORDER Carnivora
Family Mustelidae
*Mephitis mephitis* (Schreber), Striped Skunk

**Material.**—One left tibia (TMM 41172-510) from blocks 10-12, level 1; one left mandible (TMM 41172-222) from blocks 10-12, level 2; left $M_1$ (TMM 41172-773) from blocks 2-4, level 2.
**Description and Discussion.**—This material shows no differences from the corresponding parts of Recent specimens. The striped skunk is present in the area surrounding Pratt Cave but is less common there than the hognose skunk.

*Mustela frenata* Lichtenstein, Long-tailed Weasel

**Material.**—One left maxillary with $P^4$-$M^1$ and alveolus for $P^3$ (TMM 41172-1153) from block 10-12, level 2; one left $M_1$ (TMM 41172-327) from level 1 of the hearth.
**Description and Discussion.**—A comparison of the Pratt Cave material with a Recent specimen from Ohio (TMM M-1751) shows only minor differences. The protocone of the $P^4$ and the entire $M^1$ of the Pratt Cave specimen are slightly larger than in the Ohio specimen. In addition, the metacone and the posterior part of the stylar area of the $M^1$ are larger in the Pratt Cave specimen. These differences are minor and are no more than expected between specimens from

such widely separated localities. The $M_1$ cannot be distinguished from that of the Recent specimen.

The long-tailed weasel is widely distributed in the United States and Mexico, except for southwest Arizona, southeast California, and Baja California, and is recorded from Culberson County (Davis 1960: 80).

Family Canidae
*Urocyon cinereoargenteus* (Schreber), Gray Fox

**Material.**—One left $M^2$ (TMM 41172-326) from level 1 of the hearth.
**Description and Discussion.**—The Pratt Cave specimen is considerably smaller than the corresponding tooth of *Vulpes vulpes* and is somewhat smaller than the $M^2$ of *U. cinereoargenteus* from central Texas. The tooth resembles the corresponding tooth of Recent *U. cinereoargenteus* in the strong development of the outer cingulum, the relatively low paracone and metacone, and the broad inner area. In addition, the angle formed by the intersection of a line joining the paracone and metacone with one joining the protocone and metaconule is much greater in *U. cinereoargenteus* than in *V. macrotis*. The length along the ectoloph is 7.5 mm; the width normal to the ectoloph is 8.6 mm.

This species is common around Pratt Cave today.

Family Procyonidae
*Bassariscus astutus* (Lichtenstein), Ringtail

**Material.**—One left $P_4$ (TMM 41172-372) from blocks 13-15, level 2; one $M^2$ (TMM 41172-771) from blocks 8-9, level 1; one canine (TMM 41172-776) from blocks 8-9, level 2; one left $dP_4$ (TMM 41172-777) from blocks 25-27 B, level 4.
**Description and Discussion.**—These specimens cannot be distinguished from the homologous teeth of the Recent form. This is a widespread upland species in the southwestern United States and is common in the Guadalupe Mountains today.

*Procyon lotor* (Linnaeus), Racoon

**Material.**—Anterolabial part of one right $P^4$ (TMM 41172-649) from blocks 10-12, level 1.
**Description and Discussion.**—The $P^4$ has the parastyle, the anterior half of the paracone, and about one-fourth of the protocone. Although the shape and size of the parastyle of $P^4$ is variable in this species, the Pratt Cave specimen is almost identical to a Recent specimen from Sutton County, Texas (TMM M-2340).

The racoon is common along McKittrick Canyon today.

ORDER Perissodactyla
Family Equidae
*Equus* sp.

**Material.**—The distal end of one metapodial (TMM 41172-677) from level 1, blocks 16-18 R and the distal articular surface of one phalanx (TMM 41172-554) from level 3, blocks 26-28 B.
**Description and Discussion.**—These two specimens are the only indication of horses recovered from the Pratt Cave deposits to date. They represent a small form about the size of an ass. The metapodial has been slightly burned and has the anterior (dorsal) surface of the shaft broken away. It is not possible to determine on the basis of morphology whether these specimens were derived from a modern feral or domestic horse or from an extinct Pleistocene horse, but their positions in the cave and their preservation indicate they represent the former.

Both specimens were recovered from the topmost unit of the cave. In view of the C-14 dates of 2090 and 2560 years BP from level 2 of blocks 2 to 15, they apparently represent modern feral or domesticated horses.

ORDER Artiodactyla
Family Cervidae
*Odocoileus* sp.

**Material.**—Two incisors and fragments of postcranial skeleton from blocks 5–7, level 2; blocks 8–9, level 2 and silt layer of level 2; and blocks 25–27 C, level 4.
**Description and Discussion.**—This genus, as with most of the larger animals, is not well represented in the deposits of Pratt Cave. Both *O. virginianus* and *O. hemionus* are found in this region today, but the latter is much more common.

ORDER Rodentia
Family Sciuridae
*Spermophilus variegatus* (Erxleben), Rock Squirrel

**Material.**—Maxillaries, mandibles, and molars from blocks 10–12, level 2; blocks 19–21 B, level 2; blocks 22–24 A, level 2; blocks 22–24 B, levels 2, 5, 6; blocks 25–27 B, levels 5, 6; blocks 25–27 C, levels 3, 4.
**Description and Discussion.**—The material from Pratt Cave cannot be distinguished from Recent specimens in size or morphology. The limestone cliffs in McKittrick Canyon are typical of their habitat, and the rock squirrel is common there today.

*Cynomys ludovicianus* (Ord), Black-tailed Prairie Dog

**Material.**—Posterior part of one left mandible (TMM 41172–217) from level 3 of blocks 25–27 C; left $M^1$ (TMM 41172–1324) from level 5 of blocks 23–25 B; lower molar (TMM 41172–751) level 2 of blocks 8–9; lower molar (TMM 41172–755) from level 2 of blocks 4–5.
**Description and Discussion.**—The mandible is indistinguishable from the same part of the mandible of Recent specimens.

The historic range of this species included the area of Pratt Cave, although the nearest extant colony is some 20 miles distant. Man has been the most important agent in Recent range restrictions of the black-tailed prairie dog.

*Eutamias canipes* Bailey, Gray-collared Chipmunk

**Material.**—One right mandible with $M_1$ (TMM 41172–753) from level 2 of blocks 2–4.
**Description and Discussion.**—The Pratt Cave specimen resembles specimens of *E. canipes* in the Texas Natural History Collection (TNHC 135, 137) from New Mexico in size and morphology of the $M_1$. The metaconid is strongly joined to the anterior cingulum which is well defined and straight. The protoconid and hypoconid are well separated, and a well-developed mesoconid is located between them.

The specimen differs from *Spermophilus spilosoma* in its smaller size, the presence of a well-defined mesoconid, and in the subdivisions of the trigonid basin by a ridge that extends from the protoconid to the anterior cingulum. It differs from *Ammospermophilus interpres* in its slightly smaller size, presence of a well-defined mesoconid, and by the divided trigonid basin. In addition, the metalophid is better developed in *E. canipes*, and there is no well-developed cuspule on the anterior cingulum. The metaconid of *A. interpres* is more isolated from the protoconid and the cingular cuspule than is the case in *E. canipes*.

The gray-collared chipmunk is found in the higher parts of the Guadalupe Mountains, including The Bowl and Dog Canyon (Hall and Kelson 1959). It is doubtful that it signifies any change in conditions in McKittrick Canyon.

*Marmota flaviventris* (Audubon and Bachman), Yellow-bellied Marmot

**Material.**—Labial part of one left $M^3$ (TMM 41172–742) from level 2, blocks 5–7, associated with C-14 date TX-2192.
**Description and Discussion.**—The Pratt Cave specimen differs only in minor details from the $M^3$ of a Recent specimen from Colorado (TMM M–1248). The metaloph is slightly more

complicated in the Pratt Cave specimen, with a slightly better-developed metaconule. The length along the ectoloph of the Pratt Cave specimen is 5.6 mm; that of the Colorado specimen is 5.2 mm.

The occurrence of the yellow-bellied marmot in the Pratt Cave deposits indicates that some change has taken place in the environment of McKittrick Canyon since it lived there. The marmot today is found in the high mountain forests of New Mexico. Its presence in the McKittrick Canyon deposits could imply the existence of similar forests in the southern Guadalupe Mountains at some time in the past. However, Harris and Findley (1964) have pointed out that this animal lives in other habitats and have interpreted its presence in a late Pleistocene fauna from north-central New Mexico as indicating open conditions similar to those found today in central Wyoming.

Harris (1970) postulated, on the basis of its distribution in New Mexico, that the primary limiting factor in the southward and lower altitude distribution of the marmot is the availability of sufficient precipitation during the winter to provide abundant green fodder in the spring prior to the summer rains. The mountains in the southern part of New Mexico and Arizona in which marmots would be expected, but are absent, are separated from the northern mountain masses by dry areas. Harris believes this would block repopulation. He further postulated that the elimination of marmots from these mountains took place after the intervening areas had become dry, or repopulation would have taken place. This interpretation (Harris 1970; Harris and Findley 1964) has implications for the age of the Pratt Cave deposits as well as the environmental conditions. The earlier interpretations of the climatic significance of marmots in fossil and subfossil assemblages made by Stearns (1942) and Murray (1957) imply that most of the southward extensions of range of the marmot in the past date from the late Pleistocene. The interpretation of Harris that marmots survived in isolated favorable areas for significant lengths of time after the end of the Pleistocene is confirmed by the Pratt Cave specimen which is associated with a C-14 date of 2090 ± 420 years BP (TX-2192). The upper parts of McKittrick Canyon are still quite mesic and the lower portion may have been so, too, until quite recently.

Family Sciuridae—genus and species undetermined

**Material.**—One edentulous right maxillary (TMM 41172-144) from level 4 of blocks 25–27.
**Description and Discussion.**—This specimen is from a small sciurid about the size of *Ammospermophilus interpres* but is not generically or specifically identifiable.

Family Erethizontidae
*Erethizon dorsatum* (Linnaeus), Porcupine

**Material.**—Two quills (TM 41172-1106) from block 5–7, level 2.
**Description and Discussion.**—This is the only material of this species recovered from the Pratt Cave deposits. This animal is widespread in west Texas and New Mexico today where it frequently uses crevices and caves as shelters. It is part of the Recent fauna of the Guadalupe Mountains.

Family Cricetidae
*Microtus mexicanus* (Saussure), Mexican Vole

**Material.**—Two left $M^3$'s (TMM 41172–397, –398) from level 2, blocks 19–21. Two left mandibles (TMM 41172–1332, 1333) and a left maxillary (TMM 41172–1334) from level 2 of blocks 22–24 A.
**Description and Discussion.**—These two teeth are the only remains of microtines found to date. One tooth (TMM 41172–397) has three closed triangles and a fourth (inner) triangle which is confluent with the posterior loop. The other specimen (TMM 41172–398) has only two closed triangles and a third (outer) which is confluent with the posterior loop. Both conditions are found in *M. mexicanus* from Otero County, New Mexico (TNHC 2284, 2287, 2289). The $M^3$ of *M. pennsylvanicus* also shows three closed triangles and a fourth confluent with the posterior

loop. All 12 specimens of *M. pennsylvanicus* examined showed the three closed triangles on $M^3$. The teeth from Pratt Cave are referred to *M. mexicanus*.

In the southern Guadalupe Mountains this species is now restricted to elevations above 7000 ft, where it is found in grassy areas in or near coniferous forest. It is possible that in the recent past it was found at lower elevations in McKittrick Canyon and that the present restriction is a recent change, similar to the recent disappearance of *Pitymys pinetorum* from many areas of central Texas in the last 1000 years (Lundelius 1967). It is also possible that the remains of this species in Pratt Cave were brought from higher elevations by owls. Their rarity would support this hypothesis.

*Neotoma albigula* Hartley, White-throated Woodrat

**Material.**—Mandibles and $M_1$'s from blocks 2–4, level 2; blocks 8–9, level 2; blocks 10–12, levels 1, 2; blocks 13–15, level 1; blocks 19–21 A, levels 2, 3; blocks 19–21 B, levels 1, 3; blocks 22–24 A, levels 2, 3; blocks 22–24 B, level 5; blocks 22–24 C, level 5; blocks 25–27 A, level 2; blocks 25–27 B, levels 4, 5; blocks 25–27 C, levels 3, 4, 5; level 1 of the hearth.

**Description and Discussion.**—This material is assigned to this species on the basis of the absence of a dentine tract on the anteroexternal face of $M_1$ and because the width of the second loph of $M_1$ is less than 1.94 mm. The width of the second loph on the $M_1$ is not an absolutely certain criterion upon which to base the differentiation of *N. albigula* and *N. micropus*; hence, the possibility exists that not all specimens are correctly assigned.

This species is widely sympatric with *N. micropus*, including the Guadalupe region. Finley (1958) found that in Colorado, where these two species are sympatric, *N. albigula* is restricted to rocky uplands and *N. micropus*, to more open lowlands. This same situation was reported by Bailey (1905) for west Texas and holds in the Guadalupe Mountains. *N. albigula* is rare in McKittrick Canyon, however, and *N. micropus* has not been trapped there.

*Neotoma cinerea* (Ord), Bushy-tailed Woodrat

**Material.**—One right mandible with $M_{1-2}$ (TMM 41172–229) from level 2 of blocks 10–12; one right $M_1$ (TMM 41172–1104), one right $M^1$ (TMM 41172–1102), one right $M^2$ (TMM 41172–1105) from levels 1 of blocks 13–15; one left and one right mandible (TMM 41172–283, 281) from level 1 of the hearth.

**Description and Discussion.**—The specimens listed above have dentine tracts on the molars which are as well developed as in *Neotoma mexicana* but are substantially larger. The horizontal ramus of the mandible (TMM 41172–229) is deeper and more massive than that of *N. mexicana*. The basal closure of the labial re-entrants of the $M_1$, $M^1$, and $M^2$ is better developed than in *N. mexicana* or *N. micropus*. The $M_1$'s from Pratt Cave are not only larger than those of *N. mexicana* from New Mexico but are also larger than four modern specimens of *N. cinerea* from New Mexico (UNM 27795, 17860, 16250, 94). They are about the same size as the $M_1$'s from a sample of *N. cinerea* from Wyoming and specimens of *N. cinerea* from a late Pleistocene deposit from Dark Canyon Cave near Carlsbad, New Mexico (Table 1).

The difference in size between the modern *N. cinerea* from New Mexico and Wyoming suggests a north–south size cline in this species today. The large size of the Dark Canyon Cave specimens indicates that during the Pleistocene, large-sized *N. cinerea* were living farther south than today. The Pratt Cave specimens show that at least one population retained large size well into the Holocene.

The presence of this taxon, like *Marmota*, is unexpected in a fauna this young. However, it has been reported in late Pleistocene faunas from Williams Cave (Ayer 1937), Dry Cave (Harris 1970), and Burnet Cave (Murray 1957).

*Neotoma mexicana* Baird, Mexican Woodrat

**Material.**—Numerous mandibles and $M_1$'s from blocks 2–4, level 2; blocks 5–7, level 2; blocks 8–9, level 2; blocks 10–12, levels 1, 2; blocks 13–15, levels 1, 2; blocks 16–18 A, level 1; blocks 16–18 B, level 1; blocks 19–21 A, levels 1, 2, 3; blocks 19–21 B, levels 1, 2, 3; blocks 22–24 A,

levels 1, 2, 3, 4; blocks 22–24 B, levels 2, 4, 5, 6; blocks 22–24 C, levels 2, 4; blocks 25–27 A, level 2; blocks 25–27 B, levels 3, 4, 5, 6; blocks 25–27 C, levels 3, 4, 5, 6; blocks 25–27 D, levels 3, 4; level 1 of the hearth, blocks 20–21 B, level 4, and the packrat nest of block 19.

**Description and Discussion.**—Three species of *Neotoma* (*N. mexicana, N. albigula,* and *N. micropus*) have been reported from the Guadalupe Mountains. In addition, *N. cinerea*, which now occurs in northern New Mexico, and *N. floridana*, which now occurs in the eastern half of Texas, might be expected to have extended their ranges southward and westward, respectively, during the last glacial stage.

The specific identification of *Neotoma* mandibles and teeth is difficult. Recently, Dalquest et al. (1969) have suggested several criteria by which *N. floridana, N. micropus,* and *N. albigula* can be separated. According to them, the greater size of *N. floridana* is reflected in a greater breadth of the molar rows (greater than 8.7 mm) than either *N. micropus* or *N. albigula*. This character was checked in 32 Recent specimens of *N. albigula* from the Texas High Plains and 30 Recent specimens of *N. micropus* from south Texas in the Texas Natural History Collection. None of these specimens had a molar row breadth exceeding 8.6 mm. None of the few palates present in the Pratt Cave collection has a molar row breadth equal to 8.7 mm. As a result, there is no evidence of the presence of *N. floridana* from Pratt Cave.

Dalquest et al. (1969) separated *N. micropus* from *N. albigula* on the basis of the width of the second lophid of $M_1$. They found that the width of this lophid in *N. micropus* always exceeded 1.94 mm, whereas in *N. albigula* it was always less than 1.94 mm. However, this was checked in the Texas Natural History Collection specimens of *N. albigula* and *N. micropus* mentioned above with the following results: in five specimens of *N. micropus*, the width of the second lophid of $M_1$ is less than 1.94 mm; in three specimens of *N. albigula*, this width is greater than 1.94 mm. Thus this character is not completely reliable for differentiating *N. micropus* and *N. albigula*.

*Neotoma mexicana* was identified on the basis of the dentine tract on the anteroexternal side of the $M_1$. The dentine tract on $M_1$ extends one-fourth to one-third the distance from the root to the crown of an unworn tooth. The dentine tract on the $M_2$ is shorter. An examination of 27 Recent specimens of *N. albigula* from Dawson County, Texas, in the Texas Natural History Collection shows a short, incipient dentine tract in two specimens, TNHC 3144 and 1038. This could not be confused with the situation in either *N. cinerea* or *N. mexicana*. None of the Pratt Cave specimens shows the enamel islands which result from isolation of the inner parts of the re-entrant folds in deeply worn teeth as is seen in *N. cinerea*.

*N. mexicana* is common in McKittrick Canyon today where it occupies cracks and crevices in the canyon walls.

*Neotoma micropus* Baird, Gray Woodrat

**Material.**—Mandibles and $M_1$'s from blocks 2–4, level 2; blocks 5–7, level 2, blocks 8–9, levels 1,2; blocks 10–12, level 2; blocks 13–15, level 2; blocks 19–21 A, level 1; blocks 22–24 A, level 2; blocks 22–24 C, level 5; blocks 25–27 B, levels 4, 5; blocks 25–27 C, level 5.

**Description and Discussion.**—This material is assigned to this species on the basis of the absence of a dentine tract on the anteroexternal face of $M_1$ and a width of the second loph of $M_1$ more than 1.94 mm. The general ecological preferences and relationships to other species have been discussed above.

*Onychomys leucogaster* (Wied-Neuwied), Northern Grasshopper Mouse

**Material.**—One left mandible with $M_1$ (TMM 41172–1304) from level 2, blocks 8–9; one edentulous right mandible (TMM 41172–535) from level 6, blocks 26–28.

**Description and Discussion.**—These specimens have the prominent, backwardly curved coronoid process of *Onychomys*, but their $M_{1-3}$ alveolar lengths are larger than those of either of the other Pratt Cave specimens or the Recent sample of *O. torridus* (Tables 2–3). The large size of these specimens suggests that they are probably *O. leucogaster*, and they are tentatively assigned to this species on that basis.

TABLE 2. Numerical data on *Onychomys* from Pratt Cave.

| Specimen number | $LM_1$ | L lower alveolus $M_{1-3}$ | $LM^1$ | L upper alveolus $M^{1-3}$ |
|---|---|---|---|---|
| | | *Onychomys torridus* | | |
| TMM 41172-411 | 1.65 | 3.85 | - | - |
| TMM 41172-99 | - | 3.76 | - | - |
| TMM 41172-100 | - | 3.72 | - | - |
| TMM 41172-193 | - | - | 1.93 | 4.09 |
| | | *Onychomys leucogaster* | | |
| TMM 41172-535-1304 | - | 4.58 | | |
| | 1.97 | 4.03 | | |

TABLE 3. Numerical data of Recent samples of *Onychomys leucogaster* and *Onychomys torridus*, San Patricio County, Texas.

| | Sample size | Observed range | Mean ± standard error | Standard deviation | Coefficient of variation |
|---|---|---|---|---|---|
| | | *Onychomys leucogaster* | | | |
| $LM_1$ | 9 | 1.72-2.01 | 1.88±0.032 | 0.096 | 5.11 |
| Alveolus $LM_{1-3}$ | 12 | 3.77-4.48 | 4.19±0.065 | 0.225 | 5.37 |
| $LM^1$ | 8 | 2.06-2.23 | 2.15±0.023 | 0.065 | 3.01 |
| Alveolus $LM^{1-3}$ | 13 | 4.35-4.89 | 4.71±0.044 | 0.159 | 3.38 |
| | | *Onychomys torridus* | | | |
| $LM_1$ | 2 | 1.56-1.67 | 1.62 | | |
| Alveolus $LM_{1-3}$ | 2 | 3.78-3.79 | 3.785 | | |
| $LM^1$ | 2 | 1.94-2.01 | 1.98 | | |
| Alveolus $LM^{1-3}$ | 2 | 3.96 | 3.96 | | |

*Onychomys leucogaster* is known to the north of Pratt Cave in the vicinity of Carlsbad, New Mexico (Hall and Kelson 1959: 663). It is likely that its distribution extended farther to the southwest during the Pleistocene, and McKittrick Canyon provided a refuge into Holocene time.

*Onychomys torridus* (Coues), Southern Grasshopper Mouse

**Material.**—One right maxillary with $M^1$ (TMM 41172-193), one right mandible with $M_1$ (TMM 41172-411), one edentulous right mandible (TMM 41172-100), one edentulous left mandible (TMM 41172-99), all from level 2, blocks 19-21.

**Description and Discussion.**—All of the mandibles have the coronoid process strongly recurved posteriorly. The $M_1$ and $M^1$ are simple, with the high, widely exposed principal cusps characteristic of *Onychomys*.

This material is assigned to *O. torridus* on the basis of size. The lengths of $M_1$, $M^1$, and of alveoli for $M_{1-3}$ and $M^{1-3}$ are within the range of size of a Recent sample of *O. torridus* from

Trans-Pecos Texas. Only one of these measures, the $M_{1-3}$ alveolar length, overlaps the lower end of the size range of a sample of *O. leucogaster* from south Texas (Tables 2–3).

This species is present in the general area of Pratt Cave today.

*Peromyscus difficilis* (Allen), Zacatecan Deer Mouse

**Material.**—One right mandible with $M_{1-2}$ from the hearth area (TMM 41172–299), one right and one left mandible with $M_{1-2}$ from level 1 (TMM 41172–585, –1201); one right and two left mandibles with $M_{1-2}$ from level 2 (TMM 41172–1157, –1206, –97); one right mandible with $M_{1-2}$ from level 3 (TMM 41172–1266).

**Description and Discussion.**—All *Peromyscus* mandibles with low incisor root capsules are heterogeneous as to size and complexity of the teeth. The specimens listed above are large in size (length of $M_{1-2}$ greater than 3.26 mm) and have stylids and lophids present on both $M_1$ and $M_2$. The length of $M_{1-2}$ of a Recent sample of *P. difficilis* (N = 5) ranges from 3.16 mm to 3.43 mm, and both teeth are complicated with lophids and stylids as reported by Martin (1968).

*Peromyscus* sp.

**Material.**—Numerous mandibles from levels 1, 2, 3, 4, and 6.

**Description and Discussion.**—The *Peromyscus* material has presented problems of identification which have not been solved to the author's satisfaction. The extensive overlap in size and dental characters of a number of species makes definite identification of individual specimens very difficult.

Dalquest et al. (1969) have used the size of the capsule housing the root of the lower incisor to separate *P. leucopus* and *P. maniculatus* from *P. boylii* and *P. pectoralis*. They found that this capsule formed a prominent bulge on the labial side of the mandible in the first pair of species and little or no bulge in the second. In addition, an examination of mandibles of *P. difficilis* and *P. truei* shows that the former also has an inconspicuous capsule and that the latter has a slight to moderately bulged capsule.

The mandibles from Pratt Cave can be easily divided into two groups on the basis of the size of this capsule. However, it is clear from an examination of scatter diagrams of length versus width of the lower molars and frequency histograms of the length of $M_{1-2}$ that both groups are heterogeneous.

Dalquest et al. (1969) pointed out that in central and east Texas *P. maniculatus* can be distinguished from *P. leucopus* by its shorter $M_{1-2}$ but that this character does not hold for the populations in west Texas. Indeed, I have been unable to find reliable characters to differentiate these populations in west Texas.

The distribution maps of Hall and Kelson (1959) showed both species occurring in the Guadalupe Mountains, but Davis (1940) and Davis and Robertson (1944) reported only the occurrence of *P. leucopus*. The inability to separate these species makes it impossible to determine whether *P. maniculatus* was present in the Guadalupe Mountains in the past.

Those mandibles with small incisor root capsules and teeth with a low degree of development of stylids and lophs show some variation and may be heterogeneous as to species. Many are similar in size and morphology to *P. boylii rowleyi* now found in west Texas and probably represent that species.

*Reithrodontomys megalotis* (Baird), Western Harvest Mouse

**Material.**—Mandibles and maxillaries from blocks 5–7, level 2; blocks 8–9, levels 1, 2; blocks 10–12, levels 1, 2; blocks 16–18, level 1; blocks 19–21 A, level 2; blocks 19–21 B, level 3; blocks 22–24 A, level 3; blocks 22–24 C, levels 4, 5; packrat nest in block 19.

**Description and Discussion.**—The first primary fold of $M^3$ is shorter than the second primary fold and does not extend half way across the tooth. The labial folds on the $M^{1-2}$ are tight and V-shaped when viewed from the side.

*R. megalotis* is present in the Bowl area, nearly 1000 ft above McKittrick Canyon today. It is similar morphologically to *R. montanus*, which is also recorded from Trans-Pecos Texas

(Hooper 1952; Hall and Kelson 1959). All specimens of *Reithrodontomys* from Pratt Cave more closely resemble *R. megalotis* than *R. montanus*.

*Sigmodon hispidus* Say and Ord, Cotton Rat

**Material.**—Numerous mandibles and maxillaries from blocks 2–4, level 2; blocks 8–9, level 2; blocks 10–12, levels 1, 2; blocks 19–21 A, level 2; blocks 19–21 B, level 3; blocks 22–24 A, levels 2, 3; blocks 22–24 C, levels 3, 4; blocks 25–27 B, level 5; blocks 25–27 C, level 4; level 1 of the hearth.

**Description and Discussion.**—All of the *Sigmodon* material is referable to *S. hispidus*. A comparison of the Pratt Cave material with *S. ochrognathus* reveals that it is too large to be readily assigned to that species. It falls within the size range of a sample of *S. hispidus* from central Texas.

The cotton rat is widely distributed in the southern part of the United States. It is reported by the Guadalupe Mountains Park Staff (1965), and its presence in the Pratt Cave deposits is not unexpected.

Family Geomyidae

*Pappogeomys castanops* (Baird), Yellow-faced Pocket Gopher

**Material.**—Mandibles and maxillaries from blocks 2–4, level 2; blocks 8–9, levels 1 and silt layer of 2; blocks 10–12, level 1; blocks 19–21 A, level 3; blocks 22–24 A, levels 1, 2, 3; blocks 22–24 B, levels 2, 4; blocks 25–27 B, levels 3, 4, 5, 6; blocks 25–27 C, level 4; the hearth.

**Description and Discussion.**—The material referred to this species cannot be distinguished from Recent specimens. The size is large, the upper incisors are unisulcate, and $M_{1-3}$ have enamel plates only on the posterior side.

*Pappogeomys castanops* in the Pratt Cave deposits is expected. This gopher occupies deep soils relatively free of rocks (Davis 1960). In the vicinity of Pratt Cave this habitat is represented by the terrace deposits that flank the existing creek, and *P. castanops* is usually present there today. However, the periodic floods that sweep McKittrick Canyon often decimate the population.

*Geomys bursarius* (Shaw), Plains Pocket Gopher

**Material.**—One right mandible (TMM 41172-26) from level 1. One right mandibular ramus with $M_1$ (TMM 41172-302) and a left edentulous mandibular ramus (TMM 41172-693) from level 1 of the hearth; right mandibular ramus with the incisor and $P_4$ (TMM 41172-724) from level 1 of blocks 13-15; right mandibular ramus with the incisor (TMM 41172-26) from level 3 of blocks 22-24; left mandibular ramus with the incisor and $P_4$ (TMM 41172-524) from level 4 of blocks 22-24 C.

**Description and Discussion.**—The lower molars are not drawn out to points lingually as in *Thomomys*; there is a deep pit between the tooth row and the ascending ramus. The lower molars have enamel plates on posterior faces only.

The plains pocket gopher is represented by a relatively small amount of material. It is usually found in areas of sandy soil more than 4 in. deep (Davis 1960) and is not recorded in Culberson County today. The nearest record is at Monahans, Ward County, Texas (Hall and Kelson 1959). The closely related species *G. arenarius* is found no closer than El Paso County, Texas. The Pratt Cave specimens are almost exactly at the midpoint of the distributional gap between *G. bursarius* and *G. arenarius*, and may indicate that the separation of these two species is quite recent. The low frequency may indicate limited areas of appropriate soil with small populations in lowlands near the cave in the past.

*Thomomys bottae* (Eydoux and Gervais), Botta Pocket Gopher

**Material.**—Maxillaries and mandibles from blocks 2–4, level 2; blocks 5–7, level 2; blocks 8–9, levels 1, 2; blocks 10–12, levels 1, 2; blocks 13–15, levels 1, 2; blocks 19–21 A, level 3; blocks 19–21 B, levels 2, 3; blocks 22–24 A, levels 2, 3; blocks 22–24 B, level 5; blocks 22–24 C, level 4;

blocks 25–27 C, levels 3, 4, 5; level 1 of the hearth and the packrat nest of block 19.

**Description and Discussion.**—The mandibles that are referred to this species cannot be distinguished from those of modern representatives. The lower molars are drawn out to points on the lingual side. Some lower molars tend to be grooved on the labial side. The anterior lobe of $P_4$ is triangular. There is no deep pit between the tooth row and the ascending ramus of the jaw as in *Geomys*. The $M_3$ is subcircular. The incisive foramina open posterior to the anterior opening of the infraorbital canal.

This is the most abundant gopher in the Pratt Cave deposits. It is common today in McKittrick Canyon close to Pratt Cave.

*Dipodomys ordii* Woodhouse, Ord's Kangaroo Rat

**Material.**—Left mandible from blocks 8–9, level 2 silt layer (TMM 41172–688); right maxillary from blocks 10–12, level 2 (TMM 41172–254); right mandible from blocks 13–15, level 1 (TMM 41172–711); left mandible from blocks 22–24 B, level 5 (TMM 41172–658); left maxillary from blocks 25–27 B, level 4 (TMM 41172–664).

**Description and Discussion.**—The masseteric foramen opens in a fossa which is steep-walled anteriorly as is *Dipodomys spectabilis* but differs from it in its smaller size. In *D. merriami* the masseteric foramen does not lie in a deep fossa but is in a shallow depression. The Pratt Cave specimen resembles *D. ordii* in the location of a small nutrient foramen close behind $M_3$ on the crest of the ridge extending posteriorly from $M_3$. In *D. merriami* this foramen is located more posteriorly and is on the lingual side rather than on the crest of the ridge.

The $P_4$ has enamel breaks at both ends of the hypolophid. The $M_3$ is oval and has enamel breaks at both lingual and labial ends. The enamel breaks develop late in this species (Wood 1935). This specimen is apparently old, and the teeth are sufficiently worn to show the enamel breaks. The $P^4$ is roughly triangular, with the pattern worn away. The anterointernal corner has a distinct re-entrant, making the tooth asymmetrical. *D. merriami* lacks this re-entrant or has it very poorly developed. The $M^1$ is oval, with a re-entrant on the labial end. This is as found in Recent specimens of *D. ordii*. No enamel breaks are present in the Pratt Cave specimen, but according to Wood (1935), they appear late in life. In *D. merriami* the enamel breaks appear early.

*Dipodomys ordii* is uncommon below the Guadalupe Escarpment today but is abundant elsewhere in Culberson County (Davis and Robertson 1944).

*Dipodomys spectabilis* Merriam, Banner-tailed Kangaroo Rat

**Material.**—Two left mandibles (TMM 41172–683 and –712) from blocks 22–24 A and blocks 10–12, level 1; and one right mandible (TMM 41172–271) from blocks 19–21 B, level 3.

**Description and Discussion.**—The mandible resembles that of *Dipodomys spectabilis* in its size and robustness and in the presence of a broad, deep fossa on the lingual side of the ascending ramus of the mandible posterior to the $M_3$. The $P_4$ has the outline of a truncated triangle. The enamel is broken in four places—at the anterior corners and at the sides of the hypolophid. Similar breaks are present in the enamel of a Recent specimen of *D. spectabilis* (TNHC 642) from Presidio County, Texas. The $M_{1-2}$ are wider than the $P_4$. All lower molars are less compressed anteroposteriorly than those of TNHC 642 and are more like those figured by Wood (1935: fig. 88). All lower molars have enamel breaks at both the lingual and labial ends as in the Presidio County specimen.

According to Davis (1960), *D. spectabilis* is limited to low hills with sparse vegetation and hard, gravelly soil. Alluvial fans east of the Guadalupe Escarpment support large populations.

*Perognathus hispidus* Baird, Hispid Pocket Mouse

**Material.**—Abundant material from blocks 2–4, levels 2, 4; blocks 5–7, level 2; blocks 8–9, levels 1,2; blocks 10–12, levels 1, 2; blocks 13–15, levels 1, 2; blocks 19–21 A, levels 2, 3; blocks 19–21 B, level 3, blocks 22–24 A, levels 2, 3; blocks 22–24 B, level 4; blocks 25–27 B, level 5; blocks 25–27 C, levels 4, 5.

**Description and Discussion.**—In size and morphology these specimens cannot be separated from Recent specimens of this species. All bones are too large to belong to any other species of *Perognathus*, which might be expected in this area. *P. hispidus* is found in areas of friable soil and moderate vegetation over wide areas of Texas and New Mexico, yet there is but one record for the southern Guadalupe Mountains (Davis 1940).

*Perognathus merriami* Allen, Merriam's Pocket Mouse

**Material.**—Mandibles from blocks 2–4, level 2; blocks 8–9, level 2; blocks 13–15, level 2; blocks 16–18 B, level 1; blocks 19–21 A, levels 1, 2; blocks 19–21 B, levels 3, 4; blocks 22–24 C, level 4.
**Description and Discussion.**—The Pratt Cave material differs from *Perognathus flavus* in the greater posterior turning of the anterolabial cusps of $M_1$ and $M_2$, the lesser anteroposterior compression of the cross lophs of $M_1$ and $M_2$, the smaller size of the posterolabial cusps of $M_1$ and $M_2$ (especially $M_2$), and the relatively deeper mandible.

They differ from *P. nelsoni* in the relatively smaller $P_4$, the much greater posterior extension of the anterolabial cusps of $M_1$ and $M_2$, and the much less parallel transverse lophs of teeth.

They differ from *P. penicillatus* in the relatively smaller $M_3$, lower crowned teeth, greater posterior development of the anterolabial cusp of $M_1$ and $M_2$, and a relatively shorter $P_4$.

They differ from *P. flavescens* in the larger $P_4$ and the presence of an external cingulum joining the two lophs on $M_1$ and $M_2$.

*P. merriami* is widely distributed in western Texas, New Mexico, and northern Mexico; it occurs in areas of sandy or gravelly soils with sparse vegetation. Certainly it is present today in the area around Pratt Cave, but specimens are not available. The nearest record is the vicinity of Pine Springs (Davis and Robertson 1944).

ORDER Lagomorpha
Family Leporidae
*Lepus californicus* Gray, Black-tailed Jackrabbit

**Material.**—One left maxillary (TMM 41172–778) from blocks 16–18 A, level 1; one left mandible (TMM 41172–834) from blocks 5–7, level 2; two upper molars (TMM 41172–786 and –787) from blocks 2–4, level 2. Additional postcranial material not positively identifiable to species from blocks 2–4, level 2; blocks 8–9, levels 1 and silt layer of 2; blocks 10–12, levels 1, 2; blocks 13–15, levels 1, 2; blocks 19–21 A, level 3; blocks 19–21 B, level 2; blocks 22–24 A, levels 2, 3; blocks 22–24 B, levels 2, 4; blocks 22–24 C, level 3; blocks 25–27 A, level 2; blocks 25–27 B, levels 3, 4, 5, 6; blocks 25–27 C, level 4; level 1 of the hearth; block 19, packrat nest.
**Description and Discussion.**—The Pratt Cave material has been compared with *Lepus americanus, L. townsendii,* and *L. californicus*, and found to be indistinguishable from *L. californicus*. The inner and outer ends of the trigonids and talonids of the $P_3$–$M_3$ are rounded as in *L. californicus* rather than pointed as in *L. americanus*. The labial groove separating the trigonid and talonid of the lower teeth is deep and parallel-sided as in *L. californicus*. This groove is shallow in *L. americanus*. The size is the same as that of Recent specimens of *L. californicus* and is larger than the specimen of *L. americanus* available for comparison.

The upper molars of the Pratt Cave *Lepus* and Recent specimens of *L. californicus* are proportionately wider than those of *L. townsendii* and have the anterior and posterior ends less convex and more nearly parallel. The re-entrants of the upper teeth are narrower and extend closer to the labial margin of the teeth in *L. californicus* than in *L. townsendii*. The Pratt Cave *Lepus* material is similar to *L. californicus* in these characters.

There is no evidence of the presence of either *L. townsendii* or *L. americanus* in the Pratt Cave material. Both of these species might be expected in deposits of late Pleistocene age in this region.

*L. californicus* presently is widely distributed in the lowlands below Pratt Cave.

*Sylvilagus audubonii* (Baird), Desert Cottontail

**Material.**—One right edentulous maxillary (TMM 41172-36), one right maxillary with $P^2$–$M^3$ (TMM 41172–194), one left maxillary with $P^{2-4}$ (TMM 41172–37) from levels 2 and 3.

**Description and Discussion.**—*Sylvilagus audubonii* is so similar to *S. floridanus* in most cranial characters that it is extremely difficult to differentiate the two species. The palatine of *S. audubonii* has on its medial side a prominent rounded ridge which projects into the basipharyngeal canal. (This results in a rapid narrowing of the canal posteriorly.) The ridge is poorly developed in *S. floridanus* and the basipharyngeal canal narrows gradually posteriorly. The one specimen referred to *S. audubonii* shows the anterior part of this ridge on the medial surface of the palatine.

This species is common around Pratt Cave.

*Sylvilagus* sp.

**Material.**—Abundant dental and postcranial material from all levels.

**Description and Discussion.**—Most of the *Sylvilagus* material from Pratt Cave cannot be specifically identified. There is the possibility that some of it represents *S. floridanus robustus*, which is known from McKittrick Canyon today.

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# *Ground Sloth Dung of the Guadalupe Mountains*

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Eight caves in the North American continent are known to contain the dung of the extinct Shasta ground sloth (*Nothrotheriops shastense*). Four of these lie within the bounds of the Guadalupe Mountains National Park (Fig. 1). The dried feces of this large extinct herbivore have been used to reconstruct its diet and the environment in which it lived (Laudermilk and Munz 1934; Martin et al. 1961; Long et al. 1974). Through radiocarbon dating, the dung can be used to determine the time of occupation of the caves by the sloths. In this study, we compare Shasta ground sloth dung with that of other herbivores. We wish to learn more of the life history of this extinct species.

The Upper Sloth Caves (Caves 05, 08, and 09; Logan and Black 1977) are located on the west-facing escarpment of the Guadalupe Mountains at 2000 m elevation. They were first mentioned by Schultz (1943) who was present during the excavation of these caves in the 1930s. No bones identified as sloth have been recovered from test excavations. The dung recovered closely resembles that of sloths from better known deposits, such as Rampart Cave, Arizona. The stratigraphically controlled excavations of Logan in Cave 08 provide most of the material for this study. Of particular interest to us is the sloth dung in Stratum 3, Trench 1, Cave 08.

Williams Cave at 1500 m in the foothills southwest of the Guadalupe Mountains has been known for some time (Ayer 1936). Both cultural strata and underlying Pleistocene faunal deposits were removed during the course of archaeological excavations in the 1930s. Unfortunately, stratigraphic controls were imperfect. Dung identified by Laudermilk as that of the Shasta ground sloth was reported in Ayer (1936).

## METHODS

Eleven ground sloth dung samples were subjected to fractional analysis. Six were from Stratum 3, Trench 1, Cave 08. Unprovenienced sloth dung from Williams Cave was obtained for study from the Carlsbad Public Library, Carlsbad, New Mexico, and the Academy of Natural Sciences,

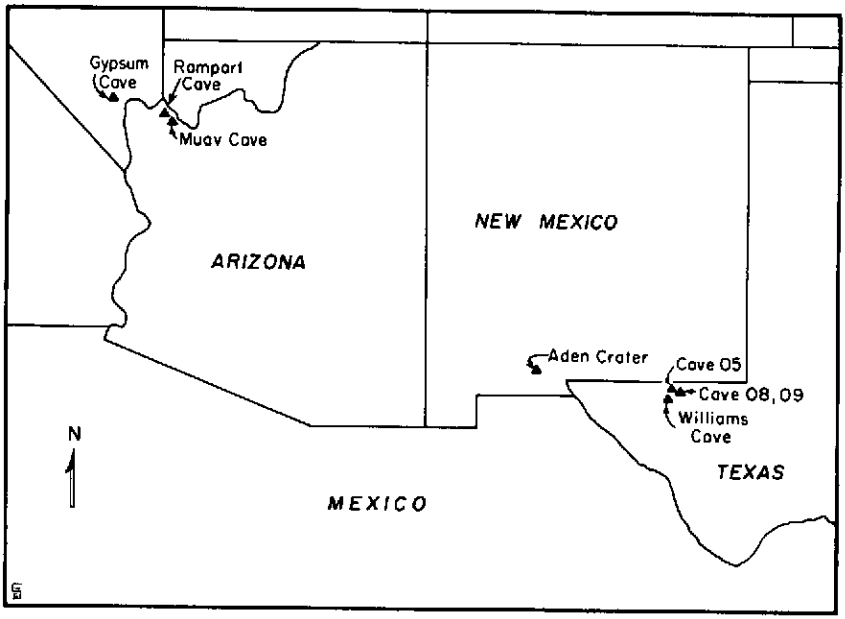


**Fig. 1.** Ground sloth dung caves of North America.

TABLE 1. Type and provenience of dung samples used in fractional and pollen analyses.

| Sample no. | Description |
|---|---|
| 1–6 | Sloth. Cave 08, Trench 1, Stratum 3, ca. 35 cm. Guadalupe Mountains, Culberson County, Texas. |
| 7–8 | Artiodactyl fecal pellets. Cave 08, Stratum 3, ca. 15 cm. Guadalupe Mountains, Culberson County, Texas. |
| 9 | Cow. Collected in the vicinity of the Upper Sloth Caves, Guadalupe Mountains, Culberson County, Texas. |
| 10–11 | Sloth. Unprovenienced dung balls from Williams Cave, Guadalupe Mountains, Texas. |
| 12 | Cow. Collected in the vicinity of Rampart Cave, Grand Canyon, Arizona. |
| 13 | Black rhinoceros. Serengeti Plain, vicinity of Olduvai Gorge, Tanzania. |
| 14 | Wild burro. Warm Sulfur Springs, Panamint Valley, California. |
| 15 | Cow. Medanos de Ricardo, Los Palomas, Argentina. |
| 16 | Cow. Hanging Rock Cave, Churchill County, Nevada. |
| 17–18 | Sloth. Unprovenienced dung balls from Rampart Cave, Grand Canyon, Arizona. |
| 19 | Sloth. Unprovenienced dung ball from Gypsum Cave, Clark County, Nevada. |
| 20 | Musk ox. Captive in the vicinity of Farmington, Vermont. |

TABLE 2. Data from fractional analysis of dung samples expressed as dry weight in grams and percent of dry weight of sample before treatment.

| Weight and Particle Size | | Sample Number | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 9 | 10 | 11 | 12 | 13 |
| Weight (g) before treatment | | 29.74 | 32.19 | 38.29 | 35.87 | 23.68 | 13.27 | 41.51 | 14.98 | 28.11 | 14.41 | 14.57 |
| Weight of Particles | | | | | | | | | | | | |
| >3.4 mm | | 3.70 | 5.89 | 10.93 | 2.26 | 4.24 | 1.41 | 0.01 | 5.20 | 7.18 | 0 | 6.24 |
| >2.0 mm | <3.4 mm | 1.61 | 4.07 | 4.28 | 1.34 | 1.93 | 0.43 | 0.08 | 0.35 | 0.72 | 0.03 | 1.42 |
| >1.0 mm | <2.0 mm | 2.53 | 3.19 | 3.01 | 1.93 | 3.62 | 1.04 | 2.09 | 1.17 | 1.64 | 1.37 | 1.65 |
| >0.6 mm | <1.0 mm | 1.17 | 1.59 | 2.11 | 1.34 | 1.50 | 0.66 | 3.01 | 0.61 | 0.74 | 1.99 | 0.75 |
| >0.3 mm | <0.6 mm | 1.32 | 1.67 | 1.70 | 2.26 | 1.50 | 0.55 | 4.02 | 0.62 | 0.77 | 2.08 | 0.77 |
| <0.3 mm | | 19.41 | 15.79 | 16.26 | 24.92 | 10.85 | 9.17 | 32.30 | 7.03 | 17.05 | 8.94 | 3.75 |
| Percent of Particles | | | | | | | | | | | | |
| >3.4 mm | | 12.44 | 18.29 | 28.55 | 7.05 | 17.92 | 10.65 | 0.02 | 34.68 | 25.55 | 0 | 42.86 |
| >2.0 mm | <3.4 mm | 5.41 | 12.65 | 11.18 | 8.07 | 8.33 | 3.26 | 0.19 | 2.36 | 2.75 | 1.94 | 9.71 |
| >1.0 mm | <2.0 mm | 8.50 | 9.90 | 8.47 | 5.38 | 15.27 | 7.83 | 5.03 | 7.81 | 5.84 | 9.50 | 11.30 |
| >0.6 mm | <1.0 mm | 3.94 | 4.93 | 5.51 | 3.73 | 6.33 | 5.00 | 7.25 | 4.10 | 2.62 | 13.82 | 5.14 |
| >0.3 mm | <0.6 mm | 4.43 | 5.19 | 4.44 | 6.29 | 6.33 | 4.18 | 9.68 | 4.15 | 2.75 | 14.46 | 5.26 |
| <0.3 mm | | 65.28 | 49.03 | 38.06 | 69.48 | 45.83 | 69.08 | 77.81 | 46.90 | 60.67 | 62.02 | 25.74 |

TABLE 2. (continued)

| Weight and Particle Size | | Sample Number | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | 14 | 15 | 16 | 17 | 18 | 19 | 20 |
| Weight (g) before treatment | | 13.15 | 22.20 | 26.81 | 15.14 | 16.91 | 6.42 | 10.45 |
| Weight of Particles | | | | | | | | |
| >3.4 mm | | 2.76 | 0.96 | 0.01 | 2.11 | 0.21 | 0.33 | 0.02 |
| >2.0 mm | <3.4 mm | 1.23 | 1.26 | 0.32 | 2.14 | 0.98 | 0.59 | 0.29 |
| >1.0 mm | <2.0 mm | 2.24 | 2.14 | 2.87 | 1.73 | 1.32 | 0.77 | 2.32 |
| >0.6 mm | <1.0 mm | 1.61 | 2.21 | 2.95 | 0.50 | 0.25 | 0.24 | 1.58 |
| >0.3 mm | <0.6 mm | 1.51 | 2.73 | 4.65 | 0.87 | 0.87 | 0.50 | 2.00 |
| <0.3 mm | | 3.80 | 12.90 | 15.99 | 7.79 | 13.27 | 3.99 | 6.21 |
| Percent of Particles | | | | | | | | |
| >3.4 mm | | 21.01 | 4.34 | 0.05 | 13.96 | 1.26 | 5.12 | 0.20 |
| >2.0 mm | <3.4 mm | 9.36 | 5.69 | 1.21 | 14.15 | 5.81 | 9.14 | 2.76 |
| >1.0 mm | <2.0 mm | 17.06 | 9.62 | 10.71 | 11.40 | 7.83 | 12.02 | 22.17 |
| >0.6 mm | <1.0 mm | 12.21 | 9.95 | 11.01 | 3.30 | 1.48 | 3.66 | 15.09 |
| >0.3 mm | <0.6 mm | 11.45 | 12.30 | 17.37 | 5.76 | 5.15 | 7.85 | 19.15 |
| <0.3 mm | | 28.91 | 58.09 | 59.64 | 51.43 | 78.48 | 62.22 | 59.37 |

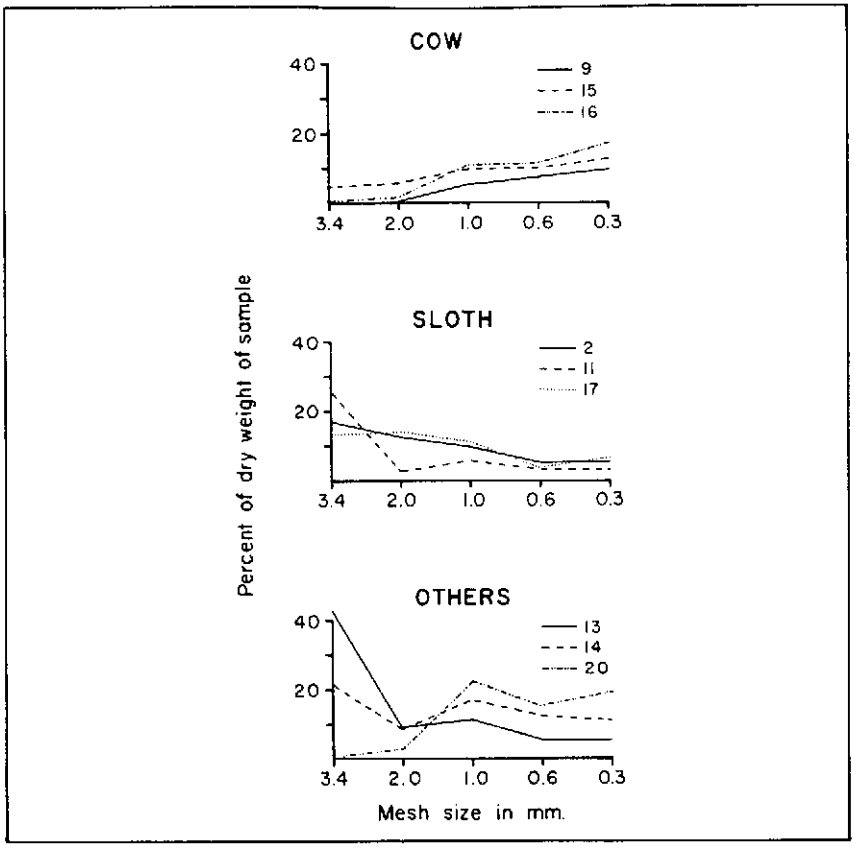


**Fig. 2.** Graphic representation of dung size-frequency distribution derived from fractional analysis. See Table 1 for an explanation of sample numbers.

Philadelphia, Pennsylvania. Fossil ground sloth dung from Rampart Cave, Grand Canyon, Arizona; and Gypsum Cave, Nevada; and modern dung samples of cow, burro, rhinoceros, and musk ox were used for comparison (Table 1).

Each dung sample was dried, weighed, and disaggregated in a solution of water and detergent. Sonic vibration proved effective in separating tightly compacted fecal material. When disaggregation was complete, the mixture was decanted through a series of five sieves of decreasing mesh size—3.4 mm, 2.0 mm, 1.0 mm, 0.6 mm, and 0.3 mm. The initial decant passing through the sieves was captured and used for pollen analysis. Fecal material from each sieve was removed, dried, and weighed separately. The weight of solubles and particles less than 0.3 mm in size was obtained by adding the weight of

TABLE 3. Pollen counts of fecal samples from Cave 08 and Williams Cave. See Table 1 for type and provenience of samples.

| | Sample no. | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Pollen types** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **10** | **11** |
| *Picea* | 4 | 6 | 1 | | | 1 | | | | |
| *Pseudotsuga* | | | 2 | | | | | | | |
| *Pinus* | 97 | 16 | 30 | 24 | | 15 | 13 | 11 | 9 | 1 |
| *Juniperus* | 2 | 1 | 9 | 3 | 2 | 4 | 3 | 3 | 6 | 16 |
| *Ostrya* | 4 | 2 | 16 | 1 | | 5 | 11 | 1 | 1 | |
| *Quercus* | 4 | | 2 | | | | 2 | 2 | 3 | 2 |
| *Acer* | 2 | | | | | 1 | | | | |
| *Celtis* | | | | | | 3 | | | | |
| Cheno-am | | 1 | | | | 2 | 1 | 1 | 10 | 57 |
| Gramineae | 15 | 37 | 8 | 6 | 19 | 34 | 73 | 135 | 16 | 20 |
| *Artemisia* | 24 | 81 | 26 | 116 | 46 | 65 | 31 | 4 | 78 | 20 |
| Short-spine Compositae | 2 | 6 | 2 | 8 | 10 | 4 | 2 | 2 | 2 | 12 |
| Long-spine Compositae | 29 | 40 | 95 | 30 | 110 | 45 | 43 | 21 | 54 | 50 |
| *Senecio*-type | | | | | | | | | | |
| *Cercocarpus*-type | 2 | 2 | 3 | 1 | 2 | | | 1 | 2 | 3 |
| *Petrophytum*-type | | | | | | | | 11 | | |
| *Prunus*-type | 1 | | | | | | | | | |
| *Potentilla*-type | | | | | | 1 | | | | |
| Scrophulariaceae | | | | 1 | | | | | 1 | 1 |
| Onagraceae | | | | 1 | | | | | | |
| Leguminosae | | | | | | | | 1 | 3 | |
| Saxifragaceae | | 1 | | 1 | 4 | 1 | | 2 | 2 | |
| *Rhus* | | 1 | | | | | | | 4 | |
| *Cylindropuntia* | | | 1 | | | | | | | |
| *Platyopuntia* | | | | | 1 | 1 | | | | |
| Caryophyllaceae | | | | | | 1 | | | | |
| *Euphorbia* | | | | | | | 1 | | | 4 |
| Malvaceae | | | | | | | | | | 1 |
| Boraginaceae | | | | 3 | 1 | | | | | |
| Polemoniaceae | | 1 | | | | | | | 1 | |
| *Arceuthobium* | 1 | | 1 | 2 | | | | | | |
| Rubiaceae | | 1 | | | 1 | 1 | 3 | | | |
| *Berberis* | | | | | | | | | 1 | |
| *Rhamnus* | | | | | | | | | | 1 |
| Solanaceae | | | | | | 1 | | | | |
| *Kallstroemia* | | | | | | | | | | 1 |
| *Larrea*-type | | | | | | | 5 | | | |
| *Sparganium–Typha* | | | | | | | 1 | | | |
| Umbelliferae | | | | | | | 1 | | | |
| Undetermined | 3 | 1 | 2 | | 1 | 1 | | | 2 | 1 |
| Unknown | 10 | 3 | 2 | 3 | 3 | 14 | 9 | 1 | 5 | 10 |
| N | 200 | 200 | 200 | 200 | 200 | 200 | 200 | 200 | 200 | 200 |
| $\sum$AP | 113 | 25 | 60 | 28 | 2 | 29 | 29 | 16 | 19 | 19 |
| Trilete, psilate spores | | | 1 | 3 | | | | | | |
| Grains per gram ($\times 10^3$) | 29.9 | 31.1 | 11.6 | | 112.6 | 6.0 | 47.9 | 124.0 | 59.3 | |

plant fragments captured in each sieve and subtracting that from the initial dry weight of the sample. Relative percentages calculated from the initial dry weight were used in comparing the samples (Table 2).

Separate pieces of samples 1, 3, 10, and 11 were submitted to the Laboratory of Isotope Geochemistry, Department of Geosciences, University of Arizona, for radiocarbon analysis. An additional sloth dung sample from a separate area in Cave 08, one from Cave 05, and artiodactyl fecal pellets from Stratum 3, Cave 08 were also dated (Table 3).

Decant recovered from the screening process was centrifuged. The remaining solids were extracted for pollen following the methods for fecal material outlined by Spaulding (1974). Before fractional analysis, a known amount of *Eucalyptus* pollen grains was added to each sample to enable us to determine the amount of fossil pollen per gram of dung (Stockmarr 1973). Two hundred pollen grains were counted in each sample and relative frequencies of each pollen type were calculated from this pollen sum (Martin 1963). *Eucalyptus* pollen and spores were counted separately and not included in the pollen sum (Table 3).

## RESULTS

Fractional separation of herbivore dung produces a size-frequency curve with trends that appear to be unique to the dung of particular species (Table 2, Fig. 2). The dung of ruminants, such as cow or musk ox, contains high percentages of fine particles. A nonruminant browser, such as rhinoceros, has very coarse dung. The size-frequency curve of burro dung is most similar to that of sloth, but has a greater percentage of fine particles. Differences in the size-frequency curves are greater between than within a species. Diets of the sloths that occupied Williams Cave and those that occupied Cave 08 differed markedly. Dung from the former site consists mostly of *Yucca* fiber, whereas dung from the latter contains mostly twigs. Size-frequency curves produced by the dung from Williams Cave and Cave 08 are quite similar (Fig. 2).

Analysis of pollen from sloth dung shows that most samples have high relative percentages of long-spine Compositae and *Artemisia* pollen (Table 3). Relative percentages of arboreal pollen (AP), particularly pine (*Pinus*), are higher in the sloth dung samples from Cave 08 than from Williams Cave. Four-wing salt-bush (*Atriplex canescens*) seeds were found in the Cave 08 sloth dung. Cheno-am (Chenopodiaceae plus *Amaranthus*) pollen is infrequent in those samples. However, cheno-am pollen is relatively abundant in the samples from Williams Cave.

The amount of *Eucalyptus* pollen counted with every 200 fossil pollen grains varies greatly. Determinations of the amount of fossil pollen per gram of sloth dung vary from 112,600 to 6000 grains per gram. It appears that much fossil and *Eucalyptus* pollen was trapped in the screens during

fractional analysis and was therefore not included in the decant used for pollen analysis. Hence, values for absolute amounts of pollen are considered to be unreliable and are not used. In future studies, a separate section of dung should be reserved for pollen analysis.

In addition to sloth dung, fossil artiodactyl fecal pellets from Stratum 3, Cave 08 were analyzed for pollen. These pellets are much larger than those dropped by deer (*Odocoileus*), sheep (*Ovis*), or modern mountain goat (*Oreamnos americanus*). They are closer in size and weight to pellets found in Rampart and Stanton's caves, Grand Canyon, Arizona, which were assigned by Iberall (1972) to the extinct Harrington's mountain goat (*Oreamnos harringtoni*). They also resemble the fecal pellets of the extant elk (*Cervus canadensis*). Bones of *Oreamnos* have been recovered from Pleistocene-age deposits in the Guadalupe Mountains (Logan, pers. comm.) and Merriam's elk (*Cervus canadensis merriami*) was present in the Guadalupes until Recent times. A radiocarbon date on the fossil pellets from Stratum 3, Cave 08 yielded an age of 11,760 ± 610 BP (radiocarbon years before present).

## DISCUSSION

Through fractional analysis we have been able to discriminate among the dung of five herbivore genera. Although our sample is small, the data indicate that ground sloth dung may be quantitatively identified without having to rely upon associated faunal remains. Variation in the relative percentages of particles greater than 2.0 mm in size are attributed to dietary differences. Sample 18 from Rampart Cave is remarkably fine textured for ground sloth dung (Table 4). Before analysis, it was noted that this sample was degraded,

TABLE 4. Radiocarbon ages of sloth dung from the Guadalupe Mountains. All age determinations are by the Laboratory of Isotope Geochemistry, Department of Geosciences, University of Arizona and are given as radiocarbon years before the present (1950; BP).

| Sample number | Radiocarbon number | Description | Age (BP) |
|---|---|---|---|
| 1 | A–1583 | Sloth dung. Cave 08, Trench 1, Stratum 3, ca. 30 cm. | 10,750±140 |
| 2 | A–1584 | Sloth dung. Cave 08, Trench 1, Stratum 3, ca. 30 cm. | 11,060±180 |
| 11 | A–1588 | Sloth dung. Williams Cave. No provenience. | 11,930±170 |
| 10 | A–1589 | Sloth dung. Williams Cave. No provenience. | 11,140±320 |
| – | A–1519 | Sloth dung. Cave 05. No provenience. | 11,590±230 |
| – | A–1533 | Artiodactyl fecal pellets. Cave 08, Stratum 3, ca. 15 cm. | 11,760±610 |
| – | A–1534 | Sloth dung. Cave 08, Stratum 3, ca. 15 cm. | 10,780±140 |
| – | A–1563 | Sloth dung. Williams Cave. No provenience. | 12,100±210 |

perhaps by fungi. It is unlike well-preserved ground sloth dung from the cave.

The plant communities existing in the area at the time the sloths occupied these caves differed markedly from those of today. Needles of Douglas fir (*Pseudotsuga menzeisii*) and southwestern white pine (*Pinus strobiformis*) were found in the dung balls from Cave 08. These macrofossils and the radiocarbon dates (Table 4) indicate that the Upper Sloth Caves were frequented during the biochronological zone designated Wisconsin 2 (W2) by Van Devender et al. (1977). The presence of spruce (*Picea*) pollen in samples 1, 2, 3, and 6 supports their assertion that, although spruce is no longer present in the macrofossil record, it had not been completely extirpated from the Guadalupe Mountains by ca. 11,000 BP. Radiocarbon ages of the Williams Cave sloth dung (Table 3) indicate that this site may have been frequented by *Nothrotheriops* during zone W1 (Van Devender et al. 1976).

The clustering of radiocarbon dates and the relatively thin layer of sloth dung found in Cave 08, Stratum 3 suggests that sloths occupied this cave only briefly. The deepest known deposit of ground sloth dung, 1.4 m in depth representing over 30,000 years of sporadic occupation, comes from Rampart Cave, Arizona. Like the sloths of Rampart Cave, those of the Guadalupe Mountains apparently did not frequent the caves during the Wisconsin maximum between ca. 24,000 and ca. 14,000 BP. At present, there is no established radiocarbon record of ground sloths in any cave during the full-glacial. Older records (pre-Wisconsin maximum) of sloths in the Guadalupe Mountains have not been established, possibly due to the poor preservation of organic matter in the deeper strata of the Upper Sloth Caves. Sloths occupied the Upper Sloth Caves coincidentally close to the time of their ultimate demise, which Long et al. (1974) place at ca. 11,000 BP.

The absence of *Nothrotheriops* from Rampart Cave from ca. 24,000 to ca. 14,000 BP cannot necessarily be attributed to unfavorable environmental factors. During the occupation of the Upper Sloth Caves, the vegetation that prevailed was typical of much higher and cooler elevations than would have surrounded Rampart Cave even during the full-glacial (Phillips and Van Devender 1974). Similarly, Shasta ground sloth extinction in the Guadalupe Mountains cannot easily be attributed to changing climate. Sloths lived in Gypsum Cave in southern Nevada at a time when the late Pleistocene climate supported Joshua-tree vegetation at 610 m (Wells and Berger 1967). The average annual precipitation and temperature needed to support such a community implies that it was probably as xeric or even more xeric than present conditions in the vicinity of the Guadalupe Mountains sloth caves.

Radiocarbon ages of the Guadalupe Mountains sloth dung are not appreciably younger than the time of Clovis big game hunters associated with mammoths which Haynes (1971) puts at 11,200 years ago. Possible exceptions are the two samples from Cave 08 (Table 4). Contamination by younger material cannot be ruled out as the cause of these younger dates.

Further effort is needed to replicate them. Possibly ground sloths lingered slightly longer in the Guadalupes than elsewhere.

## CONCLUSIONS

Fractional analysis provides a quantitative basis for distinguishing fossil sloth dung from that of other herbivores.

The late Pleistocene distribution of the Shasta ground sloth ranges from extremely xeric sites such as Gypsum Cave, Nevada, at 610 m to the semi-xeric Upper Sloth Caves of the Guadalupe Mountains at 2000 m. Wide ecological amplitude argues against any megafaunal extinction hypothesis founded upon climatic change.

Qualitative examination of Shasta ground sloth dung from Williams Cave and the Upper Sloth Caves shows considerable difference in composition. This suggests a high degree of versatility in the sloths' dietary preferences.

Results of radiocarbon analysis of dung from the Guadalupe Mountains sloth caves suggest that the animals might have lived a few hundred years longer than Long et al. (1974) suggested on the basis of dung deposits elsewhere.

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Contribution no. 749, Department of Geosciences, University of Arizona.

# *Mammals of the Guadalupe Mountains National Park, Texas*

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The Guadalupe Mountains National Park was authorized by an act of Congress on 15 October 1966 and was formally established on 30 September 1972. The park covers 76,468.6 acres located in Culberson and Hudspeth counties of Trans-Pecos Texas. The park contains the Texas portion of the uplifted Capitan Reef of Permian age. The southern end of the escarpment is marked by the prominent El Capitan. The escarpment extending northwest from El Capitan contains other impressive peaks including Guadalupe Peak, which at 8759 ft is the highest point in Texas.

The low and intermediate elevations in the park contain floral and faunal elements from the Chihuahuan Desert. The high elevations are inhabited by montane elements with Rocky Mountain affinities. These montane elements represent an island surrounded by, and in dynamic equilibrium with, the desert flora and fauna. The mountains, all canyons, and desert areas contain many fragile floral and faunal microhabitats. To preserve the natural heritage of the park, baseline data are being gathered by the National Park Service for use in development of the park's master plan.

The first mammal survey of the Guadalupe Mountains was conducted by Vernon Bailey of the U.S. Biological Survey between 9 and 25 August 1901 (Bailey 1905). His field notes and specimens are deposited in the National Museum of Natural History. During his visit,Bailey worked in Upper Dog Canyon, McKittrick Canyon, and various portions of the high country. Bailey (1905) reported 17 species inhabiting the Guadalupe Mountains and listed two additional species that possibly occurred there. The next work in the area was conducted by William B. Davis and field parties from Texas A & M University during 1938, 1939, and 1940 (Davis 1940; Davis and Robertson 1944). They worked at seven stations including McKittrick Canyon, West Dog Canyon, The Bowl, Burned Cabin, Pine Springs and Bear Canyons, Frijole, and 7 miles N Pine Springs. A total of 35 species of mammals (Davis 1940; Davis and Robertson 1944) were recorded as occurring in the Guadalupe Mountains as a result of this survey. LaVal

(1973) studied the distribution and ecology of bats in McKittrick Canyon during 1968 and 1970. He presented data on 13 species.

Our survey began in late May 1973 and continued through August 1975. The objectives of our study, which was supported by the National Park Service, were to survey the mammals occurring in the Guadalupe Mountains National Park, Texas, and to correlate their distribution with major plant associations. This inventory of the natural resources of the park is preliminary to the development of any serious management program. Therefore, we present the following accounts to serve as baseline data for future mammalian work in the park and development of the master plan for the park.

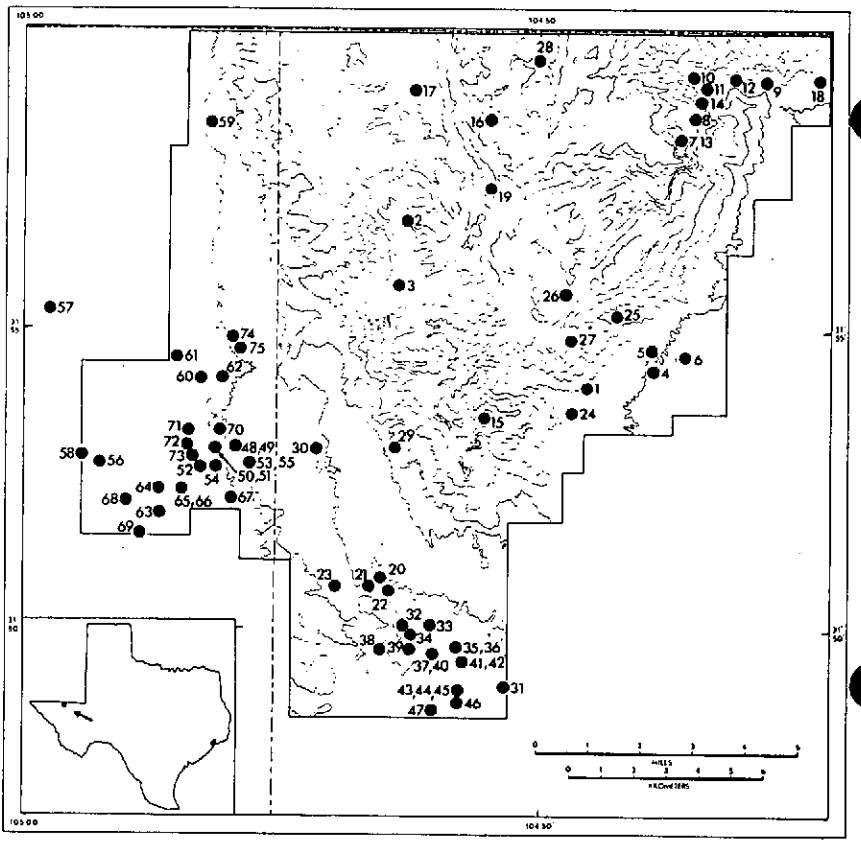


**Fig. 1.** Map showing collecting localities in the Guadalupe Mountains National Park, Texas. Numbers correspond to those given in text with the exact location of each place.

**Fig. 2.** (*Upper*) Photograph of eastern slope of Guadalupe escarpment showing Frijole and Manzanita Spring.

**Fig. 3.** (*Lower*) Photograph of a dry arroyo in McKittrick Canyon in the Guadalupe Mountains National Park, Texas.

## METHODS AND MATERIALS

During our survey of mammals of the Guadalupe Mountains National Park in 1973–75, we visited selected sites throughout the park (see below) during all seasons of the year. Rodents were collected using various types of traps including museum specials, Sherman live-traps, Victor steel traps, and

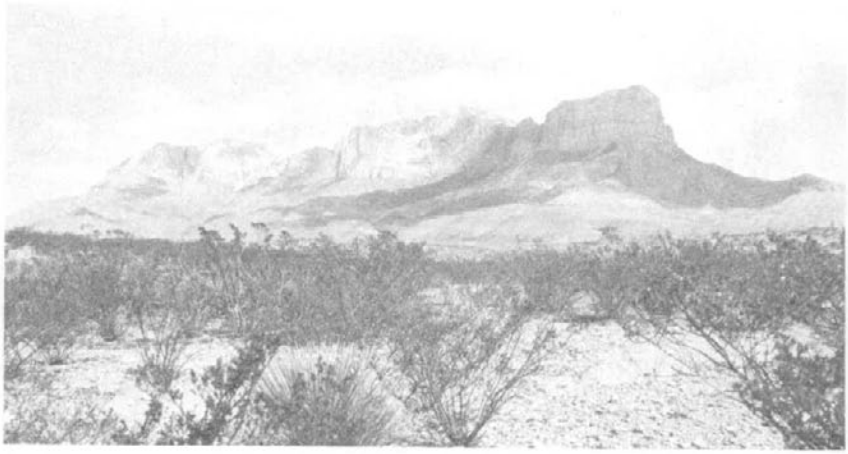

**Fig. 4.** (*Upper*) Photograph of southwestern face of El Capitan (*right*) and Guadalupe Peak (*center*) showing creosote bush community typical of the western and southern lowlands in the Guadalupe Mountains National Park, Texas.

**Fig. 5.** (*Lower*) Photograph of the coniferous forest in The Bowl area in the Guadalupe Mountains National Park, Texas.

National live traps. Bats were obtained by mist-netting, by shooting individuals as they flew at dusk, and by inspecting daytime roosts. Carnivores were taken by shooting and trapping and rabbits were obtained by shooting. All individuals taken in our work were prepared as various types of standard museum specimens. These specimens and extensive field notes made during our work are deposited in The Museum of Texas Tech University (TTU).

In addition to our material, we have examined specimens (abbreviations used to identify specimens in text) deposited in the Texas Cooperative Wildlife Collection, Texas A & M University (TCWC) and National Museum of Natural History (USNM), Washington, D.C. All cranial measurements were taken by means of dial calipers; external measurements were those recorded by the field collector. All measurements are recorded in millimeters. Specimens were karyotyped using the methods of Baker (1970).

## COLLECTING LOCALITIES

Listed below are the collecting localities visited during our survey of the mammals of the park. Locality numbers correspond to those given in Fig. 1.

Following each locality or groups of localities below is a brief description of the habitat being sampled. Four major habitats in which work was conducted are shown in Figs. 2–5. Cornely (1976) has presented a checklist of the mammals of the park with their major habitat preference.

### Culberson County

1) **Bear Canyon–Pump House** (el. 1829 m).—The ruins of a pump house containing very large water pumps are situated on the Bear Canyon trail above upper Pine Spring. The vegetation is open canyon woodland including *Quercus grisea, Juniperus pinchotii, Arbutus xalapensis, Bouteloua gracilis*, and *Bouteloua curtipendula*.

2) **Blue Ridge Campground** (el. 2438 m).—Blue Ridge Campsite is situated at the north end of Blue Ridge which extends due north of Bush Mountain. The vegetation is open woodland including *Pinus ponderosa, Quercus gambelii, Pseudotsuga menziesii, Juniperus deppeana, Bouteloua gracilis, Muhlenbergia pauciflora*, and *M. dubia*.

3) **Bush Mountain** (el. 2530 m).—Bush Mountain forms part of the western ridge of the Guadalupe Mountains. Traps were set in pine-oak meadow immediately southeast of the summit. Plants included *Pinus ponderosa, Quercus gambelii, Pseudotsuga menziesii, Juniperus deppeana, Ceanothus greggii, Cercocarpus montanus, Bouteloua gracilis, Muhlenbergia pauciflora, M. dubia*, and *Hymenoxys richardsonii*.

4) **Frijole Ranger Station** (el. 1692 m); 5) **Manzanita Spring** (el. 1676 m); 6) **Nipple Hill** (el. 1646 m).—Frijole Ranger Station, Manzanita Spring, and Nipple Hill are on the bajada east of the Guadalupe Escarpment. The vegetation is open juniper woodland and grassland including *Juniperus pinchotii, Muhlenbergia setifolia, Bouteloua gracilis, B. warnockii*, and *Parthenium incanum*.

7) **Grisham-Hunter Lodge** (el. 1615 m); 8) **½ mi. NNE Grisham-Hunter Lodge** (el. 1615 m); 9) **Half-way between Pratt Lodge and McKittrick Canyon Parking Lot** (el. 1554 m); 10) **North McKittrick Canyon at Devil's Den Canyon** (el. 1585 m); 11) **Pratt Lodge** (el. 1585 m); 12) **0.3 mi. N, 0.5 mi. E Pratt Lodge** (el. 1570 m); 13) **Stone Cabin above Grisham-Hunter Lodge** (el. 1645 m); 14) **Thrush Hollow, ¼ mi. S Pratt Lodge** (el. 1590 m).—The vegetation of the canyon walls is succulent desert, whereas the canyon floor vegetation is canyon woodland. An intermittent stream in McKittrick Canyon is the only permanent stream in Guadalupe Mountains National Park. Plants in the canyon include *Acer grandidentatum, Quercus muhlenbergii, Arbutus*

*xalapensis, Pinus ponderosa, Stipa tenuissima, Muhlenbergia emersleyi, Quercus undulata, Juniperus deppeana*, and *Dasylirion leiophyllum*.

15) **Guadalupe Peak Campsite** (el. 2439 m).—Guadalupe Peak Campsite is situated on top of the eastern escarpment due east of Guadalupe Peak. The vegetation is open coniferous woodland dominated by *Pinus ponderosa* and *Muhlenbergia pauciflora*.

16) **Lost Peak Mine** (el. 2164 m).—Lost Peak Mine is an old copper mine between Upper Dog Canyon Ranger Station and Lost Peak. The mine is on the west slope of the ridge which the trail from the ranger station to Lost Peak traverses. The vegetation is chaparral and succulent desert including *Ceanothus greggii, Cercocarpus montanus, Nolina micrantha, Dasylirion leiophyllum*, and *Quercus undulata*.

17) **Marcus Cabin-West Dog Canyon,** 6⅛ mi. N, ¾ mi. W Guadalupe Peak (el. 1905 m).—West Dog Canyon is relatively large, with a steep wall forming the east side and a more gradual slope marking the west side. Deep soil of the canyon floor is cut by dry washes. The vegetation is mixed grassland with riparian vegetation along the washes. Plants include *Muhlenbergia repens, Bouteloua gracilis, B. warnockii, Aristida glauca, Berberis haematocarpa, Fallugia paradoxa, Opuntia imbricata, Xanthocephalum sarothrae, Xanthium spinosum, Verbesina encelioides*, and *Pinus edulis*.

18) **McKittrick Canyon Parking Lot** (el. 1524 m).—The parking lot is on the canyon floor at the mouth of the canyon. Canyon floor vegetation is open grassland with succulent desert on the slopes. Species include *Agave lecheguilla, Dasylirion leiophyllum, Bouteloua eriopoda, B. gracilis, Muhlenbergia setifolia*, and *Juniperus pinchotii*.

19) **Mescalero Campground,** 4½ mi. N, ¾ mi. E Guadalupe Peak (el. 2286 m).—Mescalero is situated on top of a ridge separating West Dog Canyon drainage and South McKittrick Canyon drainage. The campsite is on the trail between Upper Dog Canyon Ranger Station and The Bowl. The vegetation is woodland including *Pinus edulis, P. ponderosa, Quercus undulata, Juniperus deppeana, Nolina micrantha, Ceanothus greggii, Rosa stellata*, and *Muhlenbergia dubia*.

20) **Patterson Hills Notch,** 3 1/16mi. S, 1⅜ mi. W Guadalupe Peak (el. 1356 m); 21) **3⅛ mi. S, 1¾ mi. W Guadalupe Peak** (el. 1341 m); 22) **3⅛ mi. S, 1⅜ mi. W Guadalupe Peak** (el. 1356 m); 23) **3¼ mi. S, 2⅜ mi. W Guadalupe Peak** (el. 1341 m).—Water erosion has cut the notch through the eastern ridge of the Patterson Hills along the Williams Ranch Road. The vegetation on the hills is succulent desert, the dry wash in the notch supports riparian vegetation, and the vegetation on the surrounding bajada is desert scrub. Species include *Larrea tridentata, Chilopsis linearis, Fallugia paradoxa, Prosopis glandulosa, Acacia neovernicosa, Brickellia laciniata, Yucca torreyi, Agave lecheguilla, Parthenium incanum*, and *Viguiera stenoloba*.

24) **Pine Springs Canyon** (el. 1768 m).—Pine Springs Canyon cuts deeply into the eastern escarpment of the mountains. The vegetation on the canyon floor is open canyon woodland with succulent desert on the slopes. Species include *Arbutus xalapensis, Juniperus deppeana, Quercus grisea, Bouteloua curtipendula, B. gracilis*, and *Dasylirion leiophyllum*.

25) **Smith Spring-Smith Canyon** (el. 1829 m).—Smith Spring is approximately one-third of the way up Smith Canyon at the end of a trail starting at Frijole Ranger Station. The vegetation around the spring is riparian woodland becoming more open toward the canyon mouth. Plants include *Juniperus deppeana, Quercus grisea, Bothriochloa* sp., *Bouteloua gracilis, Lycurus phleoides*, and *Panicum obtusum*.

26) **The Bowl** (el. 2377 m).—The Bowl is relict coniferous forest interspersed with hardwoods. In many places the young trees are growing in very dense almost impenetrable stands. The Bowl contains a man-made earthen tank which periodically holds water. Plants in The Bowl include *Pinus ponderosa, P. strobiformis, Pseudotsuga menziesii, Quercus gambelii, Muhlenbergia emersleyi, M. pauciflora*, and *Agropyron smithii*.

27) **Upper Bear Canyon Trail** (el. 2362 m).—Upper Bear Canyon Trail is a series of switchbacks which traverses a steep rocky slope with thin loose soil. The vegetation is chaparral including *Quercus undulata, Cercocarpus montanus*, and *Muhlenbergia pauciflora*.

28) **Upper Dog Ranger Station** (el. 1920 m).—The ranger station is located on the floor of Upper Dog Canyon just north of a point where the canyon becomes considerably narrower. The

deep soil of the canyon floor supports open woodland and large, mixed grass meadows. The vegetation of the washes on the eastern slope of the canyon and the canyon floor is riparian woodland. Open slopes support chaparral and succulent desert vegetation. Riparian woodland includes *Quercus muhlenbergii, Acer grandidentatum, Arbutus xalapensis, Cercocarpus montanus, Quercus undulata, Ceanothus greggii*, and *Dasylirion leiophyllum*. Open slopes include *Quercus grisea, Cercocarpus montanus, Nolina micrantha, Agave neomexicana, Ceanothus greggii, Dasylirion leiophyllum*, and *Juniperus deppeana*. Grasses on the canyon floor include *Stipa tenuissima, Muhlenbergia repens, Panicum obtusum*, and *Bouteloua gracilis*.

29) **Williams Ranch House** (el. 1524 m); 30) **½ mi. S, 2⅝ mi. W Guadalupe Peak** (el. 1356 m).—The ranch house is located near the mouth of Bone Canyon at the west base of Guadalupe Peak. The vegetation of the bajada around the house is desert scrub, whereas the slopes above are characterized by succulent desert vegetation. Succulent desert forms include *Agave lecheguilla, Dasylirion leiophyllum, Parthenium incanum*, and *Bouteloua eriopoda*. Desert scrub includes *Larrea tridentata, Prosopis glandulosa, Opuntia lindheimeri, Sporobolus contractus, Setaria leucopila, Muhlenbergia porteri, Bouteloua gracilis*, and *B. eriopoda*.

31) **Williams Ranch Road Entrance**, 4¾ mi. S, ⅞ mi. E Guadalupe Peak (el. 1311 m); 32) **4 mi. S, 1 mi. W Guadalupe Peak** (el. 1356 m); 33) **4 mi. S, ½ mi. W Guadalupe Peak** (el. 1341 m); 34) **4¼ mi. S, 1 mi. W Guadalupe Peak** (el. 1387 m); 35) **4.3 mi. S Guadalupe Peak** (el. 1349 m); 36) **4 5/16 mi. S Guadalupe Peak** (el. 1349 m); 37) **4⅜ mi. S, ½ mi. W Guadalupe Peak** (el. 1356 m); 38) **4⅜ mi. S, 1⅜ mi. W Guadalupe Peak** (el. 1372 m); 39) **4⅜ mi. S, 1⅛ mi. W Guadalupe Peak** (el. 1372 m); 40) **4½ mi. S, ½ mi. W Guadalupe Peak** (el. 1341 m); 41) **4½ mi. S, ⅛ mi. E Guadalupe Peak** (el. 1341 m); 42) **4½ mi. S, ⅜ mi. E Guadalupe Peak** (el. 1326 m); 43) **4⅞ mi. S, ⅛ mi. W Guadalupe Peak** (el. 1311 m); 44) **4⅞ mi. S Guadalupe Peak** (el 1326 m); 45) **4⅞ mi. S, ⅛ mi. E Guadalupe Peak** (el. 1326 m); 46) **5⅛ mi. S Guadalupe Peak** (el. 1311 m); 47) **5⅜ mi. S, ½ mi. W Guadalupe Peak.**—Williams Ranch Road enters near the southeastern corner of the park. The soil is very sandy in lower areas with patches of higher rockier areas. The area is bajada with desert scrub vegetation including *Larrea tridentata, Prosopis glandulosa, Xanthocephalum sarothrae, Sporobolus contractus*, and *Bouteloua eriopoda*.

**Hudspeth County**

48) **Crossroads**, 9/16 mi. S, 4 5/16 mi. W Guadalupe Peak (el. 1219 m); 49) **⅜ mi. S, 4 1/16 mi. W Guadalupe Peak** (el. 1234 m); 50) **⅝ mi. S, 4¾ mi. W Guadalupe Peak** (el. 1204 m); 51) **11/16 mi. S, 4¾ mi. W Guadalupe Peak** (el. 1204 m); 52) **⅞ mi. S, 4⅞ mi. W Guadalupe Peak** (el. 1196 m); 53) **⅞ mi. S, 4 mi. W Guadalupe Peak** (el. 1242 m); 54) **1 mi. S, 4¾ mi. W Guadalupe Peak** (el. 1204 m); 55) **1 mi. S, 3 15/16 mi. W Guadalupe Peak.**—The Crossroads is the area surrounding the junction of primitive roads due west of Williams Ranch House and immediately north of the central ridge of the Patterson Hills. This area is bajada cut by dry washes. The bajada vegetation is desert scrub with riparian vegetation in the washes. Species include *Larrea tridentata, Prosopis glandulosa, Fallugia paradoxa, Atriplex canescens, Opuntia lindheimeri, O. leptocaulis, O. imbricata*, and *Chilopsis linearis*.

56) **Lewis Well**, 11/16 mi. S, 6⅝ mi. W Guadalupe Peak (el. 1128 m); 57) **2⅞ mi. N, 7⅞ mi. W Guadalupe Peak** (outside of park) (el. 1112 m); 58) **7¾ mi. W Guadalupe Peak** (el. 1113 m).—Lewis Well is an old water well marked by a windmill tower on the bajada near the western boundary of the park. West of the well is a large, white, gypsum sand dune, patches of crusted gypsum soil, and areas of lacustrine clay. Each of these areas supports distinct plant communities. The bajada near the well is dominated by *Larrea tridentata* and *Prosopis glandulosa*. Lacustrine clay is dominated by *Atriplex canescens* and crusted gypsum soil is dominated by *Coldenia hispidissima*. The dominant on the gypsum sand dune is *Bouteloua breviseta*.

59) **Northwest Corner**, 4 mi. N, 5½ mi. W Guadalupe Peak (el. 1158 m).—The bajada in the northwest corner of the park has been grazed far less than any other area of the park west or south of the Guadalupe Mountains. This area contains the most well-developed grassland in the Hudspeth County portion of the park and may be an example of the potential natural vegeta-

tion of the creosote bajada of the park. The vegetation is mixed grassland and succulent desert plants including *Bouteloua eripoda, Sporobolus cryptandrus, Tridens muticus, Aristida pansa, Krameria glandulosa, Erioneuron pulchellum, Dyssodia pentachaeta, Viguiera stenoloba, Yucca torreyi, Prosopis glandulosa, Larrea tridentata, Opuntia lindheimeri, O. phaeacantha, O. imbricata, O. schottii, O. violacea, O. leptocaulis*, and *Fouquieria splendens*.

60) **Red Sand Dunes,** ½ mi. N, 4¼ mi. W Guadalupe Peak (el. 1189 m); 61) **1 7/16 mi. N, 5½ mi. W Guadalupe Peak** (el. 1158 m); 62) **½ mi. N, 4½ mi. W Guadalupe Peak** (el. 1204 m).—Near the western boundary of the park, due west of Shumard Peak, is an area of wind-deposited quartz sand dunes. The vegetation consists of desert scrub and scattered grasses including *Prosopis glandulosa, Atriplex canescens, Croton dioicus, Dalea scoparia, D. terminalis, Poliomintha incana, Sporobolus contractus, S. flexuosus, S. giganteus, Oryzopsis hymenoides, Panicum ramisetum*, and *Penstemon ambiguus*.

63) **Southwest Corner,** 1⅞ mi. S, 5⅞ mi. W Guadalupe Peak (el. 1135 m); 64) **1¼ mi. S, 5⅞ mi. W Guadalupe Peak** (el. 1151 m); 65) **1¼ mi. S, 5 7/16 mi. W Guadalupe Peak** (el. 1166 m); 66) **1¼ mi. S, 5 5/16 mi. W Guadalupe Peak** (el. 1173 m); 67) **1⅜ mi. S, 4¼ mi. W Guadalupe Peak** (el. 1219 m); 68) **1½ mi. S, 6½ mi. W Guadalupe Peak** (el. 1128 m); 69) **2¼ mi. S, 6¼ mi. W Guadalupe Peak** (el. 1128 m).—The southwest corner of the westernmost section of park, which is due south of Lewis Well, is bajada. This area is subjected to heavy grazing by trespassing cattle. The vegetation is desert scrub dominated by *Larrea tridenta* and *Atriplex canescens*, with scattered hummocks of *Prosopis glandulosa*.

70) **Stage Coach Hills,** 9/16 mi. S, 4 15/16 mi. W Guadalupe Peak (el. 1219 m); 71) **⅛ mi. S, 5⅜ mi. W Guadalupe Peak** (el. 1173 m); 72) **½ mi. S, 5½ mi. W Guadalupe Peak** (el. 1173 m); 73) **9/16 mi. S, 5 5/16 mi. W Guadalupe Peak** (el. 1181 m).—The Stage Coach Hills are a pair of small hills north and slightly east of the central ridge of the Patterson Hills. The vegetation of the bajada surrounding the hills is desert scrub, whereas succulent desert vegetation is found on the hills themselves. Plants include *Coldenia hispidissima, C. greggii, Larrea tridentata, Agave lecheguilla, Jatropha dioica, Opuntia lindheimeri, O. phaeacantha, Viguiera stenoloba, Sporobolus cryptandrus, Bouteloua eriopoda, Muhlenbergia porteri, Hybiscus denudatus, Fouquieria splendens*, and *Selaginella wrightii*.

74) **Tank Hill,** 1 7/16 mi. N, 4½ mi. W Guadalupe Peak (el. 1234 m); 75) **1⅜ mi. N, 4¼ mi. W Guadalupe Peak** (el. 1227 m).—Tank Hill is an isolated hill north of the Patterson Hills and due west of Bartlett Peak. The bajada surrounding the hill was firmly packed quartz and gypsum sands with scattered patches of crusted gypsum soil. The vegetation is desert scrub including *Larrea tridentata, Prosopis glandulosa, Yucca torreyi, Fouquieria splendens, Opuntia leptocaulis, Croton dioicus, Melampodium leucanthum, Sporobolus flexuosus S. nealleyi, Bouteloua eriopoda, Erioneuron pulchellum, Coldenia hispidissima*, and *Viguiera stenoloba*.

## SPECIES ACCOUNTS

### **Myotis californicus californicus** (Audubon and Bachman), California Myotis

*Specimens Examined* (13).—CULBERSON COUNTY: McKittrick Canyon, 10 (TCWC); 7 mi. N Pine Springs, 1 (TCWC); Smith Spring, 2 (TTU).

The California myotis occurs at intermediate to low elevations within the park, although it may not be found in the low bajadas to the west of the mountains. This species has a slow, fluttering flight that can be seen as they forage for insects just at dusk. Daytime retreats sought by *M. californicus* include caves, mines, and rock crevices, where they may also hibernate during the colder months of the year. Most of our specimens were taken in mist nets set over water.

All of the specimens examined are adult males taken in the months of June and August. Nine males taken in June had testes that measured 3 in length, whereas two taken in August had testes that measured 4.

We follow Bogan (1975) in use of the name combination *Myotis californicus californicus* for bats from this region. Of other species of bats occurring in the park, *Myotis californicus* is difficult to distinguish from *Myotis leibii*. The braincase arises much more abruptly in *M.*

*californicus* which is also somewhat paler than *M. leibii* particularly in coloration of the membranes. External and cranial measurements of four adult males are as follows: total length, 75, 76, 74, 83; length of tail vertebrae, 39, 40, 38, 42; length of hind foot, 6, 7, 6, 5; length of ear, 12, 13, 12, 13; length of forearm, 33.2, 32.0, 31.7, 32.8; greatest length of skull, 13.3, 13.9, 13.9, 14.1; zygomatic breadth, 8.2, 8.4, 8.6, 8.8; postorbital constriction, 3.0, 3.1, 3.1, 3.4; breadth of braincase, 6.2, 6.3, 6.3, 6.6; mastoid breadth, 6.9, 7.2, 7.0, 7.2; length of maxillary toothrow, 4.9, 5.1, 5.1, 5.1; breadth across upper molars, 5.0, 5.3, 5.2, 5.4.

**Myotis leibii ciliolabrum** (Merriam), Small-footed Myotis

*Specimens Examined* (5).—CULBERSON COUNTY: Manzanita Spring, 1 (TTU); McKittrick Canyon, 4 (TCWC).

The small-footed myotis has been obtained only at lower elevations along the eastern escarpment of the mountains. The species probably can be expected elsewhere in the park at lower elevations wherever pools of water are available. *M. leibii* seeks daytime roosts mainly in rock crevices and caves and mines.

The five specimens from the park are adult males which were taken in June. Testes measurements for four specimens from the early part of the month were all 3, whereas that of the specimen taken 23 June was 4. The specimen taken on 2 June at Manzanita Spring was undergoing annual molt.

We follow Glass and Baker (1968) for use of this trinomial combination. External and cranial measurements of the four specimens from McKittrick Canyon are as follows: total length, 78, 83, 76, 76; length of tail, 38, 41, 41, 41; length of hind foot, 6, 8, 7, 7; length of ear, 14, 11, 13, 13; length of forearm, 30.8, 33.0, 32.6, 33.8; greatest length of skull, 13.9, 13.5, 13.6, 14.0; zygomatic breadth, 8.5, 8.1, 8.1, 8.7; postorbital constriction, 3.3, 3.1, 3.1, 3.1; breadth of braincase, 6.6, 6.3, 6.0, 6.6; mastoid breadth, 7.0, 6.6, 6.5, 7.1; length of maxillary toothrow, 5.2, 4.8, 5.1, 5.1; breadth across upper molars, 5.5, 5.1, 5.2, 5.3.

**Myotis thysanodes thysanodes** Miller, Fringed Myotis

*Specimens Examined* (19).—CULBERSON COUNTY: Lost Peak, 2 (TTU); Manzanita Spring, 1 (TTU); McKittrick Canyon, 11 (TCWC); Smith Spring, 1 (TTU); The Bowl, 4 (TTU).

The fringed myotis is probably the most common member of the genus occurring in the Guadalupe Mountains National Park. The species can be expected to seek daytime shelter in rock crevices, man-made buildings, and caves and mines. The majority of our specimens were taken in mist nets set over water at night. However, two individuals from Lost Peak were caught by hand in an old mine on the opposite side of the ridge from the Lost Peak Mine. This mine is about a quarter of a mile deep and is almost horizontal with no side shafts. This species may hibernate in caves and mines in the park during the winter months.

Five adult males taken in late May and June all had testes that measured 3 in length. A male taken on 3 July had testes that measured 4, whereas individuals taken on 1 August and 7 August had testes that were 3 and 5 in length, respectively. Three adult females captured in early June each contained a single embryo that measured as follows in crown-rump length: 11 (2 June); 12 (4 June); 8 (6 June). Two females taken on 6 August were postlactating. A male taken on 7 August and a female taken on 8 August were nearing completion of annual molt.

The subspecies *thysanodes*, originally described from Kern Co., California, is widespread in the southwestern United States and clearly includes material from the Guadalupe Mountains National Park. External and cranial measurements of two adult males from McKittrick Canyon are as follows: total length, 82, 84; length of tail, 41, 40; length of hind foot, 10, 9; length of ear, 18, 17; length of forearm, 42.9, 41.4; greatest length of skull, 16.7, 17.0; zygomatic breadth, 10.5, 10.5; breadth of postorbital constriction, 4.1, 4.2; breadth of braincase, 8.0, 7.8; mastoid breadth, 8.2, 8.3; length of maxillary toothrow, 6.0, 6.5; breadth across upper molars, 6.6, 6.8.

**Myotis velifer incautus** (J. A. Allen), Cave Myotis

*Specimens Examined* (5).—CULBERSON COUNTY: McKittrick Canyon, 4 (TCWC); 4 mi. E Pine Springs Camp, 1 (TCWC).

We did not obtain specimens of this species during our studies in the park. However, the species can be expected in the park particularly at lower elevations. *M. velifer* commonly roosts in caves and mines; a population is known at Carlsbad Caverns. It is a hibernating species and may be expected in the park throughout the year.

Four of the specimens from the park were adult males taken on the following dates (testes measurements in parentheses): 4 June (5); 9 June (6); 31 July (4); 1 August (3). The one adult female was not pregnant when taken on 1 August.

Hayward (1970) has reviewed geographic variation in *Myotis velifer*. He concluded, and we concur, that populations from west Texas are assignable to the subspecies *incautus*. External and cranial measurements of two adult males are as follows: total length, 88, 96; length of tail, 40, 45; length of hind foot, 10, 10; length of ear, 15, 14; length of forearm, 43.5, 42.0; greatest length of skull, 16.8, 16.2; zygomatic breadth, 10.4, 10.3; postorbital breadth, 3.7, 3.9; breadth of braincase, 7.2, 7,3; mastoid breadth, 8.4, 8.2; length of maxillary toothrow, 6.5, 6.3; breadth across upper molars, 6.8, 6.7.

**Myotis volans interior** Miller, Long-legged Myotis

*Specimens Examined* (5).—CULBERSON COUNTY: Manzanita Spring, 1(TTU); McKittrick Canyon, 2 (TCWC); The Bowl, 2 (TTU).

This species of *Myotis* is evidently not abundant in the Guadalupe Mountains National Park. The long-legged myotis occurs in most mountain regions of Trans-Pecos Texas where it evidently prefers high, open montane woodlands (Mollhagen and Baker 1972; Davis 1960). Easterla (1973a; 1973b) found *M. volans* to occur in only two plant habitats in the Chisos Mountains. These were both woodland habitats found at the highest elevations. Four of our five specimens were taken in woodland situations. The fifth specimen was taken at Manzanita Spring along the eastern base of the mountains. At this place the vegetation consists of desert scrub grassland.

Our five specimens are all males and were taken on the following dates: 5 June; 10 June; 23 June; 8 August. Testes measurements for the first two and the last of these individuals were 3, 4, and 4. The specimen taken on 23 June was undergoing annual molt. All specimens were netted at night over water.

*Myotis v. interior* is the trinomial that is applied to populations of this species occurring in the west-central United States. Our specimens are definitely included in this taxa. External and cranial measurements for two adult males are as follows: total length, 92, 95; length of tail, 44, 45; length of hind foot, 8, 9; length of ear, 12, 12; length of forearm, 38.8, 38.6; greatest length of skull, 14.6, 14.6; zygomatic breadth, 8.9. 8.8; breadth of postorbital construction, 4.0, 3.9; breadth of braincase, 7.5, 7.0; mastoid breadth, 7.8, 7.6; length of maxillary toothrow, 5.3, 5.2; breadth across upper molars, 5.7, 5.6.

**Lasionycteris noctivagans** (Le Conte), Silver-haired Bat

*Specimens Examined* (18).—CULBERSON COUNTY: McKittrick Canyon, 16 (TCWC); The Bowl, 1 (TTU); Thrush Hollow, ¼ mi. S Pratt Lodge in South McKittrick Canyon, 1 (TTU).

This relatively rare species was obtained in relatively high numbers in the Guadalupe Mountains. The species is known in Texas from only a few localities including the Davis Mountains, Bandera County (Davis 1960:51), and on the High Plains. All of these are apparently spring or autumn migrants. The population in the Guadalupe Mountains may be in residence during all of the summer and, if so, it is the only such population in the state. Our specimens, which are all males, were taken during May and June (26 June latest date).

We have specimens from the montane areas of the park and the riparian woodland areas of McKittrick Canyon. In addition, a specimen was taken just north of the Upper Dog Ranger Station at Trail Canyon Tank. The species probably is limited to those areas supporting good

stands of trees within the park because silver-hair bats roost in trees. All of our specimens were obtained in mist nets set over water where the bats were probably coming to drink. The species is migratory and will not be found in the park during the colder months of the year.

Thirteen adult males captured in the first week of June had testes that averaged 5(4–6) in length. None of our specimens evinced molt. External and cranial measurements of five adult males from McKittrick Canyon are as follows: total length, 100, 98, 92, 91, 93; length of tail, 45, 45, 37, 40, 40; length of hind foot, 9, 10, 8, 8, 10; length of ear, 15, 14, 14, 14, 15; length of forearm, 41.9, 39.6, 38.7, 39.8, 38.8; greatest length of skull, 16.4, 16.1, 16.0, 16.0, 16.3; zygomatic breadth, 9.9, 10.0, 9.8, 9.7, 10.2; breadth of postorbital constriction, 4.0, 4.2, 4.1, 4.2, 4.2; breadth of braincase, 7.4, 7.8, 7.6, 7.6, 7.9; mastoid breadth, 8.5, 8.6, 8.5, 8.1, 8.8; length of maxillary toothrow, 5.7, 5.6, 5.7, 5.4, 5.6; breadth across upper molars, 6.5, 6.6, 6.6, 6.4, 6.8.

**Pipistrellus hesperus maximus** Hatfield, Western Pipistrelle

*Specimens Examined* (23).—CULBERSON COUNTY: Manzanita Spring, 1 (TTU); McKittrick Canyon, 13 (TCWC); 7 mi. N Pine Springs, 2 (TCWC); Pratt Lodge, McKittrick Canyon, 1 (TTU); Smith Spring, 1 (TTU). HUDSPETH COUNTY: Crossroads, 5 (TTU).

This is one of the most common and widespread species of bats occurring in the park. One can expect to see its fluttering flight anywhere in the park just before darkness during the summer months. The only place that populations of this species may be restricted within the park are in the high montane areas as we did not obtain specimens of this species in The Bowl even with extensive netting. The species does hibernate and, therefore, can be expected to be a year-round resident of the park. It roosts during the day in cracks and crevices, mines, and caves. Our five specimens from Hudspeth County were shot at dusk as they flew over a dry wash. Vegetation in the area consisted of creosote bush, mesquite, four-winged salt bush, and apache plume. All of the remaining specimens except those from north of Pine Springs (no information available for these) were taken in mist nets set over water.

Seven males taken in early June had testes that were 3 in length as did males taken on 20 May, 23 June, and 11 July. Males with testes measuring 2 in length were taken on 20 May (2) and 22 June. A female taken on 8 June contained two embryos that were 10 in crown-rump length. An adult female taken on 31 July was postlactating.

Geographic variation in the western pipistrelle was studied recently by Findley and Traut (1970). They recognized only two subspecies, with the name *P. h. maximus* being applied to populations from east of the Continental Divide. We have followed this arrangement.

**Eptesicus fuscus pallidus** Young, Big Brown Bat

*Specimens Examined* (30).—CULBERSON COUNTY: Burned Cabin, head McKittrick Canyon, 1 (TCWC); Grisham-Hunter Lodge, McKittrick Canyon, 1 (TTU); Jct. North McKittrick Canyon and Devil's Den Canyon, 2 (TTU); Manzanita Spring, 2 (TTU); McKittrick Canyon, 9 (TCWC); Pine Springs, 1 (TCWC); 2 mi. NW Pine Springs, 2 (TTU); Smith Spring, 2 (TTU); The Bowl, 9 (6 TTU, 3 TCWC); Thrush Hollow, ¼ mi. S Pratt Lodge in South McKittrick Canyon, 1 (TTU).

This insectivorous species is one of the most common bat species in the park. All of our specimens were shot as they foraged at dusk along canyons or were taken in mist nets at night along flightways. Although all of our specimens were taken from the top or along the eastern slopes of the mountains, this species probably can be expected at any locality in the park where there are pools of fresh water suitable for drinking. Because of the flight abilities of this bat, it is easily capable of foraging over the low bajadas to the west of the mountains before returning to daytime roosts in and near the mountains. Big brown bats will seek daytime shelter in abandoned buildings, rock crevices, and old mines (Barbour and Davis 1969).

In addition to the individuals listed as examined, we banded four bats of this species that were netted in The Bowl on the nights of 7 and 8 August 1973. Also two big brown bats were taken at Trail Canyon Tank just to the north of the park near Upper Dog Canyon Ranger Station (5.6 mi. S, 0.6 mi. W El Paso Gap, Eddy Co., New Mexico).

All six adult females obtained between 1 June and 23 June were pregnant. Each contained a single embryo, which measured 15 (1 June), 12 and 14 (4 June), 10 (6 June), 25 (10 June), and 23 (23 June) in crown-rump length. Testicular lengths of adult male *Eptesicus* obtained during this study were 6 (1 June), 8 (10 June), 6, 7, and 8 (23 June), 9 (12 July), 7 (13 July), 8 (6 August), and 4 (7 August). Adult males undergoing annual molt were taken on 23 June (3 individuals) and 26 June (1). Two flying young-of-the-year were netted on the night of 7 August in The Bowl.

We follow the arrangement of Engels (1936) in use of the subspecific name *E. f. pallidus* for brown bats from this area.

**Lasiurus cinereus cinereus** (Palisot de Beauvois), Hoary Bat

*Specimens Examined* (22).—CULBERSON COUNTY: Manzanita Spring, 1 (TTU); McKittrick Canyon, 12 (TCWC); 2 mi. NW Pine Springs, 5 (TTU); The Bowl, 4 (TTU).

The hoary bat is evidently a common inhabitant of the montane and wooded areas of the Guadalupe Mountains during the warmer months of the year. The species is migratory and is absent from the area during those times of the year when freezes occur. This species roosts in trees and, therefore, is most common in wooded areas; however, it is a strong flier and probably could forage throughout the park. We do have one record, Manzanita Spring, that does indicate that it forages away from wooded areas on occasion.

Both sexes are evidently resident in the mountains during at least some of the summer months. We have adult males taken on the following dates: 2 June; 3 June; 6 June; 11 June; 24 June; 26 June; 1 August; 2 August; 8 August; 4 September. Adult females, however, have been taken only on 3 June and 4 September. The adult males (9) taken in June had testes that averaged 4.9 (3–6) in length, whereas those taken in August (5) had testes that measured 6.2 (5–8). The adult female taken on 3 June in McKittrick Canyon carried two embryos that measured 20 in crown-rump length. In addition to the specimens listed above, five individuals of this species were taken just north of the park at the Trail Canyon Tank, 5.6 mi. S, 0.6 mi. W El Paso Gap, Eddy Co., New Mexico. These five specimens (one male and four females) were netted as they came to drink from the tank on the night of 3 June. The four females each contained two embryos that ranged from 14 to 17 in crown-rump length. The adult male had testes that were 4 in length. One individual of this species (male) was banded and released in The Bowl on the evening of 7 August 1973. An adult male netted on 26 June evinced annual molt over much of the dorsum.

The subspecies *cinereus* has a widespread distribution in North America and is currently the only one recognized in this geographic area.

**Plecotus townsendii pallescens** (Miller), Townsend's Big-eared Bat

*Specimens Examined* (15).—CULBERSON COUNTY: Lost Peak Mine, 1 (TTU); Manzanita Spring, 1 (TTU); McKittrick Canyon, 4 (TCWC); 7 mi. N Pine Springs, 1 (TCWC); Stone Cabin, near Grisham-Hunter Lodge, 3 (TTU); The Bowl, 4 (TTU); Upper Dog Ranger Station, 1 (TTU).

*Additional Record.*—CULBERSON COUNTY: Upper Sloth Cave (Davis 1940:74).

Townsend's big-eared bat is not a common species in the Guadalupe Mountains National Park, but it may be expected anywhere in the park at middle and upper elevations. This species commonly seeks refuge in mines or caves during the daytime and will hibernate in them during the winter. Two of our specimens—Lost Peak Mine and Upper Dog Ranger Station—were obtained from a mine and a small test shaft, respectively, as they slept during the day. The three specimens from the Stone Cabin were taken during the daytime as they slept hanging from the rafters. The remaining specimens for which we have data were netted over water, including one that was banded and released in The Bowl on 7 August 1973.

A female obtained on 6 August and the one banded in The Bowl were lactating. Other females obtained on 3 August, 6 August, and 8 August (2) evinced no reproductive activity. Testes lengths for males included the following (date of capture in parentheses): 4 (4 April); 5 (1 June); 6 (12 June); 5 (23 June). An adult female taken in The Bowl on 8 August was molting over most of its dorsum, whereas another female taken on the same night evinced no molt.

Handley (1959) revised the genus *Plecotus*. He assigned all specimens from Trans-Pecos Texas to *P. townsendii pallescens*, although he considered those living outside of the Guadalupe Mountains to be intergrades with *P. t. australis*. We have followed this arrangement. External and cranial measurements of an adult male and female are, respectively, as follows: total length, 90, 102; length of tail, 48, 45; length of hind foot, 10, 6; length of ear, 33, 37; length of forearm, 41.8, 42.9; greatest length of skull, 16.4, 16.6; zygomatic breadth, 8.8, 8.8; postorbital constriction, 3.6, 3.7; breadth of braincase, 7.7, 7.9; mastoid breadth, 9.2, 9.2; length of maxillary toothrow, 4.8, 5.3; breadth across upper molars, 5.6, 6.0.

**Antrozous pallidus pallidus** (Le Conte), Pallid Bat

*Specimens Examined* (24).—CULBERSON COUNTY: ½ mi. NNE Grisham–Hunter Lodge, South McKittrick Canyon, 1 (TTU); McKittrick Canyon, 10 (TCWC); 2 mi. NW Pine Springs, 1 (TTU); 4 mi. E Pine Springs Camp, 4500 ft., 2 (TCWC); Pratt Lodge, McKittrick Canyon, 4 (TTU); Smith Spring, 3 (TTU); The Bowl, 3 (TTU).

The pallid bat can be expected throughout the National Park. It probably is a year-round resident, hibernating in the colder months of the year. However, our specimens were all taken in the four months from May to August. All 24 specimens recorded above are males, which indicates that the females are probably forming nursery colonies elsewhere. The pallid bat is considered a common inhabitant of the Chihuahuan Desert lowland, but as our records from The Bowl indicate, it will range to high altitudes.

Average testes length for males by month were as follows (range in parentheses followed by sample size): May, 5.5 (5–6) 6; June, 5.1 (4–6) 9; July, 5.0 (5) 4; August, 7.7 (6–9) 3. Five individuals (two from Pratt Lodge and three from The Bowl) were banded during our studies. A specimen taken on 23 June was just beginning annual molt. New hair is evident under the old over most of the dorsum of four adult males taken on 11 July at Pratt Lodge. A flying young-of-the-year was netted on 7 August 1973 in The Bowl.

Our specimens are assignable to *Antrozous pallidus pallidus* as are most other populations of pallid bats occurring in the Southwest.

**Tadarida brasiliensis mexicana** (Saussure), Brazilian Free-tailed Bat

*Specimens Examined* (16).—CULBERSON COUNTY: McKittrick Canyon, 3 (TCWC); Smith Spring, 1 (TTU); The Bowl, 12 (TTU).

The Brazilian free-tailed bat is a powerful flier and can be expected anywhere in the park. However, based on our records this species must confine most of its activity to the montane areas and the eastern slopes of the mountains. This bat seeks daytime retreats in caves, mines, and old buildings; a large colony, which has been declining in recent years, occupies Carlsbad Caverns. Although the population in Carlsbad Caverns includes many adult females and their young, all of our specimens are adult males.

Free-tailed bats have a highly developed migratory pattern and will be found in the park only in the months of April to October. All of our specimens were taken in the months of June and August. In addition to the specimens listed above, 43 males were banded and released in The Bowl on the nights of 7 and 8 August 1973. One specimen also was taken on the night of 4 June just north of the Upper Dog Ranger Station at a place designated Trail Canyon Tank, 5.6 mi. S, 0.6 mi. W El Paso Gap, Eddy Co., New Mexico. Specimens evincing annual molt were taken on 23 June and 26 June, although a second specimen taken 26 June was not molting.

Populations of this species in the western United States and most of Mexico have been assigned to *T. b. mexicana*. This arrangement has been questioned by some recent investigators (Cockrum 1969). However, the systematic review of this species has not been published.

**Tadarida macrotis** (Gray), Big Free-tailed Bat

*Specimens Examined* (13).—CULBERSON COUNTY: McKittrick Canyon, 13 (TCWC).

This species has been taken in large numbers only in the Chisos (Easterla 1973b:120) and Guadalupe mountains in west Texas; other records for the species in Texas are based on single

or a few specimens. Our specimens are all adult females taken on two dates—11 June 1968 and 3 August 1970 (LaVal 1973). Our two-year survey has failed to produce additional specimens. The specimens were netted as they were coming to drink in wooded areas of lower South McKittrick Canyon. However, the area described by LaVal (1973) in which the specimens were taken was altered significantly by the floods of 1968. Whether or not a resident population of this rare species occurs in the Guadalupe Mountains National Park is not known. However, it is clear that a few, possibly migrant, individuals do use the park from time to time.

Of 12 females taken on 11 June, eight carried a single embryo each. The embryos ranged from 22 to 30 in crown-rump length and averaged 25.9. The female taken on 3 August was lactating.

This species is considered to be monotypic by modern authors (Husson 1962:258–259). External and cranial measurements of five females are as follows: total length, 130, 139, 130, 129, 126; length of tail, 52, 62, 50, 52, 50; length of hind foot, 12, 13, 12, 12, 12; length of ear, 27, 30, 29, 29, 27; length of forearm 60.8, 61.5, 59.4, 60.8, 61.3; greatest length of skull, 23.7, 23.7, 23.9, 23.2, 23.2; zygomatic breadth, 12.5, 12.5, 12.7, 12.5, 12.6; postorbital constriction, 4.2, 4.3, 4.0, 4.2, 4.2; breadth of braincase, 10.0, 10.0, 10.3, 10.3, 10.3; mastoid breadth, 11.4, 11.6, 11.7, 11.4, 11.5; length of maxillary toothrow, 8.6, 8.6, 8.7, 8.8, 8.3; breadth across upper molars, 8.8, 8.5, 8.8, 9.1, 9.0.

### **Sylvilagus audubonii neomexicanus** Nelson, Desert Cottontail

*Specimens Examined* (5).—CULBERSON COUNTY: mouth of McKittrick Canyon, 1 (TCWC); Upper Dog Ranger Station, 4 (TTU).

The desert cottontail is abundant throughout the park at lower elevations wherever there is sufficient cover to provide daytime hiding places. Our specimens from Upper Dog Ranger Station at 1920 m are from the highest elevation at which the species is presently known in the park. Although all of the specimens obtained during our studies are from this location, the species was observed at numerous other places including Williams Ranch Road Entrance, along Williams Ranch Road, and Patterson Hills Notch in Culberson County, and Lewis Well and the Crossroads in Hudspeth County. Davis (1940:82) reported sighting this species at Pine Springs, West Dog Canyon, and along the road at the east base of the mountains during his work in the Guadalupe Mountains.

On 27 July 1973, J. E. Cornely obtained a large *Crotalus atrox* near Choza Spring. Examination of the stomach contents of this snake revealed two juvenile *S. audubonii* each measuring approximately 140 in total length. An adult male taken on 31 May 1974 at Upper Dog Ranger Station had testes that measured 35 in length.

We agree with Davis and Robertson (1944:271) that desert cottontails from this part of Texas are best assigned to the subspecies *neomexicanus*. This subspecies was described based upon material from Fort Sumner, New Mexico, and is currently applied to specimens from much of west Texas and eastern New Mexico.

### **Sylvilagus floridanus robustus** (Bailey), Eastern Cottontail

*Specimen Examined* (1).—CULBERSON COUNTY: The Bowl, 1 (TTU).

The eastern cottontail may be one of the rarest species of mammals currently occurring in the Guadalupe Mountains National Park. Specimens have been recorded only from The Bowl (Davis 1940; Davis and Robertson 1944; Hall and Kelson 1951; Hall 1951b) where it evidently is confined to dense stands of Douglas fir and ponderosa pine. During our work in the areas, only two individuals were seen and this was only for a brief moment as the rabbit quickly disappeared into dense underbrush. Davis (1940) estimated that the population of this rabbit was approximately 50 individuals. The population is certainly no larger today and may be smaller. This taxon occurs only in isolated populations in the Chisos, Chinati, Davis, and Guadalupe mountains of Texas. There certainly is no interchange between these populations at the current time.

Our one specimen was a juvenile obtained on 8 June 1974 as was one specimen taken by Davis (1940) on 11 June.

The taxonomic status of this taxon is currently uncertain. Beginning with Nelson's revision (1909) of the genus, this rabbit was considered a distinct species, *S. robustus*. This taxonomic arrangement prevailed until 1951 when Hall and Kelson (1951:56) presented evidence indicating that this rabbit was best considered to be a member of the widespread species *S. floridanus*. Davis (1960) has chosen, however, to retain the specific status for this rabbit under the name *Sylvilagus robustus*. We have chosen to follow Hall and Kelson's revision until further evidence is available. Clearly, this rabbit is closely related to *S. floridanus* but further study may prove its specific distinctness.

**Lepus californicus texianus** Waterhouse, Black-tailed Jackrabbit

*Specimens Examined* (5).—CULBERSON COUNTY: mouth McKittrick Canyon, 5000 ft, 1 (TCWC); Upper Dog Ranger Station, 2 (TTU); Williams Ranch Road Entrance, 1 (TTU). HUDSPETH COUNTY: Lewis Well, 1 (TTU).

The black-tailed jackrabbit is a common inhabitant of the Chihuahuan Desert portions of the park, where its distribution is almost identical with the desert cottontail, *Sylvilagus audubonii*. The highest elevation at which this species has been taken or observed within the park is 1920 m in Upper Dog Canyon. In addition to the localities from which specimens were obtained, individuals of *L. californicus* were observed at the following places: Northwest Corner; Southwest Corner; Patterson Hills Notch; Stage Coach Hills; Crossroads; Williams Ranch House; near Marcus Cabin in West Dog Canyon; near the lower end of Bear Canyon Trail; Nipple Hill. Black-tailed jackrabbits are herbivores and are known to forage on grasses and low brush.

The two adult females taken on 2 and 3 June 1973 were pregnant and lactating. The specimen taken on 2 June contained five embryos—three in the right uterine horn and two in the left. Two of the embryos in the right horn were being reabsorbed. The crown-rump length of the normal embryos was 11. The female taken on 3 June possessed three embryos in the right uterine horn and none in the left. These embryos measured 45 in crown-rump length. A subadult male taken on 25 July 1973 at the Williams Ranch Road Entrance had testes measuring 17 in length and was molting on the posterior portion of the dorsum and onto the flanks.

We have assigned our specimens to the taxon *Lepus californicus texianus* on geographic grounds. This name is currently applied to jackrabbits occurring in much of west Texas, New Mexico, and north-central Mexico (Hall and Kelson 1959:283).

**Eutamias canipes canipes** Bailey, Gray-footed Chipmunk

*Specimens Examined* (34).—CULBERSON COUNTY: head of Dog Canyon, 7000 ft, 2 (USNM); Guadalupe Mts., 7000 ft, 3 (USNM); McKittrick Canyon, 5900 ft, 1 (TCWC); The Bowl, 22 (19 TCWC, 3 TTU); Upper Dog Ranger Station, 6 (TTU).
*Additional Record.*—CULBERSON COUNTY: Guadalupe Mountains, 8000 ft (Davis 1940:78).

The gray-footed chipmunk is confined to the higher elevations of the park; the lowest elevation at which the species has been taken is 1800 m in McKittrick Canyon, which is a mesic, wooded area. The species is evidently most abundant in and near The Bowl and in Upper Dog Canyon. In addition to specimens taken during this study, individuals of this species were sighted at Bush Mountain, near Mescalero Campground, and in the upper portions of South McKittrick Canyon. All capture sites where the gray-footed chipmunk has been seen are in or near forested areas. One specimen was obtained as it climbed in a small Douglas fir tree. The Guadalupe Mountains National Park is the only area in Texas where this chipmunk occurs.

A female taken on 6 August 1973 in The Bowl contained four embryos that measured 28 in crown-rump length. Two females taken on 3 and 9 June in Upper Dog Canyon evinced no gross reproductive activity. Three male gray-footed chipmunks had the following testes length (capture dates in parentheses): 18 (31 May); 17 (31 May); 5 (9 June). Three individuals taken in our study were undergoing molt. A male taken on 31 May was molting in a large band across the dorsum approximately half-way between the head and rump. The other two individuals were

molting in only small areas. A female taken on 3 June was molting on the chest and a female taken on 6 August was molting in two small areas on the rump.

*Eutamias canipes* is currently considered to occur in restricted montane habitats of the Guadalupe, Sacramento, White, Capitan, and Gallinas mountains of Texas and New Mexico. There is probably little genetic interchange between isolated populations at the present time. Fleharty (1960) recognized a subspecies, *E. c. sacramentoensis*, as occurring in the Sacramentos northward, thus restricting *E. c. canipes* to the Guadalupe Mountains of Texas and adjacent New Mexico. We follow Fleharty's arrangement here.

External and cranial measurements of four specimens (two males, two females) of *E. c. canipes* deposited in the National Museum of Natural History are as follows (holotype given last): total length, 210, 235, 220, 230; length of tail, 96, 105, 97, 104; length of hind foot, 32, 35, 33, 35; greatest length of skull, 33.9, 36.7, 36.0, 36.5; zygomatic breadth, 18.0, 19.2, 19.7, 19.[illegible]; interorbital breadth, 7.2, 7.2, 7.8, 8.0; postorbital breadth, 11.4, 11.7, 11.9, 11.6; mastoid breadth, 16.2, 16.7, 17.0, 17.2; length of nasals, 10.3, 11.9, 11.4, 11.6; length of maxillary toothrow, 5.6, 4.7, 5.6, 5.9; length of palatal bridge, 10.9, 12.1, 11.8, 11.8.

**Ammospermophilus interpres** (Merriam), Texas Antelope Squirrel

*Specimens Examined* (8).—CULBERSON COUNTY: south of Guadalupe Mountains, 1 (USNM); mouth McKittrick Canyon, 5000 ft, 1 (TCWC); 7 mi. N Pine Springs, 1 (TCWC); below Pine Springs, 2 (TTU); Upper Dog Ranger Station, 3 (TTU).
*Additional Records.*—CULBERSON COUNTY: Frijole, about 5600 ft (Davis 1940:77); Pine Springs Camp, 5300 ft (Davis 1940:77).

The Texas antelope squirrel is characteristic of the middle to lower elevations of the Guadalupe Mountains National Park. The species has not been taken or seen at elevations higher than 1920 m at Upper Dog Ranger Station. Evidently, this squirrel is restricted to rocky areas along the escarpment of the mountains as pointed out by Findley et al. (1975:114). Our three specimens from Upper Dog were trapped near piles of rock. In addition to the places listed above, individuals of this species were sighted on the rocky slope above Williams Ranch House in an area dominated by sotol, lecheguilla, and ocotillo, around Nipple Hill, Northwest Corner, and near the road immediately below Williams Ranch House.

None of the specimens taken during our study evinced reproductive activity. Two females taken on 5 June 1973 were young of the year. An adult male taken on 30 May 1966 was molting in a broad band across the nape of the neck and extending onto the head and shoulders.

The species *Ammospermophilus interpres* occupies a relatively restricted geographic range in Chihuahua and Coahuila, Mexico, Texas, and New Mexico. The species is relatively uncommon within the park, but extensive areas of its preferred rocky desert habitat are included in the park. Unless major environmental changes occur, this species should present no major management problems.

The five species of the genus *Ammospermophilus* occupy allopatric geographic ranges. The distribution of *A. interpres* is approached by that of *A. harrisii* and *A. leucurus* in New Mexico. The relationships of those species (Findley *et al.* 1975) are currently under investigation at the University of New Mexico. For the time being, we considered *A. interpres* to be a distinct, monotypic species. External and cranial measurements of two adult females (mouth of McKittrick Canyon and south of Guadalupes) are as follows: total length, 228, 220; length of tail, 71, 67; length of hind foot, 40, 39; greatest length of skull, 41.5, 41.1; zygomatic breadth, 24.3, 23.4; interorbital constriction, 10.3, 9.8; postorbital constriction, 14.1, 14.5; mastoid breadth, 20.7, 19.6; length of maxillary toothrow, 6.8, 7.2.

**Spermophilus spilosoma marginatus** Bailey, Spotted Ground Squirrel

*Specimens Examined* (6).—CULBERSON COUNTY: Williams Ranch Road Entrance, 1 (TTU). HUDSPETH COUNTY: Tank Hill, 1 7/16 mi. N, 4½ mi. W Guadalupe Peak, 1 (TTU); Lewis Well, 4 (TTU).

The specimens of spotted ground squirrel herein reported are the first known from the park area, although Davis and Robertson (1944) reported them from elsewhere in Culberson Co.

This species evidently is confined to the Chihuahuan Desert areas of the western bajada. In addition to the animals obtained during our study, spotted ground squirrels were sighted near the Crossroads and in the Southwest Corner of the park. The specimen taken at Williams Ranch Road Entrance was trapped under a creosote bush where the ground was rocky. Two specimens from Lewis Well were trapped in sandy soil west of the well where gypsum sand dunes enter the park. The spotted ground squirrel does not appear to be abundant in the park.

A female taken at Tank Hill on 15 August 1974 was lactating, whereas two females taken at Lewis Well on 18 and 19 May 1974 evinced no reproductive activity. A female from the Williams Ranch Road Entrance had four placental scars in the left uterine horn when trapped on 26 July 1973. A male from Lewis Well had testes that were 17 long on 19 May 1974. This male evinced molt on the head and shoulders; the remainder of the pelage evidently was old as it was faded and harsh in appearance.

The type locality for the subspecies *marginatus* is Alpine, Brewster Co., Texas. Clearly, our material from Guadalupe Mountains National Park is indistinguishable from spotted ground squirrels from this region of Texas.

**Spermophilus variegatus grammurus** (Say), Rock Squirrel

*Specimens Examined* (17).—CULBERSON COUNTY: Guadalupe Mountains, 2 (USNM); 2 mi. E mouth of McKittrick Canyon, 5000 ft, 1 (TCWC); ¼ mi. up McKittrick Canyon, 5300 ft, 1 (TCWC); McKittrick Canyon, 5900 ft, 1 (TCWC); 7 mi. N Pine Springs, 2 (TCWC); 1½ mi. S Pine Springs, 1 (TCWC); Pratt Lodge, 1 (TCWC); Upper Dog Ranger Station, 7 (TTU); West Dog Canyon, 1 (TCWC).

*Additional Record.*—CULBERSON COUNTY: Frijole, about 5600 ft (Davis 1940:76).

Rock squirrels are the most common sciurid occurring in the park and are abundant particularly in areas of rock outcroppings. The species was abundant in Upper Dog Canyon during our studies where they fed on the berries of *Juniperus deppeana* and acorns and found refuge in the numerous rocky areas. Davis (1940:77) recorded seeing an individual of this species ascend the vertical flowering stalk of a century plant and feed on the fruit of the plant. Bailey (1905:85–86) records this species as feeding on the berries of *Juniperus pachyphloea*, acorns of the gray oak, cactus fruits (*Opuntia engelmanni* and *Cereus stramineus*), and walnuts (*Juglans rupestris*). In addition to the localities listed above, individuals of this species were seen near the Burned Cabin at the head of McKittrick Canyon, in Shumard Canyon above the Williams Ranch House, and near the Williams Ranch House. On 24 June 1973, a rock squirrel was seen drinking from the horse tank in the corral at Frijole. Davis (1940) reported seeing this species at 7000 ft above Pine Springs Canyon and along the north rim of North McKittrick near the state line. Based upon our own and earlier records, therefore, this species occurs as low as 1524 m along the west face of the mountains and to at least 5000 ft (1524 m) along the east slope and as high as 7000 ft (2134 m) in suitable habitats. Bailey (1905) concluded that the species occurred between 4000 (1220 m) and 7000 ft in the Guadalupes.

A female taken at Upper Dog Ranger Station on 26 June 1974 contained five embryos that measured 18 in crown-rump length, whereas another female taken on 26 June 1973 at this place carried four embryos that measured 5. Testes of a male taken on 31 May 1974 were 16 long. This male was evidently undergoing molt on its head region. The remainder of the pelage appeared to be extremely worn. A nonpregnant female taken on 27 July 1974 had completed molt on the anterior half of its body and was in the process of molting in the remaining areas, being particularly evident on its rump.

The name *Spermophilus variegatus grammurus* is the scientific name applied to most rock squirrels occurring in Trans-Pecos Texas and New Mexico. Our specimens lack the black head region as do other members of this subspecies (Howell 1938:143).

**Cynomys ludovicianus** (Ord), Black-tailed Prairie Dog

*Specimen Examined* (1).—CULBERSON COUNTY: near Guadalupe Mountains, 1 (USNM).

Although this species once occurred in numerous areas in the vicinity of the Guadalupe Mountains, evidently only one melanistic individual that was once held in the National Zoo was

ever preserved. The species has been extirpated from the area occupied by the park through the direct activity of man. Prairie dogs were eradicated by means of poison because they were believed to directly compete with cattle for food in the short-grass prairies.

Bailey (1905:89–90) reported seeing prairie dogs on the main ridge of the mountains in New Mexico and into Dog Canyon in Texas. The name of this canyon was derived from the presence of this species. Davis (1940:77–78) did not collect any specimens but did see active colonies at the base of Nipple Hill, 3 mi. N of Nipple Hill along U.S. Highway 62-180, and near the entrance of Pine Springs Canyon. He also reported seeing a group of old burrows at the mouth of McKittrick Canyon. Clearly, a number of widely scattered colonies of this species once existed in the Guadalupe Mountains National Park. A recent attempt by Roger Reisch of the National Parks Service to re-introduce this species near Nipple Hill was unsuccessful. If a future attempt to re-introduce prairie dogs is planned, the most promising location is the site of an abandoned town near Pine Springs where remnants of the old mounds are still evident. At the present time a corral for visitors' horses occupies this site. A prerequisite for successful establishment of a new prairie dog town would be the relocation of this corral.

Hollister (1916:19–21), in his revision of the genus, pointed out that the distinction between the two subspecies—*C. l. ludovicianus* and *C. l. arizonensis*—of black-tailed prairie dog was based upon average differences in cranial measurements and color. He admitted that the subspecies were weakly defined and that one individual specimen could not be allotted with any certainty. Recently, Pizzimenti (1975) has reviewed members of this genus and he has decided, based upon his studies, to consider *C. ludovicianus* as a monotypic species. We have followed this latter arrangement.

**Thomomys bottae guadalupensis** Goldman, Botta's Pocket Gopher

*Specimens Examined* (17).—CULBERSON COUNTY: Bear Canyon Pump House, 1 (TTU); Burned Cabin, head of McKittrick Canyon, 5 (TCWC); Dog Canyon, 6800 ft, 2 (USNM); Manzanita Spring, 1 (TTU); McKittrick Canyon, 4 (USNM); Nipple Hill, 1 (TTU); mouth Pine Springs Canyon, 1 (TCWC); Upper Bear Canyon Trail, 2 (TTU).

This species of pocket gopher occurs at moderate to high elevations within the park. Although no specimens were obtained from the top of the mountains, the specimens from Upper Bear Canyon Trail were taken near the summit and pocket gopher activity, undoubtedly of this species, was noted near the summit of Guadalupe Peak, Bush Mountain, Blue Ridge Campground, and Lost Peak. *T. bottae* occurs in shallow, rocky soil often in association with *Agave lecheguilla*. This pocket gopher frequently feeds on the roots of lecheguilla and will kill individual plants.

*Thomomys bottae guadalupensis* was described originally by Goldman (1936), with the holotype from McKittrick Canyon, although we did not find any pocket gophers in this area during our survey. The subspecies was distinguished on the basis of pale coloration and details of cranial morphology. As currently understood, this taxon is confined to the Guadalupe Mountains. It is worthy of note that we did not find this species to be abundant anywhere within the park. However, we believe that this subspecies will be in no danger as long as its preferred food of lecheguilla remains abundant.

External and cranial measurements of two adult males (holotype given first) from McKittrick Canyon and two adult females from Burned Cabin, respectively, are as follows: total length, 218, 218, 195, 200; length of tail, 64, 64, 60, 58; length of hind foot, 29, 29, 29, 28.5; greatest length of skull, 38.2, 38.0, 34.6, 37.0; zygomatic breadth, 23.7, 23.3, 21.7, 22.3; interorbital breadth, 6.7, 6.8, 7.2, 6.7; squamosal breadth, 19.9, 18.9, 15.0, 15.4; length of nasals, 12.4, 13.8, 11.3, 13.0; palatal length, 23.8, 24.7, 21.9, 23.2; length of maxillary toothrow, 8.1, 8.5, 7.3, 7.8.

**Pappogeomys castanops parviceps** Russell, Yellow-faced Pocket Gopher

*Specimens Examined* (5).—CULBERSON COUNTY: 7 mi. N Pine Springs, 1 (TCWC); mouth Pine Springs Canyon, 1 (TCWC). HUDSPETH COUNTY: 1⅛ mi. N, 4¼ mi. W Guadalupe Peak, 2 (TTU); Lewis Well, 1 (TTU).

*Additional Record.*—CULBERSON COUNTY: foot of Pine Canyon (= Pine Springs Canyon), Guadalupe Mts., 5740 ft (Russell 1968).

During our work in the Guadalupe Mountains National Park, we took specimens of the yellow-faced pocket gophers at only two localities, both in the western portion of the park. Although we extensively searched the area of Pine Springs Canyon where the species had been taken previously, we did not find any evidence that the species currently occurs there. The two localities where we trapped members of this taxon were areas of firmly packed quartz and gypsum sand, with scattered patches of crusted gypsum soil. The species did not appear to occur outside of these soil types at these two places. Our specimens were relatively pale in coloration, probably corresponding to the light coloration of the soil in which they lived.

An adult female taken on 17 August contained a single embryo that measured 40 in crown-rump length and a female taken on 7 August carried two embryos that measured 10. Two females taken on 14 August and 7 October were nonpregnant.

External and cranial measurements of four adult females (one from each locality listed, in order listed) were as follows: total length, 238, 243, 242, 238; length of tail, 66, 62, 75, 62; length of hind foot, 33, 33, 33, 32; condylobasal length, 44.0, 44.5, 43.8, 44.7; zygomatic breadth, 26.6, 27.7, 27.8, 27.9; interorbital constriction, 7.0, 7.0, 6.6, 6.8; mastoid breadth, 25.8, 25.8, 25.8, 26.3; squamosal breadth, 20.3, 19.4, 19.2, 19.0; length of nasals, 14.6, 15.4, 15.8, 15.3; length of maxillary toothrow, 9.3, 8.9, 8.7, 8.8; palatal length, 29.3, 30.1, 29.4, 30.2. These measurements are in agreement with those given by Russell (1968:674) for *P. c. parviceps*; therefore, we assign them to that subspecies.

**Pappogeomys castanops perplanus** (Nelson and Goldman), Yellow-faced Pocket Gopher

*Specimens Examined.*—None.

*Additional Record.*—CULBERSON COUNTY: foot of Pine Canyon (= Pine Springs Canyon), Guadalupe Mts., 5740 ft (Russell 1968:653).

In Russell's (1968) recent revision of the genus *Pappogeomys*, he divided the subspecies of *P. castanops* into two groups—*excelsus* subspecies-group and *subnubilus* subspecies-group. The two groups were distinguished mainly on the basis of cranial size, especially measurements of cranial length, with the *excelsus* subspecies-group being much the larger. Russell (1968) believed that the two subspecies-groups occurred sympatrically in Pine Springs Canyon with no evidence of intergradation. Of the two adult females in a series of five specimens in the Academy of Natural Sciences in Philadelphia from the foot of Pine Springs Canyon, he assigned one to *P. c. perplanus* in the *excelsus* subspecies-group and one (plus the three younger specimens) to *P. c. parviceps* in the *subnubilis* subspecies-group. He assigned one adult female to *P. c. perplanus* because of its large size (condylobasal length, 48.2) and the other to *P. c. parviceps* because of its much smaller size (condylobasal length, 45.3).

During our work in the Guadalupe Mountains, we never obtained *P. castanops* east of the mountains although we searched extensively for their mounds and trapped several *Thomomys bottae* in the area. Changing environmental conditions or intraspecific competition may have eliminated this species from east of the mountains in the park at least for the present time.

**Perognathus flavus gilvus** Osgood, Silky Pocket Mouse

*Specimens Examined* (21).—CULBERSON COUNTY: 3 1/16 mi. S, 1⅜ mi. W Guadalupe Peak, 1 (TTU); 4⅜ mi. S, 1⅜ mi. W Guadalupe Peak, 1 (TTU); Marcus Cabin, West Dog Canyon, 1 (TTU); Nipple Hill, 2 (TTU); Patterson Hills Notch, 1 (TTU); Williams Ranch Road Entrance, 9 (TTU). HUDSPETH COUNTY: 1 mi. S, 3 15/16 mi. W Guadalupe Peak, 1 (TTU); Lewis Well, 1 (TTU).

*Additional Record.*—CULBERSON COUNTY: 7 mi. N Pine Springs, 5300 ft (Davis and Robertson 1944:268).

The silky pocket mouse occurs in grassland and desert habitats in the park. The highest elevation at which we obtained a specimen was 1905 m in West Dog Canyon. Most of our specimens were taken on the desert bajadas west and south of the mountains. At the Williams Ranch Road

Entrance, where our largest sample was obtained, the vegetation is dominated by creosote bush and mesquite with grasses of the genera *Sporobolus* and *Bouteloua*. All pocket mice are basically granivores and divide the seed resources on the basis of size, availability, and species preference.

A female taken on 17 June evinced two placental scars. Females taken on 19 August, 6 October, and 7 October were nonpregnant. Testes measurements for males were as follows (dates of capture in parentheses): 6 (25 July); 5 (26 July); 4 (28 July); 3 (6 October). Specimens taken on 17 June and 25 July were undergoing seasonal molt. In both specimens, molt had progressed onto the posterior third of the dorsum.

Until recently (Wilson 1973), two species of silky pocket mouse—*P. flavus* and *P. merriami*—were recognized in the area of the Guadalupe Mountains National Park. However, Wilson (1973) and later Findley et al. (1975) presented data to show that the two species intergrade and that populations previously called *P. merriami gilvus* were intermediate between the two species. We have followed this arrangement pending additional data. Wilson (1973) favored retention of the subspecific name *gilvus* for the intermediate populations.

The silky pocket mouse is the smallest of the four species of *Perognathus* occurring in the park. It can be distinguished easily from the other species by its overall size and soft silky pelage. External and cranial measurements of three males and two females, respectively, from the Williams Ranch Road Entrance are as follows: total length, 104, 113, —, —, 99; length of tail, 50, 54, —, —, 45; length of hind foot, 12, 16, 16, 11, 15; length of ear, 5, 6, 6, 7, 6; greatest length of skull, 20.8, 20.8, 21.0, 19.5, 19.6; zygomatic breadth, 10.6, 11.1, 10.9, 10.2, 10.1; interorbital breadth, 4.4, 4.3, 4.3, 4.1, 3.9; mastoid breadth, 12.3, 12.0, 12.3, 11.3, 11.4; length of maxillary toothrow, 2.8, 3.0, 2.9, 2.9, 2.8; interparetal width, 3.9, 3.3, 3.4, 2.7, 3.1; interparietal length, 2.8, 2.8, 2.8, 2.8, 2.4.

**Perognathus hispidus paradoxus** Merriam, Hispid Pocket Mouse

*Specimen Examined* (1).—CULBERSON COUNTY: head of Dog Canyon, 6800 ft, 1 (USNM).

The only specimen of this species that has been taken in the park was obtained by Vernon Bailey in 1901. This specimen was taken near Bailey's camp at approximately 6800 ft near a place that we would term Upper Dog Ranger Station.

Because this species was not taken during Davis' or our survey, we believe that this species has been extirpated from the park. We would suggest that this extirpation may have been caused by overgrazing or increasing environmental aridity which have altered the grassy habitat of this species.

This is the largest-sized species of pocket mouse that has occurred in the Guadalupe Mountains National Park. Measurements for the species are given by Glass (1947).

**Perognathus intermedius intermedius** Merriam, Rock Pocket Mouse

*Specimens Examined* (30).—CULBERSON COUNTY: Nipple Hill, 1 (TTU); Williams Ranch House, 20 (TTU); Williams Ranch Road Entrance, 1 (TTU). HUDSPETH COUNTY: Crossroads, 1 (TTU); 11/16 mi. S, 4¼ mi. W Guadalupe Peak, 1 (TTU); ⅜ mi. S, 4 1/16 mi. W Guadalupe Peak, 2 (TTU); 1 mi. S, 3 15/16 mi. W Guadalupe Peak, 2 (TTU); Northwest Corner, 2 (TTU).

*Additional Record.*—CULBERSON COUNTY: 7 mi. N Pine Springs (Davis and Robertson 1944:268).

The rock pocket mouse occurs in the grassland and desert habitats of the park, although it is evidently most abundant on the desert bajadas west of the mountains. The highest elevation that we have taken a specimen is 1646 m at Nipple Hill. This species was taken basically in areas where creosote bush, mesquite, and saltbush dominate the vegetation.

Two nonpregnant females were taken on 15 June and 13 July.

*Perognathus intermedius* and *P. penicillatus* are intermediate in size between the smaller *P. flavus* and larger *P. hispidus* from the park. The two former species can be distinguished easily from the latter two on the basis of external and cranial size. However, we have found it to be

extremely difficult to distinguish *P. intermedius* and *P. penicillatus* especially in the field. To identify our material, we have used the characteristics given by Hoffmeister and Lee (1967:367–368). These characteristics seem to separate specimens of the two species from the park quite easily in the laboratory.

We have applied the same *P. intermedius intermedius* to our specimens following Hall and Kelson (1959:501). External and cranial measurements of two males and three females from Williams Ranch House are, respectively, as follows: total length, 188, 174, 168, 165, —; length of tail, 109, 100, 99, 96, —; length of hind foot, 22, 20, 19, 19, 20; length of ear, 7, 8, 7, 8, 8; greatest length of skull, 25.3, 24.8, 23.2, 23.6, 23.4; zygomatic breadth, 12.3, 12.5, 11.8, 11.6, 12.1; interorbital breadth, 6.3, 6.3, 6.1, 5.8, 6.1; mastoid breadth, 13.3, 13.2, 12.6, 12.5, 13.0; length of maxillary toothrow, 3.8, 3.4, 3.5, 3.5, 3.5; interparietal width, 7.7, 7.0, 7.2, 7.3, 7.2; interparietal length, 3.7, 3.4, 3.1, 3.0, 2.8.

**Perognathus penicillatus eremicus** Mearns, Desert Pocket Mouse

*Specimens Examined* (83).—CULBERSON COUNTY: ½ mi. S, 5½ mi. W Guadalupe Peak, 10 (TTU); ½ mi. S, 4¾ mi. W Guadalupe Peak, 1 (TTU); 3 1/16 mi. S, 1⅜ mi. W Guadalupe Peak, 1 (TTU); 3¼ mi. S, 2⅜ mi. W Guadalupe Peak, 5 (TTU); 4⅜ mi. S, ½ mi. W Guadalupe Peak, 12 (TTU); Nipple Hill, 2 (TTU); Williams Ranch Road, 4⅞ mi. S, ⅛ mi. E Guadalupe Peak, 7 (TTU); Williams Ranch House, 1 (TTU); Williams Ranch Road Entrance, 15 (TTU). HUDSPETH COUNTY: Crossroads, 11 (TTU); 1 7/16 mi. N, 4½ mi. W Guadalupe Peak, 1 (TTU); ⅜ mi. S, 4 1/16 mi. W Guadalupe Peak, 1 (TTU); 11/16 mi. S, 4¾ mi. W Guadalupe Peak, 1 (TTU); ⅞ mi. S, 4 mi. W Guadalupe Peak, 5 (TTU); 1¼ mi. S, 5⅞ mi. W Guadalupe Peak, 1 (TTU); 1¼ mi. S, 5 7/16 mi. W Guadalupe Peak, 3 (TTU); 1⅞ mi. S, 5⅞ mi. W Guadalupe Peak, 2 (TTU); Lewis Well, 2 (TTU); Stagecoach Hills, 2 (TTU).

The desert pocket mouse can be expected in the grassland and desert habitats of the park. It is most abundant west of the mountains, but has been taken at Nipple Hill east of the mountains. Nipple Hill is also the highest elevation at which the species was taken in the park. This species occupies much the same habitat in the park as *P. intermedius* and has been taken with it at six localities including Nipple Hill, Williams Ranch Road Entrance, Williams Ranch House, ⅜ mi. S, 4 1/16 mi. W Guadalupe Peak, 11/16 mi. S, 4¾ mi. W Guadalupe Peak, and the Crossroads. It is of interest to note that *P. penicillatus* was the most abundant species at Williams Ranch Road Entrance, whereas *P. intermedius* was the more abundant at Williams Ranch House. Generally, *P. penicillatus* was the more abundant of the two species in the park.

Females carrying minute embryos were taken on 28 May (3 embryos) and 26 July (no number given). None of the four females taken between 5 and 7 October evinced reproductive activity. Testes measurements for males of *P. penicillatus* were as follows (dates of capture in parentheses): 6 (21 May); 6 (13 July); 4 (28 July); 4 (22 August). A female taken on 26 July was undergoing seasonal molt on the posterior portion of the dorsum.

We follow Hoffmeister and Lee (1967) in application of the name *Perognathus penicillatus eremicus* to desert pocket mice from the park. External and cranial measurements for one male and three females, respectively, from Williams Ranch Road Entrance are as follows: total length, 152, 155, 164, 164; length of tail, 90, 84, 85, 90; length of hind foot, 22, 25, 22, 21; length of ear, 8, 8, 8, 8; greatest length of skull, 25.8, 24.7, 25.2, 25.0; zygomatic breadth, 14.1, 13.1, 13.2, 13.5; interorbital breadth, 6.7, 6.2, 6.5, 6.3; mastoid breadth, 13.6, 12.7, 12.7, 12.8; length of maxillary toothrow, 3.7, 3.5, 3.6, 3.7; interparietal width, 7.5, 7.2, 7.4, 7.0; interparietal length, 3.6, 4.0, 3.5, 3.4.

**Dipodomys merriami merriami** Mearns, Merriam's Kangaroo Rat

*Specimens Examined* (436).—CULBERSON COUNTY: ½ mi. S, 2⅝ mi. W Guadalupe Peak, 11 (TTU); 3 1/16 mi. S, 1⅜ mi. W Guadalupe Peak, 7 (TTU); 3¼ mi. S, 2⅜ mi. W Guadalupe Peak, 10 (TTU); 4¼ mi. S, 1 mi. W Guadalupe Peak, 37 (TTU); 4 5/16 mi. S Guadalupe Peak, 24 (TTU); 4⅜ mi. S, 1⅛ mi. W Guadalupe Peak, 4 (TTU); 4⅜ mi. S, ½ mi. W Guadalupe Peak, 56 (TTU); 4½ mi. S, ½ mi. W Guadalupe Peak, 23 (TTU); 4½ mi. S, ⅛ mi. E Guadalupe Peak, 21 (TTU); 4½ mi. S, ⅜ mi. E Guadalupe Peak, 1 (TTU); 4⅞ mi. S Guadalupe Peak, 13 (TTU);

4⅞ mi. S, ⅛ mi. E Guadalupe Peak, 28 (TTU); 5⅛ mi. S Guadalupe Peak, 1 (TTU); Patterson Hills Notch, 8 (TTU); 7 mi. N Pine Springs, 9 (TCWC); Williams Ranch House, 4 (TTU); Williams Ranch Road Entrance, 40 (TTU). HUDSPETH COUNTY: Crossroads, 38 (TTU); 4 mi. N, 5½ mi. W Guadalupe Peak, 3 (TTU); 1 7/16 mi. N, 4½ mi. W Guadalupe Peak, 6 (TTU); ½ mi. N, 4¾ mi. W Guadalupe Peak, 8 (TTU); ½ mi. N, 4½ mi. W Guadalupe Peak, 6 (TTU); ⅛ mi. S, 5⅜ mi. W Guadalupe Peak, 8 (TTU); ½ mi. S, 5½ mi. W Guadalupe Peak, 16 (TTU); 11/16 mi. S, 4¾ mi. W Guadalupe Peak, 4 (TTU); 1 mi. S, 3 15/16 mi. W Guadalupe Peak, 3 (TTU); 1¼ mi. S, 5⅞ mi. W Guadalupe Peak, 2 (TTU); 1⅞ mi. S, 5⅞ mi. W Guadalupe Peak, 9 (TTU); Lewis Well, 22 (TTU); Stagecoach Hills, 4 (TTU).

Merriam's kangaroo rat is the most common kangaroo rat in the park. It is distributed widely at lower elevations and is able to utilize the hard rocky desert floor as well as the deeper sandy areas. Because of their desert adaptation and adaptation for saltation, kangaroo rats are of prime interest to park visitors and individuals could be caged easily in an interpretive center. Such interpretive displays in conjunction with an educational program in understanding signs made by kangaroo rats should prove of value to the park visitors.

The diets of Ord's and Merriam's kangaroo rats were the subject of an extensive study published in this volume (O'Connell 1977) and the interested person is referred to her work. In summary, she found the diet of *D. merriami* to consist of seeds, greenery, and insects. Relative to the diet of *D. ordii, D. merriami* eats greater quantities of insects, especially in the winter months.

Reproductive data for females are discussed below. In a sample of 27 females collected on 23 and 24 February, none was pregnant; in a sample of 28 females collected on 22 March, none was pregnant; in a sample of six females collected on 20 April, none was pregnant. In a sample of 11 females collected on 17 to 21 May, 10 were not pregnant and one female contained two embryos with a crown-rump length of 3. In a sample of seven females collected on 30 June, five were not pregnant and two contained two embryos each with a crown-rump length of 4 and 12. A female collected on 26 July was not pregnant. In a sample of 35 females collected on 8 to 23 August, 22 were not pregnant and 13 were pregnant with two embryos each. Crown-rump length for the embryos of each female were 2, 3, 4, 15, 18, 23, 24, 24, 29, 29, 32, 33, and 37. In a sample of 14 females collected on 5 to 7 October, none was pregnant. From these data it would appear that the normal number of embryos per litter is two and it appears unlikely that a single female produces more than one litter per year. In every case observed above, a single embryo was found in each horn of the uterus. The onset of breeding appears to be toward the end of May and to cease before October.

Testicular length for males was as follows (mean, range in parentheses, and number): February, 10 (4–13) 24; March, 9 (4–12) 37; April, 8 (6–11) 5; May, 11 (9–12) 11; June, 10 (5–13) 13; July, 9 (4–12) 8; August, 11 (6–13) 31; October, 5 (4–9) 12. The above data suggest that males have enlarged testes from February to August during which time most males have scrotal testes. During October the testes size is reduced and none of the males had scrotal testes.

Specimens were observed in molt from February to October.

We have followed the systematic arrangement of Lidicker (1960) in applying the name *Dipodomys merriami merriami* to our specimens from the park.

**Dipodomys ordii ordii** Woodhouse, Ord's Kangaroo Rat

*Specimens Examined* (75).—CULBERSON COUNTY: 4⅜ mi. S, ½ mi. W Guadalupe Peak, 1 (TTU); 4⅞ mi. S Guadalupe Peak, 1 (TTU); 5⅛ mi. S Guadalupe Peak, 2 (TTU); Williams Ranch Road Entrance, 23 (TTU). HUDSPETH COUNTY: Crossroads, 2 (TTU); 2⅞ mi. N, 7⅞ mi. W Guadalupe Peak, 3 (TTU); 1⅜ mi. N, 4¼ mi. W Guadalupe Peak, 1 (TTU); ½ mi. N, 4¾ mi. W Guadalupe Peak, 20 (TTU); 7¾ mi. W Guadalupe Peak, 1 (TTU); 9/16 mi. S, 5 5/16 mi. W Guadalupe Peak, 1 (TTU); 1½ mi. S, 6½ mi. W Guadalupe Peak, 1 (TTU); 1⅞ mi. S, 7⅞ mi. W Guadalupe Peak, 8 (TTU); Lewis Well, 10 (TTU); Stagecoach Hills, 1 (TTU).

Our records indicate that *Dipodomys ordii* is associated with the deeper sandy areas on the western side of the park and within this localized habitat the species is relatively abundant. All specimens were collected between the elevations of 1230 to 1350 m.

The diets of Ord's kangaroo rat and Merriam's kangaroo rat are described in detail in this volume (O'Connell 1977), and anyone interested in specifics is referred to her work. Briefly, this species eats seeds, greenery, and insects, with the major portion of the diet consisting of seeds (mainly of grasses). Ord's kangaroo rat is primarily an opportunistic feeder.

In a sample of five females collected on 23 and 24 February, only one was pregnant carrying an embryo measuring 7 in crown-rump length in each horn of the uterus. Two females taken on 18 May, a female taken on 29 June, and a female taken on 25 July were not pregnant. In a sample of six females taken on 10 to 22 August, two were pregnant. Each pregnant female contained an embryo in each horn of the uterus with the crown-rump length of the embryos being 4 for those of one female and 35 for the other. In a sample of three females from 7 October, one female contained a minute embryo in each horn and the other two were not pregnant. Testicular length for nine males collected in February ranged from 9 to 12, for a male collected in March it was 12, for three males collected in May it was 8, 13, and 12. Ten males collected in August had testicular lengths that ranged from 8 to 14 and the testicular length of a male collected in October was 11.

Specimens were observed in molt during June and August.

According to the most recent revision of this species by Setzer (1949), *Dipodomys ordii ordii* is the subspecies occurring in the Guadalupe Mountains National Park. *D. ordii* and *D. merriami* are similar in external size and coloration; however, the two species are distinguished easily because *D. ordii* has five toes on its hind feet, whereas *D. merriami* has only four.

**Dipodomys spectabilis baileyi** Goldman, Banner-tailed Kangaroo Rat

*Specimens Examined* (3).—CULBERSON COUNTY: 4 5/16 mi. S Guadalupe Peak, 1 (TTU). HUDSPETH COUNTY: 3/8 mi. S, 4 1/16 mi. W Guadalupe Peak, 1 (TTU); 11/16 mi. S, 4¾ mi. W Guadalupe Peak, 1 (TTU).

Specimens of the banner-tailed kangaroo rat were obtained from the park for the first time during our study. Our collecting data suggest that this species is limited to the western and southwestern boundaries of the park. This is the largest of the kangaroo rats found in the park and is distinguished easily from the other two species by the large tuft of white hairs on the distal portion of the tail. Banner-tailed kangaroo rats build conspicuous dens that form mounds with several large entrances. Such mounds are infrequent where we observed banner-tailed kangaroo rats in the park but if some mounds prove to be accessible to park visitors, they would provide a unique ecological feature for observation.

A female collected on 23 March did not contain embryos. Testicular length of males was 14 for a specimen obtained on 29 June and 16 for a specimen from 15 August. Individuals collected on 29 June and 15 August were molting.

There has not been a recent systematic review of this species and we follow Hall and Kelson (1959) in assigning our specimens to *D. s. baileyi*.

**Reithrodontomys megalotis megalotis** (Baird), Western Harvest Mouse

*Specimens Examined* (34).—CULBERSON COUNTY: 4⅞ mi. S, ⅛ mi. E Guadalupe Peak, 1 (TTU); Marcus Cabin, West Dog Canyon, 1 (TTU); Pine Springs Campground, 1 (TTU); The Bowl, 3 (2 TCWC, 1 TTU); Upper Dog Ranger Station, 27 (TTU); Williams Ranch Road, 4¼ mi. S, 1 mi. W Guadalupe Peak, 1 (TTU).

The western harvest mouse occurs at moderate to high elevations throughout the park wherever grass occurs. Apparently, it is most common at moderate elevations, but has been taken during our study and by Davis (1940:79–80) in grassy meadows in The Bowl. Harvest mice are basically granivorous and are probably dependent upon the presence of grass for their continued existence in the park. Population estimates for this species in the park are given by August et al. (1977).

A female taken on 19 August in Upper Dog Canyon contained five embryos that measured 16 in crown-rump length, whereas females taken on 26 January, 6 April, and 24 July evinced no

reproductive activity. Testes lengths for males were as follows: April, 4, 4; June, 5, 7, 8; July, 10; August, 8, 9. A female taken on 18 August was in subadult pelage. None of our 14 skins was from individuals undergoing seasonal molt.

The subspecies *R. m. megalotis* is widespread in the western United States and northern Mexico. This name has been applied to all members of the species from Trans–Pecos Texas. The last systematic revision of the group was by Howell (1914).

**Peromyscus boylii rowleyi** (J. A. Allen), Brush Mouse

*Specimens Examined* (95).—CULBERSON COUNTY: Bush Mountain, 3 (TTU); ½ mi. NNE Grisham–Hunter Lodge, South McKittrick Canyon, 1 (TTU); Guadalupe Mountains, 7800 ft, 1 (USNM); Guadalupe Mountains, Dog Canyon, 6800 ft, 2 (USNM); Guadalupe Mountains, head of McKittrick Canyon, 7800 ft, 1 (USNM); Guadalupe Peak Campground, 1 (TTU); 4⅜ mi. S, ½ mi. W Guadalupe Peak, 1 (TTU); 5⅛ mi. S Guadalupe Peak, 1 (TTU); Junction North McKittrick Canyon and Devil's Den Canyon, 1 (TTU); Lost Peak, 1 (TTU); Marcus Cabin, West Dog Canyon, 1 (TTU); McKittrick Canyon, 8 (TCWC); Nipple Hill, 1 (TTU); Pine Springs Campground, 1 (TTU); Pratt Lodge, McKittrick Canyon, 2 (TTU); Smith Canyon, 4 (TTU); The Bowl, 30 (19 TCWC, 11 TTU); Upper Dog Ranger Station, 23 (TTU); Williams Ranch Road Entrance, 1 (TTU).

The brush mouse can be expected throughout the park, with the possible exception of the lowland desert areas of the western portion. The westernmost record that we have in our material is from 4⅜ mi. S, ½ mi. W Guadalupe Peak at an elevation of 1356 m. The brush mouse is evidently most abundant at moderate to high elevations in the park because our largest samples are from The Bowl and Upper Dog Ranger Station. During the summer of 1973 when we trapped intensively in McKittrick Canyon for more than a week, the rodent populations were extremely low, with only four *Peromyscus boylii* and one *P. pectoralis* being obtained. These specimens were taken on rocky hillsides, where sotol and agave predominated under low oak trees. This habitat was similar to a number of areas where the species was taken elsewhere in the park. In The Bowl, the brush mouse was taken under large stands of conifers, but succulents were not present. A number of specimens were trapped in a log cabin in The Bowl. In the area of Williams Ranch Road Entrance, no oaks or conifers were present but the brushy vegetation was dominated by creosote bush with scattered mesquite.

Of the seven species of the genus *Peromyscus* occurring in the park, *P. boylii* is evidently the most common. Pregnant females of *P. boylii* were taken on the following dates: 22 March, three embryos (4 in crown-rump length); 6 April, minute (no number given); 23 June, two embryos (23); 6 August, four embryos (4). Nonpregnant females were obtained in May, June, and July. Testes measurements for adult males obtained in our study are as follows: 22 March, 12; 31 May, 4, 12; 1 June, 5; 2 June, 10; 3 June, 13; 4 June, 14; 5 June, 11; 9 June, 10, 12; 13 June, 8; 23 June, 11; 6 August, 14, 15, 15, 15. Four adult females were found to evince molt on various areas of the dorsum on the following dates: 12 June; 23 June; 25 June; 6 August.

We follow Schmidly (1973) in assigning our specimens to *P. b. rowleyi*. Relationships of all *Peromyscus* occurring in the park will be discussed in a subsequent publication.

**Peromyscus difficilis nasutus** (J. A. Allen), Rock Mouse

*Specimens Examined* (39).—CULBERSON COUNTY: Blue Ridge, 1 (TTU); Blue Ridge Campground, 3 (TTU); Bush Mountain, 4 (TTU); Guadalupe Peak Campground, 4 (TTU); Guadalupe Mountains, McKittrick Canyon, 7800 ft, 1 (USNM); Lost Peak, 3 (TTU); Mescalero Campground, 2 (TTU); Pine Springs Campground, 1 (TTU); The Bowl, 6 (3 TCWC, 3 TTU); Upper Dog Ranger Station, 16 (TTU).

*Additional Record.*—CULBERSON COUNTY: 2 mi. E Pine Springs (Diersing and Hoffmeister 1974:213).

The rock mouse occurs at moderate to high elevation within the park. Our lowest record of occurrence of this species is 1768 m at Pine Springs Campground. However, Diersing and Hoffmeister (1974) reported two specimens from 2 mi. E of Pine Springs which is at an approxi-

mate elevation of 1600 m. As the common name of this mouse suggests, it was generally taken in rocky situations; at many of the higher elevation localities it was taken sympatrically with *P. boylii*.

Two females containing embryos were taken during our study. One taken on 3 June carried four that measured 4 in crown-rump length and one taken on 1 July carried five that measured 3. The average testes length of three males taken on 30 May was 8.3, of six males taken on 9 to 11 June was 9.8, and of a single male trapped on 26 June was 7. Adults that evinced molt were taken on 30 May (2), 3 June, and 10 June.

The rock mouse was first reported as occurring in Texas, based upon specimens from 2 mi. E Pine Springs and McKittrick Canyon (Diersing and Hoffmeister 1974:213). Our additional specimens confirm the presence of the species and indicate that it is relatively abundant and occurs throughout the Guadalupe Mountains of Texas. We follow the systematic arrangement of Hoffmeister and de la Torre (1961) in using the name *Peromyscus difficilis nasutus* for these mice. Relationships of *Peromyscus* occurring in the park will be discussed in a subsequent publication.

**Peromyscus eremicus eremicus** (Baird), Cactus Mouse

*Specimens Examined* (42).—CULBERSON COUNTY: ½ mi. S, 2⅝ mi. W Guadalupe Peak, 6 (TTU); 3 1/16 mi. S, 1⅜ mi. W Guadalupe Peak, 1 (TTU); 3¼ mi. S, 2⅜ mi. W Guadalupe Peak, 1 (TTU); 4 mi. S, ½ mi. W Guadalupe Peak, 2 (TTU); Williams Ranch Road, 4¼ mi. S, 1 mi. W Guadalupe Peak, 11 (TTU); Williams Ranch Road, 4 5/16 mi. S Guadalupe Peak, 2 (TTU); Williams Ranch Road, 4⅞ mi. S, ⅛ mi. E Guadalupe Peak, 4 (TTU); 5⅛ mi. S Guadalupe Peak, 1 (TTU); Nipple Hill, 2 (TTU); 7 mi. N Pine Springs, 2 (TCWC). HUDSPETH COUNTY: Crossroads, 6 (TTU); ⅜ mi. S, 4 1/16 mi. W Guadalupe Peak, 3 (TTU); Northwest Corner, 1 (TTU).

This species occurs in most areas of the xeric lowlands of the park. It is particularly abundant in the rocky areas of the western portion of the park where desert scrub vegetation, including creosote bush and mesquite, dominates. Many specimens were taken on bajadas where *Dipodomys merriami* was also captured. On the eastern side of the park the vegetation around Nipple Hill and north of Pine Springs contained more grasses.

Three adult females taken on 26 January, 20 May, and 15 August were not pregnant. Three adult males had testes lengths of 9, 12, and 11 on 26 January, 15 August, and 23 August, respectively.

We have followed the subspecific arrangement given in Hall and Kelson (1959:607) for this species. Relationships of all *Peromyscus* occurring in the park will be discussed in a subsequent publication.

**Peromyscus leucopus tornillo** Mearns, White-footed Mouse

*Specimens Examined* (20).—CULBERSON COUNTY: ½ mi. S, 2⅝ mi. W Guadalupe Peak, 1 (TTU); 5⅛ mi. S Guadalupe Peak, 2 (TTU); 5⅜ mi. S, ½ mi. W Guadalupe Peak, 1 (TTU); Marcus Cabin, West Dog Canyon, 1 (TTU); Pine Springs Campground, 5 (TTU); Williams Ranch Road Entrance, 2 (TTU); Williams Ranch Road, 4⅞ mi. S, ⅛ mi. E Guadalupe Peak, 5 (TTU). HUDSPETH COUNTY: Crossroads, 1 (TTU); Lewis Well, 1 (TTU); Stage Coach Hills, 1 (TTU).

*Additional Record.*—CULBERSON COUNTY: Frijole, about 5600 ft (Davis 1940:80).

The white-footed mouse appears to occur at moderate to low elevations throughout the park, but nowhere is it abundant. The species evidently is most common in the grassy areas near the Pine Springs Campground and in the desert scrub vegetation along Williams Ranch Road. The highest elevation at which we recorded this species was 1905 m in West Dog Canyon where the vegetation was mixed grassland with riparian vegetation along the washes.

An adult female taken on 24 July contained a single embryo that measured 7 in crown-rump length; another female taken on 6 October was pregnant but the number of embryos was not recorded. Nonpregnant adult females were taken on the following dates: 26 January; 22 March;

20 May; 7 October. Three adult males collected on 26 January had testes lengths of 12, 13, and 13. A specimen taken on 26 January evidenced molt in a small area on the head and neck; the remainder of the pelage was adult.

Our *P. leucopus* are pale in coloration and should be assigned to *P. l. tornillo* which was originally described from El Paso, El Paso County, Texas (Mearns 1896). Relationships of all *Peromyscus* occurring in the park will be discussed in a subsequent publication.

**Peromyscus maniculatus blandus** Osgood, Deer Mouse

*Specimens Examined* (63).—CULBERSON COUNTY: ½ mi. S, 2⅜ mi. W Guadalupe Peak, 1 (TTU); 3¼ mi. S, 2⅜ mi. W Guadalupe Peak, 1 (TTU); 4 mi. S, ½ mi. W Guadalupe Peak, 5 (TTU); 4.3 mi. S Guadalupe Peak, 1 (TTU); 4⅜ mi. S, ½ mi. W Guadalupe Peak, 1 (TTU); Williams Ranch Road, 4½ mi. S, 1 mi. W Guadalupe Peak, 2 (TTU); Williams Ranch Road, 4⅞ mi. S, ⅛ mi. E Guadalupe Peak, 11 (TTU); 5⅛ mi. S Guadalupe Peak, 4 (TTU); Williams Ranch Road, 5⅜ mi. S, ½ mi. W Guadalupe Peak, 5 (TTU); Nipple Hill, 1 (TTU); Patterson Hills Notch, 3 (TTU); 7 mi. N Pine Springs, 1 (TCWC); Williams Ranch Road Entrance, 9 (TTU). HUDSPETH COUNTY: Crossroads, 9 (TTU); Lewis Well, 1 (TTU).

The deer mouse occurs in xeric lowland areas in much the same areas as *Peromyscus eremicus*. On the western bajadas, it was captured among creosote bush and mesquite. The area around Lewis Well was somewhat more sandy than other areas in the western portion of the park, but our specimen was taken in an area of desert scrub vegetation. Two specimens were taken along the eastern front of the mountains in areas that are xeric but contain more grasses than the western lowlands.

Adult males were taken with the following testes measurements (dates of capture in parentheses): 9 (22 March); 10 (19 May); 8 (20 May); 7 (30 June); 10 (12 July); 14 (13 July); 12 (26 July); 12, 13 (10 August); 11 (22 August); 10, 11 (6 October). An adult female trapped on 13 July was carrying three embryos that measured 10 in crown-rump length. Two subadults captured on 13 July were molting from subadult to adult pelage.

Of the 19 skins that we have available, 16 are the light gray coloration typical of *Peromyscus maniculatus blandus*. However, the other three specimens (one each from Williams Ranch Road Entrance, 4⅞ mi. S, ⅛ mi. E Guadalupe Peak, and Crossroads) are predominately buffy in color. Because the majority of specimens resemble *P. m. blandus* in color, we have assigned our specimens to this subspecies. Relationships of all *Peromyscus* occurring in the park will be discussed in a subsequent publication.

**Peromyscus pectoralis laceianus** Bailey, White-ankled Mouse

*Specimens Examined* (20).—CULBERSON COUNTY: 7 mi. N Pine Springs, 15 (TCWC); Manzanita Spring, 1 (TTU); Nipple Hill, 2 (TTU); 0.3 mi. N, 0.5 mi. E Pratt Cabin, McKittrick Canyon, 1 (TTU); Upper Dog Ranger Station, 1 (TTU).

We found the white-ankled mouse to be relatively uncommon during our survey of the park's mammals. Specimens were obtained at only four localities along the eastern and northern boundaries of the park. The habitats in which this species was taken include woodlands and grasslands at Nipple Hill and Manzanita Spring and riparian woodland in McKittrick Canyon and at Upper Dog Ranger Station. It is probably significant that we did not obtain this species at higher elevations or on the desert lowlands of the western portion of the park.

Adult females taken on 26 January and 15 July were nonpregnant. Adult males captured on 3 June, 23 June, and 29 July had testes that measured 11, 11, and 12, respectively. An adult male taken on 23 June was molting over much of its dorsum.

The most recent systematic review of this species was by Schmidly (1972:113–138) and we have followed his subspecific arrangement. Relationships of all *Peromyscus* occurring in the park will be discussed in a subsequent publication.

**Peromyscus truei truei** (Shufeldt), Piñon Mouse

*Specimens Examined* (4).—CULBERSON COUNTY: Marcus Cabin, West Dog Canyon, 3 (TTU); Upper Dog Ranger Station, 1 (TTU).

Our specimens of the piñon mouse are the first recorded from the state of Texas. The nearest previous record was 15 mi. S Weed, Otero Co., New Mexico, in the southern part of the Sacramento Mountains (Findley et al. 1975). The only two localities of record are at intermediate elevations (1905 m and 1920 m) in the extreme northern portion of the park. Throughout its geographic range the piñon mouse is most common in piñon-juniper woodlands. Our specimens were taken in riparian woodlands that included the juniper, *Juniperus deppeana*, and in West Dog Canyon the piñon pine, *Pinus edulis*.

One of our specimens is an adult female that was carrying four embryos measuring 5 when captured on 24 July. This specimen was also molting on the lower flanks. A male taken on 2 June had testes measuring 11.

The most recent systematic review of this species was by Hoffmeister (1951). Relationships of all *Peromyscus* occurring in the park will be discussed in a subsequent publication.

**Onychomys torridus torridus** (Coues), Southern Grasshopper Mouse

*Specimens Examined* (63).—CULBERSON COUNTY: ½ mi. S, 2⅝ mi. W Guadalupe Peak, 1 (TTU); 3¼ mi. S, 2⅜ mi. W Guadalupe Peak, 2 (TTU); 4 mi. S, 1 mi. W Guadalupe Peak, 7 (TTU); 4¼ mi. S, 1 mi. W Guadalupe Peak, 4 (TTU); 4 5/16 mi. S Guadalupe Peak, 2 (TTU); 4⅞ mi. S, ⅛ mi. E Guadalupe Peak, 16 (TTU); 5⅛ mi. S Guadalupe Peak, 5 (TTU); 7 mi. N Pine Springs, 1 (TCWC); Williams Ranch Road Entrance, 8 (TTU). HUDSPETH COUNTY: Crossroads, 7 (TTU); 1⅜ mi. N, 4¼ mi. W Guadalupe Peak, 5 (TTU); 2¼ mi. S, 6¼ mi. W Guadalupe Peak, 2 (TTU); Lewis Well, 2 (TTU).

The southern grasshopper mouse is found at lower elevations in the desert habitat of the park. Because it is almost entirely carnivorous, it is unique among the rodents of the park. Its primary food source is insects (Horner et al. 1964; Bailey and Sperry 1929), but other food items include scorpions, other arthropods, and mammals. Grasshopper mice have a remarkable behavior associated with the killing of prey (Bailey and Sperry 1929; Cole and Wolf 1970; Cyr 1972; Horner et al. 1964). With mammals which are nearly as large as grasshopper mice, individuals of *Onychomys* attack this prey from behind and bite them through the cranium, which results in instant death. *Onychomys* also has special means of handling arthropods which have protective devices such as scorpions, whip scorpions, and beetles of the genera *Eleodes* and *Chlaenius*. When attacking scorpions and whip scorpions, they bite off the tail before killing the animal. With *Eledoes* and *Chlaenius* (beetles which emit defensive secretions), *Onychomys* grabs these

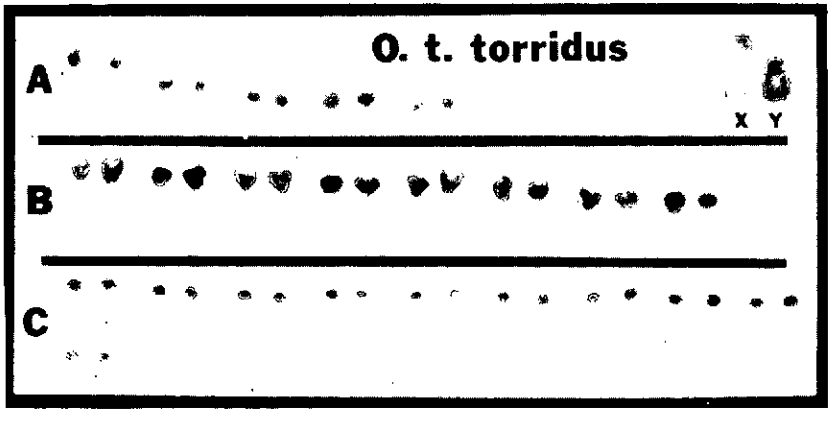


**Fig. 6.** C-band karyotype of *Onychomys torridus*, male, from the Crossroads, Guadalupe Mountains National Park, Texas.

beetles with its forepaws and jams its abdomen into the sand to avoid contact with the secretions. Information concerning the unique predatory behavior of this species would probably prove of interest to park visitors who wish to learn more about the park's ecosystem.

Although limited data have been published on the chromosomal variation in *O. torridus*, data from Baker's laboratory suggest several different chromosomal races occur within this species. Therefore the karyotype characteristic of individuals from the park is presented in Fig. 6.

Pregnant females have been collected in June, July, and August. Date of collection, number of embryos, and crown-rump length are as follows: 29 June, four embryos with crown-rump length of 16; 25 July, three embryos of 18; 26 July, four embryos of 15; 10 August, three embryos of 24; 20 August, four embryos of 7. Nonpregnant females were collected on 20 August and on 6 and 7 October. Date of collection and testicular length (in parentheses) of adult males were 10 August (11 and 16); 22 August (15); 23 August, (10, 18, and 23); 7 October (5). Adults were observed molting in July and October.

The literature relevant to this species is reviewed by McCarty (1975) and is an excellent source for reference to the biology of *Onychomys torridus*.

**Sigmodon hispidus berlandieri** Baird, Hispid Cotton Rat

*Specimens Examined* (19).—CULBERSON COUNTY: Guadalupe Mountains, 1 (USNM); Guadalupe Mountains, Dog Canyon, 6800 ft, 3 (USNM); Marcus Cabin, West Dog Canyon, 1 (TTU); Pine Springs Campground, 4 (TTU); Smith Canyon, 3 (TTU); Upper Dog Ranger Station, 4 (TTU); Williams Ranch House, 1 (TTU); Williams Ranch Road, ½ mi. S, 2⅝ mi. W Guadalupe Peak, 1 (TTU). HUDSPETH COUNTY: Lewis Well, 1 (TTU).

Hispid cotton rats are known from low to moderate elevations within the park, with Upper Dog Canyon being the highest locality from which they have been taken. The species is most abundant in the grassy areas along the eastern slopes and northern interior canyons of the mountains. However, three specimens were taken along the west slope. Two of these from Williams Ranch House area were taken from local grassy situations. The specimens from Lewis Well was taken in an *Atriplex-Larrea* scrub area. The presence of *S. hispidus* on the west side of the Guadalupe escarpment may be an indication of more widespread grasslands at an earlier time. This species was not reported previously from within the park.

Four pregnant hispid cotton rats (number of embryos in parentheses) were taken on 23 June (4, 5) and 25 July (3, 4). The following testes measurements were recorded from males captured in the park: 26 January, 20; 23 June, 24; 25 June, 20; 23 July, 18; 19 August, 17; 7 October, 17. Two juvenile specimens (both females) were taken on 26 January at the Pine Springs Campground. Two adult specimens (23 June and 19 August) were undergoing seasonal molt when captured.

The subspecies, *S. h. berlandieri*, is currently regarded as occurring throughout west Texas and most of northern Mexico. The latest systematic review of cotton rats from this area was by Bailey (1902a).

**Neotoma albigula albigula** Hartley, White-throated Woodrat

*Specimens Examined* (38).—CULBERSON COUNTY: Guadalupe Mountains, 1 (USNM); Guadalupe Mountains, Dog Canyon, 6800 ft, 1 (USNM); Marcus Cabin, West Dog Canyon, 2 (TTU); Nipple Hill, 1 (TTU); 7 mi. N Pine Springs, 5300 ft, 7 (TCWC); Upper Dog Ranger Station, 20 (TTU); Williams Ranch House, 1 (TTU). HUDSPETH COUNTY: Crossroads, 3 (TTU); 4 mi. N, 5½ mi. W Guadalupe Peak, 1 (TTU); Tank Hill, 1 (TTU).
*Additional Record.*—CULBERSON COUNTY: Frijole, about 5600 ft (Davis 1940:81).

Three species of woodrats (*Neotoma albigula, N. mexicana*, and *N. micropus*) occur within the boundary of the park. An extensive study (Cornely 1977) of the ecological distribution of these species is published in this volume and we will only briefly summarize his results in the following three accounts.

*Neotoma albigula* occurs around the perimeter of the mountains and on the floors of Upper Dog and West Dog canyons which penetrate the mountain mass. On the west side of the park

the white-throated woodrat is found primarily in or along edges of dry washes extending westward from the mountains. The white-throated woodrat is the species which has built most of the conspicuous woodrat dens within the park. These dens are constructed of any available material and would serve as an excellent item of interest for park visitors. Of particular interest should be the role that these nests play as a unique ecological situation that benefits many of the park's other species of animals.

Number and size of embryos and date of collection of pregnant females were as follows: 20 May, 2 embryos with a crown-rump length of 38; 27 June, 1 embryo with a crown-rump length of 37; 29 July, 1 embryo with a crown-rump length of 40; 26 August, 5 embryos with a crown-rump length of 2. A post-lactating female was collected on 3 June. Adult females containing no embryos were collected on 15, 25, and 27 June. Testes length for males and dates collected were as follows: 31 May, 7; 2 June, 11, 11; 26 June, 15; 29 June, 19; 23 July, 13; 20 August, 7; 26 August, 7. Adult specimens were molting on 20 and 27 May, 27 June, and 23 July.

We follow Hall and Kelson (1959) in assigning these to *N. albigula albigula*. Even though *N. albigula* and *N. mexicana* form a contact zone in Upper Dog Canyon, a chromosomal analysis failed to reveal any indication of hybridization between the two species. *Neotoma albigula* and *N. micropus* are also in contact in the southwestern part of the park (Cornely 1977); however, chromosomal analysis failed to reveal any hybridization in the specimens that we obtained.

**Neotoma mexicana mexicana** Baird, Mexican Woodrat

*Specimens Examined* (32).—CULBERSON COUNTY: Guadalupe Mountains, 7000 ft, 4 (USNM); 5⅛ mi S Guadalupe Peak, 1 (TTU); The Bowl, 6 (5 TTU, 1 TCWC); Upper Dog Ranger Station, 15 (TTU). HUDSPETH COUNTY: ⅝ mi. S, 4¾ mi. W Guadalupe Peak, 1 (TTU); 11/16 mi. S, 4¾ mi. W Guadalupe Peak, 2 (TTU); ⅞ mi. S, 4⅞ mi. W Guadalupe Peak, 1 (TTU); ⅞ mi. S, 4 mi. W Guadalupe Peak, 1 (TTU); 1¼ mi. S, 5 7/16 mi. W Guadalupe Peak, 1 (TTU); Lewis Well, 1 (TTU).

*Additional Record.*—CULBERSON COUNTY: 7 mi. N Pine Springs, 5300 ft (Davis and Robertson 1944:270).

*Neotoma mexicana* is distributed throughout Guadalupe Mountains National Park at elevations above 1500 m. The Mexican woodrat is saxicolous and builds its nests in inaccessible rock crevices where they would not be observed by park visitors. This species does frequent wooden houses such as the cabin in The Bowl and perhaps might be observed by park visitors under such circumstances. Cornely (1977) has detailed the ecological distribution of this species. Mexican woodrats in the log cabin in The Bowl were observed eating acorns which they had gathered in large quantities.

Dates of collection of pregnant females and reproductive data are as follows: 4 June, 2 embryos (crown-rump length, 18), 2 (5); 20 August, 2 (40); 26 August, 3 (22). Adult females containing no embryos were collected on 3 June and 20 August. Testicular lengths for adult males were 19 and 20 for two males collected on 4 June, 17 for a 6 August specimen, and 15 for a specimen from 8 August. Molting was observed for adult specimens collected in June and August.

We have followed Hall and Kelson (1959) for our systematic arrangement of this species.

**Neotoma micropus canescens** J. A. Allen, Southern Plains Woodrat

*Specimens Examined* (5).—CULBERSON COUNTY: 4 mi. S, ½ mi. W Guadalupe Peak, 2 (TTU); 4⅜ mi. S, ⅛ mi. E Guadalupe Peak, 2 (TTU). HUDSPETH COUNTY: Crossroads, 1 (TTU).

The southern plains woodrat has a limited distribution within the park and is first recorded for the park based on the specimens collected during our survey (see Cornely, this volume for a detailed analysis of the habitat of the species). *N. micropus* is restricted to the lower elevations in the southwestern quarter of the park and is locally abundant. As is the case with *N. albigula*, this species builds conspicuous dens under prickly pear, cholla, and possibly other large plants, but its limited distribution in the park makes the houses of this species less likely to be viewed by park visitors. Although *N. micropus* and *N. albigula* are in contact in the southern portion of the park, there is virtually no sympatry between them.

A female collected on 23 August contained three embryos with a crown-rump length of 30. An adult female collected on 9 August contained no embryos.

We follow Birney (1973) in assigning our specimens to *N. m. canescens*.

**Microtus mexicanus guadalupensis** Bailey, Mexican Vole

*Specimens Examined* (82).—CULBERSON COUNTY: Blue Ridge, 1 (TTU); Guadalupe Mountains, 10 (USNM); Guadalupe Peak Campground, 4 (TTU); The Bowl, 41 (32 TCWC, 9 TTU); Upper Dog Ranger Station, 26 (TTU).

The Mexican vole is a montane species probably occurring no lower in the mountains than 1920 m at Upper Dog Ranger Station. Although this species is locally abundant, it is restricted to open montane meadows. Because this habitat is limited in the park, the status of this vole and its habitat will need continued monitoring. The population of Mexican voles in the Guadalupe Mountains National Park is isolated from other populations of the species, with the nearest population being on the Sacramento Mountains of New Mexico. This species is best considered a relict with Rocky Mountain affinities and is therefore one of the unique features of the park. Because of the unique and precarious status of this species, an intensive study of its biology has been undertaken by Wilhelm (1977).

One female taken on 8 August contained three embryos that measured 4 in crown-rump length. Males were found to have the following testes measurements (dates of capture in parentheses): 7, 3 (5 April); 8.5, 10 (6 April); 11 (2 June); 4 (4 June); 9 (1 July); 11 (21 July); 9 (7 August); 10 (26 August). A nonpregnant adult female taken on 11 June evinced a seasonal molt over most of its posterior dorsum. Another female taken on 9 August was molting on the dorsum, but it was impossible to determine whether this was a seasonal or maturational molt.

The taxon *Microtus mexicanus guadalupensis* was described originally by Bailey (1902b) on the basis of specimens from the Guadalupe Mountains. As this taxon is currently understood, populations occurring in the Manzano, Capitan, and Sacramento mountains in New Mexico are also included in it. The status of all of these populations is being reviewed by D. E. Wilhelm. External and cranial measurements of the male holotype (USNM 109, 191), three adult male topotypes, and means (extremes in parentheses) for four adult female topotypes are as follows: total length, 152, 145, 147, 150, 142.5 (130–150); length of tail vertebrae, 34, 34, 34, 34, 33.8 (30–36); length of hind foot, 20, 19, 19, 20, 18.8 (18–19); greatest length of skull, 27.1, 25.6, 25.8, 26.1, 25.2 (24.7–25.8); zygomatic breadth, 16.0, 14.6, 15.2, 15.5, 14.8 (14.4–15.1); interorbital constriction, 3.4, 3.1, 3.2, 3.3, 3.2 (3.1–3.3); mastoid breadth, 12.4, 12.0, 11.8, 12.1, 11.6 (11.3–11.8); length of nasals, 7.1, 7.2, 7.2, 7.5, 7.1 (7.0–7.2); length of maxillary toothrow, 7.3, 6.2, 6.4, 6.3, 6.3 (6.1–6.9); length of palatal bridge, 5.7, 5.8, 5.5, 5.2, 5.6 (5.4–5.7).

**Erethizon dorsatum couesi** Mearns, Porcupine

*Specimens Examined* (3).—CULBERSON COUNTY: Bone Springs, 1 (TTU); The Bowl, 1 (TTU); Upper Dog Ranger Station, 1 (TTU).

*Additional Record.*—CULBERSON COUNTY: Burned Cabin, head of McKittrick Canyon, 7500 ft (Davis 1940:82).

Although we obtained only three specimens of porcupine during our work in the park, it is quite common in the area. It can be expected anyplace in the park where there is sufficient woody vegetation to meet its dietary needs. For example, we saw individuals at the north end of the Patterson Hills and in the Patterson Hills Notch where some riparian vegetation occurs along the washes, with creosote bush and mesquite being the dominant shrubs. Individuals also were sighted near Frijole and several places in McKittrick Canyon. The individuals sighted at Frijole on 15 May were an adult accompanied by a young.

This is one of the more conspicuous species of mammal occurring in the park and should be included in any interpretative program for the park. Evidence of the activity of this species can be seen on many of the trees where they have gnawed away the bark. Porcupines will take refuge in trees or rock dens (see Davis 1940:82). Because this species is awkward and slow-moving on the ground and unable to escape easily when treed, extra precautions must be taken to protect them from park visitors.

The specimen from Bone Springs consists of a partial skull that was picked up. The other two specimens were nonpregnant females taken on 4 and 9 June.

We follow Hall and Kelson (1959:782) in assigning our specimens to *E. d. couesi* on geographic grounds.

**Canis latrans texensis** Bailey, Coyote

*Specimens Examined.*—None.

Our search of the literature and museum collections has revealed no record of specimens of the coyote being taken within the boundaries of the park. Davis and Robertson (1944:265) report the species from elsewhere in Culberson County. We heard coyotes at night and received reports from park personnel of sightings of coyotes within the park during our work in the area, but we did not obtain a specimen. Clearly, this species is present within the park, but has escaped collection because of its secretive habits. It is probably one of the more abundant and certainly one of the most significant predators occurring within the park.

Coyotes were heard howling at night by our field parties at the following locations: McKittrick Canyon Parking Lot; Williams Ranch Road Entrance; Crossroads; Northwest Corner; Red Sand Dunes. Dave Cunningham reported to us that there are coyotes in West Dog Canyon and at Coyote Peak. John Chapman reported seeing a coyote cross the road with a freshly killed rabbit near McKittrick Canyon, and Cornely inspected a pup that had been killed on the highway near the Williams Ranch Road Entrance on 13 August 1974.

Coyotes from the Guadalupe Mountains National Park most likely belong to the subspecies *C. l. texensis* as this is the subspecies to which Davis and Robertson (1944:265) and Jackson (1951:279) assigned other specimens from Culberson County.

**Canis lupus monstrabilis** Goldman, Gray Wolf

*Specimen Examined* (1).—CULBERSON COUNTY: Guadalupe Mountains, summit of mountains near New Mexico line, 1 (USNM).

The only specimen of the gray wolf from the park is a skull which was obtained by Vernon Bailey on 24 August 1901. The following is a quotation from his field notes which are on file at the National Bird and Mammal Laboratories, Department of the Interior: "These big wolves are said to be especially troublesome in the Guadalupe Mountains and to kill much stock, mostly calves and cows. One ranchman said they had killed over 40 head of cattle for him in the past three years and that he had been unable to kill any of the wolves. The skull sent in shows their size to be very large. The color of this one was light gray." This species has been extirpated from the park probably as the result of predator control activities.

This specimen was assigned to the subspecies *C. l. monstrabilis* by Goldman (1944:468). Cranial measurements for this specimen are as follows (specimen unsexed but undoubtedly a male): condylobasal length, 247.0; zygomatic breadth, 141.0; interorbital constriction, 44.1; postorbital constriction, 40.5; mastoid breadth, 84.5; length of nasals, 95.3; length of maxillary toothrow, 104.7; palatal length, 128.3.

**Urocyon cinereoargenteus scottii** Mearns, Gray Fox

*Specimens Examined* (4).—CULBERSON COUNTY: Bear Spring, 5700 ft, 1 (TCWC); McKittrick Canyon, 1 (TCWC); The Bowl, 8200 ft, 1 (TCWC); Upper Dog Ranger Station, 1 (TTU).

The gray fox is evidently one of the more abundant carnivores occurring in the Guadalupe Mountains National Park. All specimens examined were obtained in wooded or canyon situations. Our specimen was trapped, using sardines for bait, along the road leading to the ranger station in Upper Dog Canyon. Davis (1940:76) reported that the individual from Bear Spring was shot as it stalked a cottontail. A fox was observed by Cornely on 9 June 1974 near Bush Mountain, and another was sighted by Baker at Pine Springs Campground in August 1974.

The specimen from Upper Dog Ranger Station was an adult male that possessed testes measuring 17 in length when taken on 31 May.

As currently understood, the name *Urocyon cinereoargenteus scottii* is applied to gray foxes from the park. The subspecies has a widespread occurrence throughout the southwestern United States and northern Mexico. External and cranial measurements of a specimen from The Bowl (female) and one from Bear Spring (male) are as follows: total length, 940, 1080; length of tail, 395, 468; length of hind foot, 129, 142; length of ear, 76, 83; greatest length of skull, 121.1, 131.3; condylobasal length, 114.7, 128.0; zygomatic breadth, 65.2, 66.9; interorbital constriction, 22.4, 26.7; postorbital constriction, 28.0, 27.9; mastoid breadth, 43.4, 46.2; length of maxillary toothrow, 46.4, 53.9; length of palate, 56.9, 63.3.

**Ursus americanus amblyceps** Baird, Black Bear

*Specimens Examined.*—None.
*Additional Record.*—The Bowl (Davis 1940:74).

In 1901, Bailey found bears to be common on the upper slopes of the almost inaccessible canyons of the Guadalupe Mountains. In the head of McKittrick Canyon they had worn paths to their feeding areas on the oak and juniper ridges and to waterholes in upper portions of the canyon. Evidence of feeding activity of bears was present throughout the upper parts of the canyon and on the adjacent ridges. Bailey (1905:188) believed that the bears were feeding on acorns, juniper berries, and berries of *Berberis fremonti* in August.

Davis (1940:74) estimated the black bear population in the Guadalupe Mountains to be not greater than 25 individuals in the late 1930s. He also had reports of the species in upper McKittrick Canyon as well as Blue Ridge, Frijole, and the rim of the mountains about 5 miles SE of Guadalupe Peak.

During 1973–74, a bear and bear sign were observed in The Bowl and Upper Dog Canyon. Roger Reisch estimated that there was only a single bear in the park at this time. Clearly, the population of black bear in the Guadalupe Mountains has declined significantly in recent years. This is probably due to hunting pressures. However, with complete protection of the areas within the park, the black bear population can be expected to increase again with immigrants reaching the area from the Sacramento Mountains in New Mexico where there is a significant population.

The subspecies *U. a. amblyceps*, which is believed to occur throughout west Texas and New Mexico, was described based upon material from Grant Co., New Mexico (see Hall and Kelson 1959:866–867).

**Ursus arctos** Linnaeus, Grizzly Bear

*Specimens Examined.*—None.

The only known specimen of the grizzly bear in Texas is from the Davis Mountains taken in 1890 (Bailey 1905; Davis 1974). It is supposed that this bear may have entered the area from New Mexico by way of the Guadalupes. Bailey (1932:362–363) believed that specimens "indicate a probable range for the species along the Guadalupe, Sacramento, White, Capitan, Manzano, and possibly the Jemez Mountains . . ." of New Mexico. He stated that "in 1901, while camped at the head of Dog Canyon in the Guadalupe Mountains near the New Mexico and Texas boundary line, the writer found tracks of very large bears that were evidently of the grizzly group, though apparently no grizzlies had been killed there for some time." Bailey received a report from the Forest Service of grizzlies in the Guadalupes in 1909. We believe that there is sufficient evidence to include the grizzly bear in the historic mammalian fauna of the Guadalupe Mountains, although there were probably never large numbers of the species in the area.

Because of the large size of grizzlies and the fact that they kill some livestock, they were quickly exterminated from most of their former range. They most certainly were gone from the Guadalupes early in this century.

Numerous species and subspecies have been described for grizzly bears. However, modern writers agree that there is only one species involved in the complex. The subspecific arrangement within the species awaits thorough review.

**Bassariscus astutus flavus** Rhoads, Ringtail

*Specimens Examined* (3).—CULBERSON COUNTY: Lower McKittrick Canyon, 0.2 mi. N, 0.4 mi. W Pratt Lodge, 5150 ft, 1 (TTU); The Bowl, 1 (TCWC); Upper Dog Canyon, 1 (TTU).

The ringtail is probably quite common in the park but it seldom is seen because it frequents rocky, inaccessible habitats. The two specimens that we obtained were found dead, but not as the result of our activity. The specimen from The Bowl was a skeleton picked up by Davis (1940). Davis (1940) reported signs of this species as being abundant in The Bowl and along the cliffs of McKittrick Canyon. He found by examination of the feces that insects constituted a large part of the diet of this species. Ringtails have been observed on the stone fence around the house at Frijole.

One of our specimens consists of an unsexed skeleton picked up on 24 June 1974. The other specimen (Upper Dog Canyon) was prepared as a standard museum skin and skull. This individual is a nonpregnant adult female found on 29 November 1975.

Standard cranial measurements of the unsexed individual from The Bowl are as follows: greatest length of skull, 81.8; condylobasal length, 79.0; zygomatic breadth, 52.9; interorbital constriction, 16.4; postorbital constriction, 16.9; mastoid breadth, 36.0; length of maxillary toothrow, 30.7; palatal length, 36.7. We assign our specimens to *B. a. flavus* which occupies a wide geographic range in Texas, Oklahoma, New Mexico, Colorado, and northeastern Mexico (Hall and Kelson 1959:881).

**Procyon lotor mexicanus** Baird, Raccoon

*Specimens Examined* (4).—CULBERSON COUNTY: 0.3 mi. N, 0.5 mi. E Pratt Lodge, McKittrick Canyon, 1 (TTU); Upper Dog Ranger Station, 3 (TTU).

The raccoon apparently has not been reported from the Guadalupe Mountains previously. However, we found the species to be relatively abundant in the riparian communities in the canyons along the eastern slopes and northern interior canyons of the mountains. They are already a nuisance at the Pine Springs Campground, where they raid the trash cans. In addition to the places listed, raccoons were sighted in West Dog Canyon, in main McKittrick Canyon, and Frijole. This species can be expected anywhere in the park where sources of water are associated with wooded areas.

Two specimens from Upper Dog Ranger Station are unsexed, pick-up skulls. The other two specimens are nonpregnant, subadult females.

We have assigned our specimens to *Procyon lotor mexicanus* based upon distributional data. Goldman (1950:54) assigned a specimen from El Paso to this subspecies; Bailey (1905:194) allocated a specimen from Pecos to *mexicanus*. Based upon this evidence, it seems likely the subspecies *mexicanus* inhabits the Guadalupe Mountains, but the final decision must await the obtaining of adult specimens from the area.

**Mustela frenata neomexicana** (Barber and Cockerell), Long-tailed Weasel

*Specimens Examined.*—None.

No specimens of the long-tailed weasel were obtained during our work. However, Mr. Roger J. Reisch sighted a specimen on or about 23 September 1975 at a place 3.2 mi. S, 3.4 mi. W Guadalupe Peak on the Hudspeth–Culberson County line. Although this location is just outside of the park boundary, it clearly indicates that long-tailed weasels are living in the area. In addition to sighting the animal, Reisch also collected some fecal material at a presumed den. The fecal material is composed almost entirely of insect hard parts. In recent years, long-tailed weasels also have been observed in the vicinity of Calsbad Caverns and on ranches adjacent to the Guadalupe Mountains National Park. Davis and Robertson (1944) reported a specimen from near Kent in southern Culberson County. This individual was noted to be eating a woodrat (*Neotoma albigula*) prior to collection.

We follow Hall (1951a:333–338) in assigning long-tailed weasels from this region to *Mustela frenata neomexicana*.

**Taxidea taxus berlandieri** Baird, Badger

*Specimens Examined.*—None.

No specimens of badger were taken during our study. However, the diggings of this species were sighted at a number of places, especially near the base of El Capitan in the vicinity of Guadalupe Spring. Tony Burgess saw a badger on Williams Ranch Road in the summer of 1973. Bailey in his 1901 field notes (on file at National Fish and Wildlife Laboratories) stated that "A few badger holes found all over the Mts." Davis and Robertson (1944) recorded several sightings in southern Culberson County although no specimens were obtained. Long (1972:750) reports a specimen from Carlsbad, Eddy County, New Mexico. Clearly the badger has been, and remains, a member of the mammalian fauna of the park.

We follow the taxonomic arrangement given by Long (1972) for the North American badger.

**Spilogale gracilis leucoparia** Merriam, Spotted Skunk

*Specimens Examined* (2).—CULBERSON COUNTY: Pine Springs, 1 (TCWC); Williams Ranch House, 1 (TTU).

Spotted skunks are relatively rare (possibly due to their secretive habits) throughout Trans-Pecos Texas. They are inhabitants of rocky and brushy areas and may be expected wherever these occur in the park. Our specimen from Williams Ranch House was trapped in a live trap baited with sardines. The trap was placed in a wash immediately above the house. The specimen is an adult male that possessed testes measuring 20 in length when taken on 16 June.

Van Gelder (1959) recognized a single species of spotted skunks in the United States under the name *S. putorius*. Specimens from the Guadalupe Mountains clearly fall within the geographic range of *S. p. leucoparia* as he defined it. Subsequently, Mead (1967, 1968a, b) has presented convincing evidence that two species of spotted skunks occur in the United States, with the names *S. gracilis* for the western species and *S. putorius* for the eastern. We have chosen to follow Mead's evidence for use of the specific name *gracilis* and have followed Van Gelder's use of the subspecific name.

**Mephitis mephitis varians** Gray, Striped Skunk

*Specimens Examined* (5).—CULBERSON COUNTY: 7 mi. N Pine Springs, 3 (TCWC); Upper Dog Ranger Station, 1 (TTU); Williams Ranch House, 1 (TTU).

Although specimens of striped skunks are available only from intermediate elevations in the park, the species has been sighted at the Patterson Hill Notch, near Grisham–Hunter Lodge in South McKittrick Canyon, and in The Bowl indicating that the striped skunks may be expected anywhere in the park. This species feeds primarily on insects and small vertebrates. As pointed out by Findley et al. (1975), the striped skunk is highly susceptible to highway mortality; therefore, with increased vehicular traffic in the park, this species may be affected.

Both of our specimens from the park are subadults. The female taken on 4 June was non-pregnant; the male had testes measuring 20 when taken on 15 June.

*Mephitis mephitis varians* occurs from Nebraska to northern Mexico. This was the name applied by Davis and Robertson (1944:264) to specimens from the area although they stated that specimens from 7 mi. N Pine Springs exhibited some characteristics of *M. m. estor* which occurs to the west. External and cranial measurements of two females from 7 mi. N Pine Springs are as follows: total length, 712, 629; length of tail, 350, 308; length of hind foot, 65, 66; greatest length of skull, 70.2, 66.4; condylobasal length, 65.0, 63.2; zygomatic breadth, 41.6, 40.8; interorbital constriction, 19.1, 20.0; postorbital constriction, 17.9, 18.8; mastoid breadth, 35.6, 34.9; length of maxillary toothrow, 20.8, 21.6; palatal length, 27.0, 25.6.

**Conepatus mesoleucus mearnsi** Merriam, Hog-nosed Skunk

*Specimens Examined* (8).—CULBERSON COUNTY: Burned Cabin, head of McKittrick Canyon, 1 (TCWC); McKittrick Canyon, 4 (TCWC); The Bowl, 3 (2 TCWC, 1 TTU).

The hog-nosed skunk may be the most abundant of the three species of skunks occurring in the Guadalupe Mountains National Park. Hog-nosed skunks may be expected to occur any-

where within the park boundaries, although it will be most abundant in areas of high insect populations, which it uses as its main source of food. Members of this species have been seen at Frijole and Blue Ridge Campground in addition to the places listed above. Considerable digging activity of this species was noted, during our work, along the road leading to Pratt Lodge in McKittrick Canyon.

Our specimen from The Bowl is a subadult male obtained on 8 June 1974. Testes of this individual were 13 in length.

The subspecies *C. m. mearnsi* is currently considered to occur throughout most of Texas, adjacent New Mexico, and northern Mexico. External and cranial measurements of an adult male (Burned Cabin) and female (McKittrick Canyon), respectively, are as follows: total length, 605, —; length of tail, 238, —; length of hind foot, 70, 65; length of ear, 27, 23; greatest length of skull, 74.2, 67.7; condylobasal length, 69.2, 62.6; zygomatic breadth, 47.4, 41.2; interorbital constriction, 23.2, 21.7; postorbital constriction, 18.7, 18.8; mastoid breadth, 39.9, 36.8; length of maxillary toothrow, 21.9, 20.5; palatal length, 29.5, 27.2.

**Felis concolor azteca** Merriam, Mountain Lion

*Specimens Examined.*—None.

Evidently no specimens of the mountain lions have been preserved from the Texas portion of the Guadalupe Mountains, although the species has occurred there in the past and probably still occurs in limited numbers. Bailey in his notes (on file at National Fish and Wildlife Laboratories) stated that mountain lions were "Common in the Mts. where the numerous rock cliffs and canyons furnish them excellent cover. Fresh tracks seen above and below our camp in the head of Dog Canyon. Panthers are said to kill a good deal of stock, mainly colts, and most of the ranchmen keep hounds for hunting them and other 'varments.'" Bailey (1932:289) stated that "during 1916 the hunters of the Bureau of Biological Survey killed 9 [mountain lions] in the Guadalupe Mountain region," of New Mexico.

Davis (1940:76) noted mountain lions rarely occurred in the Guadalupe Mountains of Texas. He did examine the skin of a mountain lion that had been killed several years earlier near Burned Cabin in upper McKittrick Canyon. We believe that several mountain lions (probably less than five) have been at least part-time residents of the park in recent years. In 1973, a female and two yearlings were reportedly killed just north of the park boundary in New Mexico. These lions were allegedly killing sheep and then returning to the safety of the park. In the summer of 1975, an almost identical incident occurred in the same area. This time an adult lion was captured, tranquilized, and removed from the area. One of the problems with the Guadalupe Mountains National Park is that it is too small to completely contain the normal home range of many of the larger, wide-ranging species such as the mountain lion. During the summer of 1973, one of us (Cornely) saw large cat tracks, probably of this species, in The Bowl. We also received two other reliable reports of mountain lion tracks being seen in The Bowl at other times during the same summer.

The major source of food of this species in the Southwest is mule deer (Davis 1974:134). With the increasing population of this food item in the park, the mountain lion can be expected to continue to include the park within its current distribution as long as there are populations of this cat in areas adjoining the park.

The taxonomic status of mountain lions occurring in the park is somewhat in question. Goldman (1946) in his systematic review of the species assigned specimens from central and southern Hudspeth County to *F. c. stanleyana*. The nearest record to the park was a specimen from 25 mi. north of Van Horn (stated to be in Hudspeth County by Goldman). In this same work Goldman assigned specimens from New Mexico to *F. c. azteca*, including one from Queen in southwestern Eddy County. Davis (1940) assigned the skin that he had examined from Burned Cabin to *F. c. azteca*; however, without stating a reason Davis and Robertson (1944) assigned this same specimen to *F. c. stanleyana*. We tentatively have assigned the mountain lions that occur in the park to *F. c. azteca* because, based upon all reports that we have received, they are entering the park from the north in New Mexico and not from the south. However, documented specimens are needed before this assignment can be made definite.

**Felis rufus baileyi** (Merriam), Bobcat

*Specimen Examined* (1).—CULBERSON COUNTY: The Bowl, 1 (TCWC).

The only specimen available from the Guadalupe Mountains is a male collected on 22 June 1939 in The Bowl. However, we had reports and a sighting of bobcats during our work in the area. On 16 August 1973, one of us (Cornely) saw a bobcat cross the road just inside the park in Upper Dog Canyon at 5:00 p.m. Another bobcat wandered into the yard of the ranger in Upper Dog Canyon in the summer of 1973. This individual had numerous porcupine quills embedded in its face and obviously had not eaten for a long time. It died after all efforts to help it failed. The rangers also reported the presence of bobcats in West Dog Canyon. Several bobcats have been trapped in recent years just north of the park in New Mexico according to local ranchers. Bailey in his notes (on file at National Fish and Wildlife Laboratories) indicated that bobcats were common in the mountains and that he saw numerous tracks and a few skins at ranches. Davis (1940:76) found by examination of scats that bobcats in The Bowl were living in late June almost entirely upon small mammals, especially rabbits.

We follow Anderson (1972:386–387) in use of the generic name *Felis* for bobcats previously known under the name *Lynx*. The subspecific name *F. r. baileyi* has been applied to bobcats throughout the southwestern United States and northern Mexico. Cranial measurements of our specimen are as follows: greatest length of skull, 119.5; condylobasal length, 108.3; zygomatic breadth, 83.8; interorbital breadth, 23.9; postorbital breadth, 39.6; mastoid breadth, 55.9; length of maxillary toothrow, 35.6; palatal length, 45.8.

**Cervus elaphus merriami** Nelson, Merriam's Elk

*Specimens Examined.*—None.

There are apparently no verified records of the native elk in Texas. However, Bailey (1905) wrote "several old ranchmen have told me, they ranged south to the southern part of the Guadalupe Mountains, across the Texas line. I could not get an actual record of one killed in Texas, or nearer than 6 or 8 miles north of the line. . . ." Later, Bailey (1932), writing about New Mexico, stated "Merriam's elk is now probably extinct; certainly it no longer occurs in New Mexico. Forty years ago it was common in the Sacramento, White, and Guadalupe Mountains east of the Rio Grande. . . ." According to Murie (1951), Merriam's elk ranged through only a few mountain areas of Arizona, New Mexico, and Texas, isolated by surrounding arid lands. We believe that it is relatively safe to include the native elk, *C. e. merriami*, as a member of the mammalian fauna of the Guadalupe Mountains. This subspecies probably became extinct prior to 1900 in the area.

We follow McCullough (1969) in use of the specific name *C. elaphus* for North American elk. We have followed McCullough (1969) and Findley et al. (1975) in considering Merriam's elk to be a subspecies of the more wide-ranging *C. elaphus*. The exact taxonomic status of this elk will never be determined but our arrangement seems most logical to us. *Cervus elaphus merriami* was apparently larger than *C. e. nelsoni* and *C. e. roosevelti*, had more massive antlers, and paler coloration.

**Cervus elaphus nelsoni** Bailey, Rocky Mountain Elk

*Specimen Examined* (1).—CULBERSON COUNTY: Upper Dog Ranger Station, 1 (TTU).

Forty-four Rocky Mountain elk were introduced into the Guadalupe Mountains in 1928 (Davis and Robertson 1944). They were imported from the northern Rockies by Judge J. C. Hunter and associates and released in McKittrick Canyon. In 1934 (Wright and Thompson 1934) the herd numbered approximately 60. At that time the elk were concentrated on the slopes of McKittrick Canyon near the streambed and were destroying the vegetation. In 1938 (Davis 1940) the size of the herd was reportedly approximately 400. It is very unlikely that the herd could have increased that rapidly. We estimate the present elk population to be 150 or less.

During our work we observed elk throughout the high country, with the notable exception of the Guadalupe Peak–El Capitan area. They have been sighted in Upper Dog Canyon, West Dog Canyon, Cox Tank, Frijole, Bush Mountains, and The Bowl. In addition to the above areas, Davis (1940) observed elk on Blue Ridge and in McKittrick Canyon.

The Guadalupe elk herd is probably the southernmost free-ranging population of Rocky Mountain elk. Although the ingestion of succulent vegetation provides some water for the elk and mule deer in the Guadalupes, they may be under serious stress from lack of water during the driest months of the year.

In the summer of 1975, two young of the year were observed in Pitchfork Canyon behind Upper Dog Ranger Station. Although this is proof that the elk are successfully reproducing, the status herd is questionable and is currently the subject of intensive study. Although introduced, the elk are a valuable component of the fauna of Guadalupe Mountains National Park. Nothing is more exciting to the back country hiker than the sudden appearance of a magnificent bull elk, which is one reason why the elk is the one mammal that park visitors often ask about.

**Odocoileus hemionus crooki** (Mearns), Mule Deer

*Specimens Examined* (7).—CULBERSON COUNTY: McKittrick Canyon, 2 (TCWC); Smith Spring, 1 (TTU); The Bowl, 1 (TCWC); Upper Dog Ranger Station, 3 (TTU).

The mule deer is extremely abundant in the park and its numbers can be expected to continue to increase with protection. The major natural predators of mule deer—mountain lions and wolves—have been greatly reduced in numbers or eliminated from the region. We observed mule deer throughout the park area, but the species was observed most often along the slopes and on top of the mountains in areas of dense brush and trees. Mule deer are browsers; their food habits have been studied extensively in the New Mexico portion of the Guadalupe Mountains (Anderson et al. 1965, 1970; Snyder 1961; Kittams et al. 1977).

All of our specimens are skulls that were picked up from individuals that probably died of natural causes. Davis (1940:84) reported a specimen carrying a near full-term fetus when taken on 27 June. During our work, a fawn was observed watering at the horse corral at the Upper Dog Ranger Station on 29 May.

We follow Cowan (1956:334) in use of the subspecific name *crooki* for mule deer from the park. Mule deer can be distinguished from the white-tailed deer because their antlers fork dichotomously, with prongs being about equal in size, whereas in those of the white-tailed deer the prongs appear to arise vertically from a main beam.

**Odocoileus virginianus texanus** (Mearns), White-tailed Deer

*Specimens Examined.*—None.

We know of no scientific specimens of the white-tailed deer from the Guadalupe Mountains National Park. However, Bailey made the following entry in his field notes during his work in the area in 1901 (notes on file with National Bird and Mammal Laboratories, Department of the Interior): "A few white-tail deer are said to be found along the east side of the Guadalupe Mts. but they are rare. A ranchman who had lived in the Mts. for 15 years said he had seen but 3 or 4. No doubt they straggle across from the edge of the Staked Plains where they are common." During our work in the park, mule deer were found to be extremely common but no white-tailed deer were sighted. We can find no justification for the following statement by Davis (1974:257), at least for areas within the park boundaries: ". . . in the Guadalupe Mountains the white-tail occurs almost entirely in the foothills; the mule deer, in the higher mountains." We believe that this species was never abundant in the Guadalupe Mountains and the few individuals present were probably extirpated by hunting pressures by man.

According to Kellogg (1956:35), most of the white-tailed deer in Texas are assignable to the subspecies *O. v. texanus*. We have followed this arrangement.

**Antilocapra americana americana** (Ord), Pronghorn

*Specimen Examined* (1).—New Mexico Guadalupe Mountains, at east base of mountains, 1 (USNM).

The only record of a pronghorn from near the park is based upon a skull picked up by Bailey in 1901. Writing about this species in his notes (on file with National Bird and Mammal Laboratories, Department of the Interior), Bailey stated: "A few antelope remain on the plains along the sides of the Guadalupe Mts. and come up on the foothills and in the side valleys. We saw

tracks in Dog Canyon just below our camp. A skull with horns was picked up at the east base of the Mts." Nelson (1925) estimated the pronghorn populations of Culberson and Hudspeth counties to be 75 and 125, respectively, but none was reported from the area of the park. Buechner (1950) plotted the distribution of pronghorns in Trans-Pecos Texas but all herds were from either to the south or to the west of the park. Buechner (1950) also presents detailed ecological and life history data for this species in Trans-Pecos Texas. Evidently, pronghorns, which are basically a grassland species, were never abundant in this area. The species was extirpated from the area probably by hunting pressures or by grazing pressures of cattle.

The specimen is from near the zone of intergradation between *A. a. americana* and *A. a. mexicana*. We have followed Bailey's (1932) assignment of this specimen to the former subspecies. The skull is that of an adult male, with the following measurements: condylobasal length, 275.5; palatal length, 160.5; length of maxillary toothrow, 70.0; squamosal breadth, 80.7; length of nasals, 107.0; length of horn core, 40.6; breadth of horn core, 23.4.

**Bison bison bison** (Linnaeus), Bison

*Specimens Examined.*—None.

According to Allen (1877), the bison did occur in Texas west of the Pecos River but by 1840 they "no longer ranged west of the Pecos River, either in Texas or New Mexico. . . ." Allen (1877:526) reports that on a survey of the area led by Pope in 1854, "Mr. J. H. Byrne, in his diary of the expedition, reports meeting *bois de vache* 'for the first time' at Camp No. 10, near Ojo del Cuerbo, or Salt Lakes, west of the Guadaloupe Mountains, and in the Valley of the Rio Grande. This is the only allusion to buffalo or buffalo 'sign' contained in the narrative. . . ." Findley et al. (1975:335) report a specimen from Carlsbad, Eddy County, New Mexico.

We believe that the bison did occur during historical times in the area now occupied by the Guadalupe Mountains National Park, at least at lower elevations where grassland areas were found. The numbers may have never been great and they were probably gone from the area by the middle of the 19th century.

**Ovis canadensis mexicana** Merriam, Mountain Sheep

*Specimens Examined* (3).—CULBERSON COUNTY: McKittrick Canyon, Guadalupe Mountains, 2 (USNM); Guadalupe Mountains, 1 (USNM).

Bailey (1905:70–75) reports hunting mountain sheep in the Guadalupe Mountains. The stomachs of two individuals that he shot contained *Cercocarpus parvifalius, Philadelphus microphyllus*, common wild onion, and a small amount of grass. Bailey's field notes (on file at the National Bird and Mammal Laboratories, Department of the Interior), written during his work in August 1901, state that: "Mountain sheep are fairly common in the rough part of the range south of Dark Canyon, mainly south of the Texas line. We found where they had been in the head of Dog Canyon and McKittrick, and Mr. Frank who lives in Gunsight Canyon told me that they were common around his place and in Double Canyon. Mr. Frank has lived in these Mts. for about 15 years and has probably killed more sheep than anyone else in the range, merely shooting them when they came in sight of his ranch when he needed meat, never more than 5 at a time, or 2 in warm weather, as he could not use the meat of a greater number. . . . He thinks the sheep have increased and are more numerous now than 15 years ago. He has counted 30 in a band but usually finds them in small bands of 5 to 10, sometimes all old rams, or all ewes and kids, or in mixed bands."

Davis and Taylor (1939) and Davis (1940) estimated that no more than 25 bighorns were in the Guadalupe Mountains in the late 1930s. They had reports of sightings of mountain sheep in 1939 from the east rim of the mountains above Frijole, near El Capitan, north rim of McKittrick Canyon, and west rim of mountains near Guadalupe Peak. Davis (1940) also saw two mounted heads that were from sheep taken in 1909 on Guadalupe Peak. Gross (1960) summarizes records of bighorns in the Guadalupes between 1940 and 1960. Only a few scattered reports were received during this time.

Mountain sheep no longer occur in the Guadalupe Mountains. The species undoubtedly was eliminated from the area by the activities of man. The exact causes of their extermination are

unknown, but were probably one or a combination of hunting pressures, diseases introduced by domestic sheep, or grazing competition of domestic livestock. Of the three specimens preserved from the Guadalupe Mountains, two are large, adult males with magnificent sets of horns. The other skull is that of a much younger unsexed individual. The Guadalupe Mountains are well within the geographic range of *O. c. mexicana* as currently understood (Hall and Kelson 1959:1031).

Serious consideration should be given to a reintroduction of this unique species to the park. Sighting this magnificent species would be a treat for the backpackers and hikers and the addition of this species would help return the park ecosystem to its original condition. Care should be taken concerning the possible origin of the stock for reintroduction, with the reintroduced stock being most like those that were extirpated. A careful evaluation of the extent and condition of potential mountain sheep habitat must be completed before reintroduction plans are undertaken. Also the potential for spread of disease from domestic sheep to the introduced population must be evaluated.

## DISCUSSION

Our field work and survey of the literature indicate that 65 species of mammals have occurred in the area now occupied by the Guadalupe Mountains National Park during historic times. Of the 65 species, 13 species are bats, three rabbits, 29 rodents, 14 carnivores, and six artiodactyls. Another nine species possibly occur or possibly have occurred in the park including *Notiosorex crawfordi, Myotis evotis, Euderma maculatum, Lasiurus borealis, Spermophilus mexicanus, Tamiasciurus hudsonicus, Onychomys leucogaster, Vulpes macrotis*, and *Dicotyles tajacu* (an individual, probably from an introduced population, was reportedly sighted in the park).

### Extirpated Species

Of the 65 species known from the park, nine are believed to have been extirpated from the area. Most, if not all, of these species have disappeared as the direct result of human activity.

*Cynomys ludovicianus*.—Bailey (1905) reported prairie dogs to be abundant along the main ridge of the mountains in Dog Canyon, which derived its name from the numerous colonies of this species in the area. Davis (1940) reported scattered "towns" along the eastern edge of the mountains. The species is no longer present in the park although there are colonies in the general area. Prairie dogs were removed from the area by direct human activity through the use of poisons because they were believed to directly compete with cattle for food.

*Perognathus hispidus paradoxus*.—Only one specimen of this species has been taken from the park area. Hispid pocket mice are primarily grassland inhabitants. The species was probably eliminated from the area by alteration of this habitat either by overgrazing or environmental changes.

*Canis lupus monstrabilis*.—According to Bailey gray wolves were especially troublesome in the Guadalupe Mountains and were said to kill much stock. One specimen was preserved from the park area. This species was extirpated from the park as the result of predator control activities.

*Ursus arctos*.—The grizzly bear probably has occurred in the Guadalupe Mountains in the past. The species has been removed from much of its

former geographic range, probably because of its large size and the fact that it does kill some livestock.

*Cervus elaphus merriami.*—The geographic range of this extinct subspecies of elk once included the Guadalupe Mountains. This subspecies probably was removed by the increasing aridity of the region and hunting pressures.

*Odocoileus virginianus texanus.*—White-tailed deer were never abundant in the park area and probably were removed by hunting pressure.

*Antilocapra americana americana.*—Bailey reported seeing pronghorn along the sides of the Guadalupe Mountains and in the foothills. The species was probably never abundant in the area. They probably were eliminated by hunting pressure and habitat alteration.

*Bison bison bison.*—The bison was probably removed from the area of the park by hunting or environmental change by the middle of the 19th century.

*Ovis canadensis mexicana.*—Mountain sheep were relatively common in the mountains during Bailey's survey in 1901. Herds of 30 individuals were reported to Bailey by local ranchmen. Davis, in 1940, estimated that no more than 25 bighorns remained in the mountains. Mountain sheep undoubtedly were eliminated from the area by a combination of hunting pressures of man, diseases introduced by domestic sheep, and grazing competition of domestic livestock.

**Species Rare in the Park**

Five species are rare in their distribution in the Guadalupe Mountains National Park. Four of these five species are confined to the montane regions of the park. This is definitely the most fragile habitat in the park. The montane habitat essentially represents an island that is in dynamic equilibrium with the Chihuahuan Desert and grassland that surrounds it on three sides.

*Sylvilagus floridanus robustus.*—This is probably the rarest species still occurring in the park. It is evidently confined to the Douglas fir and ponderosa pine stands in The Bowl. The taxon is confined to Chisos, Chinati, Davis, and Guadalupe mountains of Texas. There is evidently no interchange between these populations at this time; therefore, if the population in the Guadalupe Mountains is lost, no natural repopulation would be expected.

*Eutamias canipes canipes.*—Gray-footed chipmunks are confined to the wooded areas of the higher elevations of the park. This taxon is known only from the Guadalupe Mountains; therefore, its existence must be protected. *E. c. sacramentoensis*, the only other subspecies of this species, is known only from the Sacramento, White, Capitan, and Gallinas mountains of New Mexico, indicating the very restricted distribution of the entire species.

*Ammospermophilus interpres.*—The Texas antelope ground squirrel occupies a relatively restricted geographic range in northern Mexico, Texas, and New Mexico. Within the park this species occurs in the lower grassland

and desert areas. The species is relatively rare within the park, but extensive areas of its preferred rocky desert habitat are included in the park. However, because these areas will be receiving heavy human impact, the status of this unique species should be monitored in the future.

*Thomomys bottae guadalupensis*.—This taxon of pocket gopher is endemic to the Guadalupe Mountains. Nowhere did we find this gopher to be abundant. It is distributed primarily in the montane and valley areas, but we did obtain a specimen near Nipple Hill. We believe that this species will be in no real danger as long as its preferred food of lecheguilla remains abundant.

*Microtus mexicanus guadalupensis*.—This subspecies of the Mexican vole is restricted to the Guadalupe Mountains of Texas and the Manzano, Capitan, and Sacramento mountains in New Mexico. There is no evidence for genetic interchange among these populations at the present time. Although this species is locally abundant in the Guadalupe Mountains National Park, it is restricted to open montane meadows. Because this habitat is limited in the park and subject to heavy human usage, the status of the Mexican vole and its habitat will need continued monitoring.

**Mammalian Faunal Relationships within the Park**

Within the park, we recognize four mammalian distributional zones (Fig. 7). These are based upon major vegetational types (Gehlbach 1967, undated; Warnock undated) and the distribution of some indicator species of mammals. For a species to be a good indicator, it should be relatively abundant and its distribution should be restricted, or nearly so, to the zone for which it is an indicator. The four zones that we recognize and their indicator species of mammals are as follows: desert—*Dipodomys merriami, D. spectabilis, Spermophilus spilosoma, Onychomys torridus*, and *Neotoma micropus*; grassland—*Perognathus hispidus, Sigmodon hispidus*, and *Reithrodontomys megalotis*; riparian woodland—*Procyon lotor*; montane—*Sylvilagus floridanus, Peromyscus boylii, Neotoma mexicana,* and *Microtus mexicanus*.

The grassland habitat was found to contain the most mammalian species (41) and the montane the least with 27 (Table 1). The number of mammalian species shared between habitats is shown in the upper portion of Table 1. The highest Burt Coefficient of Similarity between habitats was between the Montane and Riparian Woodland. The Grassland Zone had a relatively high coefficient with all habitats. The lowest coefficient was between the Montane and Desert zones which share only eight mammalian species. Clustering of the Burt Coefficients (Fig. 8) using the Unweighted Pair Group Method Using Arithmetic Means groups Desert and Grassland mammalian faunas together and the Riparian Woodland clusters closely with the Montane.

These results indicate that the Desert and Montane mammalian faunas are quite distinct. The Grassland mammalian fauna seems to be transitional

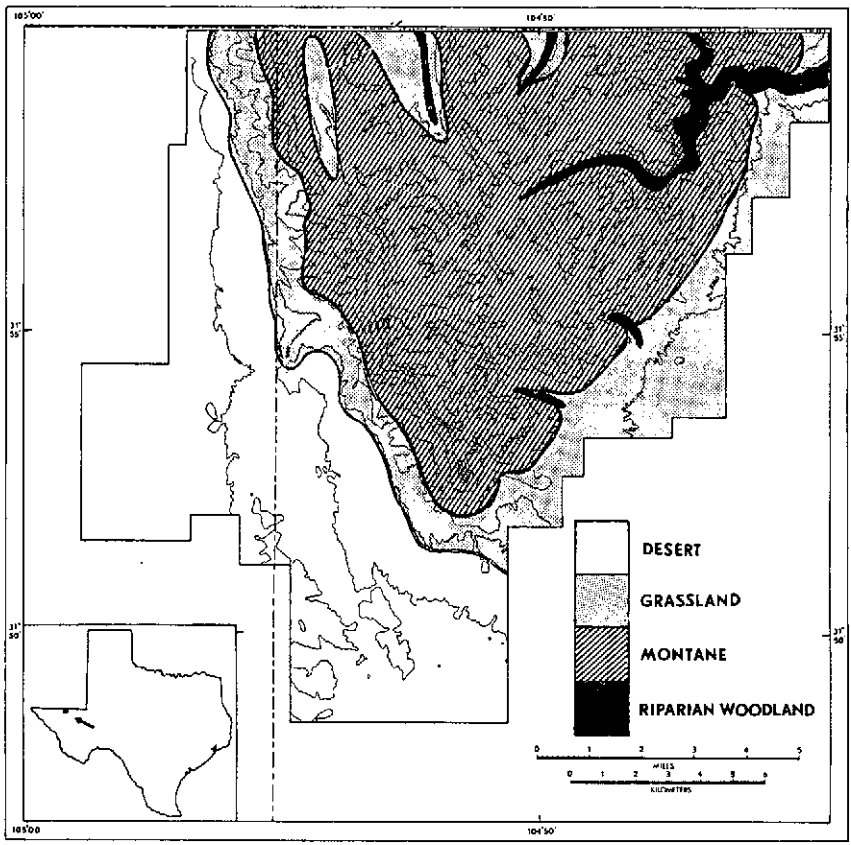


**Fig. 7.** Mammalian distributional zones in the Guadalupe Mountains National Park, Texas. See text for discussion.

TABLE 1. Similarity of mammalian faunas occurring in the four mammalian distributional zones recognized in the Guadalupe Mountains National Park, Texas. Boldface numbers on the diagonal represent the total number of mammalian species occurring in each zone. The numbers above the diagonal represent the number of species shared between zones, whereas the numbers below the diagonal represent the Burt Coefficients of Similarity between the zones.

| Distributional Zone | Desert | Grassland | Riparian woodlands | Montane |
|---|---|---|---|---|
| Desert | **31** | 24 | 12 | 8 |
| Grassland | 67 | **41** | 24 | 18 |
| Riparian Woodland | 39 | 67 | **31** | 22 |
| Montane | 28 | 53 | 76 | **27** |

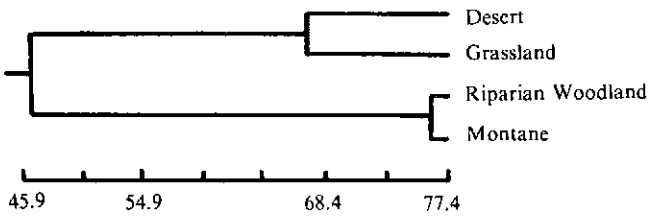


**Fig. 8.** Phenogram resulting from the clustering (Unweighted Pair Group Method Using Arithmetic Means) of Burt Coefficients of Similarity among mammalian distributional zones as given in Table 1.

between that of the Desert and Montane-Riparian Woodland faunas. This would account for high number of species in the grasslands and high coefficients with all other faunas. However, we have chosen to recognize this zone because there are some mammalian species which are limited to the grassland and would probably be eliminated from the park if the Grasslands are eliminated. The Montane and Riparian Woodland mammalian faunas are the most similar. This is reasonable because the habitats are in close geographic proximity and both represent relatively mesic habitats.

It is the Montane mammalian fauna that gives the Guadalupe Mountains National Park its unique character. Several species present in this area are at, or near, the southern limit of their distribution and represent a southern attenuation of the Rocky Mountain fauna of New Mexico. This montane island at the edge of the Chihuahuan Desert, and in dynamic equilibrium with it, is one reason that park was preserved and is the reason that a sound management plan must be developed and followed for the park.

**Comparisons of Mammalian Faunas from Guadalupe Mountains National Park with those from Other Geographic Areas**

We compared the mammalian fauna of the Guadalupe Mountains National Park with other specific areas from which we believe a relatively complete mammalian fauna is known. We chose areas within the same geographic region as the Guadalupe Mountains as follows (references in parentheses are those used to develop the faunal list given in Table 2): Big Bend National Park, Texas (Borell and Bryant 1942; Easterla 1973a, 1973b); Sierra Vieja Mountains, Texas (Blair and Miller 1949; specimens in collection at Texas Tech University); Davis Mountains, Texas (Blair 1940; specimens in collection at Texas Tech University); northwestern Chihuahua, Mexico (Anderson 1972); Sacramento Mountains, above 5000 ft, New Mexico (Findley et al. 1975); Tularosa Basin below 5000 ft, New Mexico (Blair 1941; Findley et al. 1975); Lubbock County, Texas (Bailey 1905; Davis 1974; specimens in collection at Texas Tech University). The Big Bend National Park, Sierra Vieja Mountains, and Davis Mountains represent

TABLE 2. Species of mammals occurring in selected geographic areas of Texas, New Mexico, and Chihuahua. A plus sign indicates that the species has been recorded from the given area. Records are taken from literature cited in text and specimens deposited in The Museum of Texas Tech University.

| Species | Guadalupe Mountains National Park | Big Bend National Park | Sierra Vieja Mountains, Texas | Davis Mountains, Texas | Northwestern Chihuahua, Mexico | Sacramento Mountains, New Mexico | Tularosa Basin, New Mexico | Lubbock County, Texas |
|---|---|---|---|---|---|---|---|---|
| *Didelphis virginiana* | | + | | | | | | + |
| *Notiosorex crawfordi* | | + | | + | | | + | + |
| *Cryptotis parva* | | | | | | | | + |
| *Sorex nanus* | | | | | | + | | |
| *Sorex vagrans* | | | | | | + | | |
| *Mormoops megalophylla* | | + | + | + | | | | |
| *Leptonycteris nivalis* | | + | | | | | | |
| *Myotis auriculus* | | | | | + | | | |
| *Myotis californicus* | + | + | + | | + | | + | |
| *Myotis leibii* | + | + | + | + | + | | | |
| *Myotis lucifugus* | | | | | + | + | | |
| *Myotis thysanodes* | + | + | + | + | + | + | | |
| *Myotis velifer* | + | + | + | + | + | | | |
| *Myotis volans* | + | + | + | + | + | + | + | |
| *Myotis yumanensis* | | + | + | + | + | | | |
| *Pipistrellus hesperus* | + | + | + | + | + | + | | |
| *Lasiurus borealis* | | | + | + | + | | | + |
| *Lasiurus cinereus* | + | + | + | + | + | + | | + |
| *Lasionycteris noctivagans* | + | | | + | | + | | + |
| *Eptesicus fuscus* | + | + | + | + | + | + | | |
| *Plecotus phyllotis* | | | | | + | | | |
| *Plecotus townsendii* | + | + | + | | + | + | | |
| *Euderma maculatum* | | + | | | | | | |
| *Antrozous pallidus* | + | + | + | + | + | | + | |
| *Tadarida brasiliensis* | + | + | + | + | + | + | + | + |
| *Tadarida femorosacca* | | + | | | | | | |
| *Tadarida macrotis* | + | + | + | + | | + | + | |
| *Eumops perotis* | | + | | | | | | |
| *Sylvilagus audubonii* | + | + | + | + | + | | + | + |
| *Sylvilagus floridanus* | + | + | + | + | + | + | | + |
| *Lepus californicus* | + | + | + | + | + | | + | + |
| *Lepus collotis* | | | | | + | | | |
| *Eutamias canipes* | + | | | | | + | | |
| *Eutamias dorsalis* | | | | | + | | | |
| *Eutamias minimus* | | | | | | + | | |
| *Ammospermophilus interpres* | + | + | + | | | | + | |
| *Spermophilus mexicanus* | | + | | + | | | | |
| *Spermophilus spilosoma* | + | + | | + | + | | + | + |
| *Spermophilus tridecemlineatus* | | | | | | + | | + |

TABLE 2. (continued)

| Species | Guadalupe Mountains National Park | Big Bend National Park | Sierra Vieja Mountains, Texas | Davis Mountains, Texas | Northwestern Chihuahua Mexico | Sacramento Mountains, New Mexico | Tularosa Basin, New Mexico | Lubbock County, Texas |
|---|---|---|---|---|---|---|---|---|
| *Spermophilus variegatus* | + | + | + | + | + | + | + | |
| *Cynomys ludovicianus* | + | | + | + | | | + | + |
| *Tamiasciurus hudsonicus* | | | | | | + | | |
| *Sciurus nayaritensis* | | | | | + | | | |
| *Thomomys bottae* | + | + | + | + | | + | + | |
| *Thomomys umbrinus* | | | | | + | | | |
| *Pappogeomys castanops* | + | + | + | + | | + | + | + |
| *Geomys arenarius* | | | | | | | + | |
| *Geomys bursarius* | | | | | | | | + |
| *Castor canadensis* | | + | | | | + | | |
| *Perognathus flavescens* | | | | | | | + | |
| *Perognathus flavus* | + | + | + | + | + | | + | + |
| *Perognathus hispidus* | + | | | + | + | | + | + |
| *Perognathus intermedius* | + | | | | + | | + | |
| *Perognathus nelsoni* | | + | + | + | | | | |
| *Perognathus penicillatus* | + | + | + | + | + | | + | |
| *Dipodomys merriami* | + | + | + | + | + | | + | |
| *Dipodomys nelsoni* | | | | | + | | | |
| *Dipodomys ordii* | + | + | | + | + | | + | + |
| *Dipodomys spectabilis* | + | | + | + | + | | + | |
| *Reithrodontomys fulvescens* | | + | | + | + | | | |
| *Reithrodontomys megalotis* | + | | + | + | + | + | + | + |
| *Reithrodontomys montanus* | | | | + | + | | | + |
| *Peromyscus boylii* | + | + | | + | + | + | | |
| *Peromyscus difficilis* | + | | | | | + | + | |
| *Peromyscus eremicus* | + | + | + | + | + | | + | |
| *Peromyscus leucopus* | + | + | | + | + | | + | + |
| *Peromyscus maniculatus* | + | + | + | + | + | + | + | + |
| *Peromyscus pectoralis* | + | + | + | + | | | | |
| *Peromyscus truei* | + | | | | | + | + | |
| *Baiomys taylori* | | | | | + | | | |
| *Onychomys leucogaster* | | | | + | + | + | + | + |
| *Onychomys torridus* | + | + | | + | + | | + | |
| *Sigmodon fulviventer* | | | | | + | | | |
| *Sigmodon hispidus* | + | | | + | + | | + | + |
| *Sigmodon ochrognathus* | | + | + | + | | | | |
| *Neotoma albigula* | + | + | + | + | + | + | + | + |
| *Neotoma mexicana* | + | | | + | + | + | | |
| *Neotoma micropus* | + | + | + | + | | | + | + |
| *Microtus longicaudus* | | | | | | + | | |
| *Microtus mexicanus* | + | | | | | + | | |
| *Zapus princeps* | | | | | | + | | |

TABLE 2. (continued)

| Species | Guadalupe Mountains National Park | Big Bend National Park | Sierra Vieja Mountains, Texas | Davis Mountains, Texas | Northwestern Chihuahua, Mexico | Sacramento Mountains, New Mexico | Tularosa Basin, New Mexico | Lubbock County, Texas |
|---|---|---|---|---|---|---|---|---|
| *Erethizon dorsatum* | + | + | + | + | + | + | + | + |
| *Canis latrans* | + | + | + | + | + | + | + | + |
| *Canis lupus* | + | + | | + | | + | | |
| *Urocyon cinereoargenteus* | + | + | + | + | + | + | | + |
| *Vulpes macrotis* | | + | | + | + | | + | |
| *Vulpes velox* | | | | | | | | + |
| *Vulpes vulpes* | | | | | | | | + |
| *Ursus americanus* | + | + | | + | | + | | |
| *Ursus arctos* | + | | | + | + | | | |
| *Bassariscus astutus* | + | + | + | + | | + | | |
| *Procyon lotor* | + | + | + | + | + | + | | + |
| *Mustela frenata* | + | | | | | + | | + |
| *Spilogale putorius* | + | + | + | + | + | | + | + |
| *Mephitis macroura* | | + | + | + | + | | | |
| *Mephitis mephitis* | + | + | + | + | + | | + | + |
| *Conepatus mesoleucus* | + | + | + | + | | | | |
| *Taxidea taxus* | + | + | + | + | + | | | + |
| *Felis concolor* | + | + | + | + | + | + | + | |
| *Felis rufus* | + | + | + | + | + | + | + | + |
| *Odocoileus hemionus* | + | + | + | + | + | + | + | |
| *Odocoileus virginianus* | + | + | | + | + | + | | + |
| *Cervus elaphus* | + | | | | | | | |
| *Dicotyles tajacu* | ' | + | + | + | | | | |
| *Antilocapra americana* | + | + | + | + | + | | | + |
| *Bison bison* | + | | | + | + | | | + |
| *Ovis canadensis* | + | + | | | + | | | |

other mountain ranges in Trans–Pecos Texas. Northwestern Chihuahua is a part of the Chihuahuan Desert south of the Rio Grande. The Tularosa Basin is a low-lying desert region which is a northern extension of the Chihuahuan Desert and contains the White Sands National Monument. The Sacramento Mountains are the southern extension of the Rocky Mountains in New Mexico which most closely approaches the Guadalupe Mountains. Lubbock County, Texas, is located in the southern Great Plains.

The total mammalian fauna of the Guadalupe Mountains National Park shows the highest similarity with that occurring in the Davis Mountains, Texas (Table 3). High similarity is also shown to the total mammalian fauna

TABLE 3. Similarity of the total mammalian faunas occurring in eight selected geographic areas of Texas, New Mexico, and Chihuahua. Boldface numbers on the diagonal represent the total number of mammalian species occurring in each area. The numbers above the diagonal represent the number of species shared between areas, whereas the numbers below the diagonal represent the Burt Coefficients of Similarity between the area.

| Geographic Areas | Guadalupe Mountains National Park, Texas | Big Bend National Park, Texas | Sierra Vieja Mountains, Texas | Davis Mountains, Texas | Northwestern Chihuahua, Mexico | Sacramento Mountains, New Mexico | Tularosa Basin, New Mexico | Lubbock County, Texas |
|---|---|---|---|---|---|---|---|---|
| Guadalupe Mountains National Park, Texas | **65** | 49 | 43 | 53 | 47 | 34 | 37 | 30 |
| Big Bend National Park, Texas | 0.77 | **65** | 45 | 55 | 43 | 28 | 31 | 25 |
| Sierra Vieja Mountains, Texas | 0.76 | 0.78 | **50** | 47 | 37 | 23 | 28 | 22 |
| Davis Mountains, Texas | 0.80 | 0.83 | 0.80 | **67** | 50 | 29 | 35 | 33 |
| Northwestern Chihuahua, Mexico | 0.73 | 0.67 | 0.65 | 0.76 | **64** | 24 | 31 | 28 |
| Sacramento Mountains, New Mexico | 0.62 | 0.51 | 0.49 | 0.52 | 0.44 | **44** | 17 | 17 |
| Tularosa Basin, New Mexico | 0.70 | 0.58 | 0.63 | 0.64 | 0.58 | 0.40 | **42** | 22 |
| Lubbock County, Texas | 0.57 | 0.48 | 0.49 | 0.62 | 0.54 | 0.40 | 0.54 | **40** |

of the Big Bend National Park and Sierra Vieja Mountains, Texas. Intermediate similarity values were obtained with northwestern Chihuahua and the Tularosa Basin, New Mexico, and the lowest similarity values were found to be with the mammalian faunas of the Sacramento Mountains, New Mexico, and Lubbock County, Texas. A clustering of the similarity coefficients (Fig. 9) shows the four Trans–Pecos mountain ranges in one cluster, with the Guadalupe Mountains National Park being the most distinct of the group. The remaining four geographic areas form a series with decreasing similarity to these mountains—northwestern Chihuahua, Tularosa Basin, Lubbock County, and Sacramento Mountains.

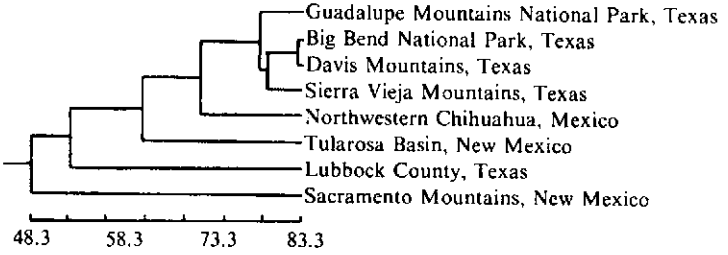


**Fig. 9.** Phenogram resulting from the clustering (UPGMA) of Burt Coefficients of Similarity among the total mammalian faunas of selected geographic areas in Texas, New Mexico, and Chihuahua as given in Table 3.

These results indicate that the total mammalian fauna of the Guadalupe Mountains National Park should be considered most closely related to that of other montane regions of Trans–Pecos Texas. The mammalian fauna is most distinct from those of the Sacramento Mountains and Lubbock County but 23 and 30 species, respectively, are shared between these areas and the Guadalupe Mountains National Park.

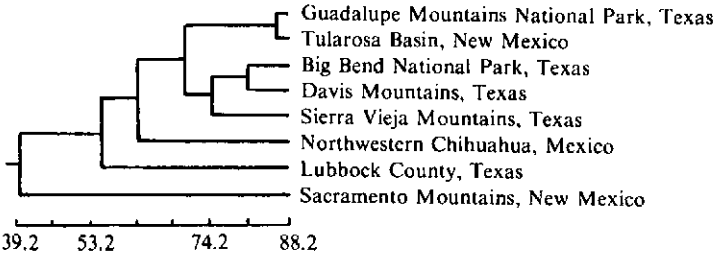


**Fig.10.** Phenogram resulting from the clustering (UPGMA) of Burt Coefficients of Similarity among the rodent faunas of selected geographic areas in Texas, New Mexico, and Chihuahua as given in Table 4.

TABLE 4. Similarity of [illegible] faunas occurring in eight selected geographic areas of [illegible], New Mexico, and Chihuahua. Boldface numbers on the diagonal represent the total number of rodent species occurring in each area. The numbers above the diagonal represent the number of rodent species shared between areas, whereas the numbers below the diagonal represent the Burt Coefficients of Similarity between areas.

| Geographic Areas | Guadalupe Mountains National Park, Texas | Big Bend National Park, Texas | Sierra Vieja Mountains, Texas | Davis Mountains, Texas | Northwestern Chihuahua, Mexico | Sacramento Mountains, New Mexico | Tularosa Basin, New Mexico | Lubbock County, Texas |
|---|---|---|---|---|---|---|---|---|
| Guadalupe Mountains National Park, Texas | **29** | 18 | 16 | 23 | 19 | 13 | 24 | 13 |
| Big Bend National Park, Texas | 0.69 | **23** | 15 | 21 | 14 | 8 | 16 | 9 |
| Sierra Vieja Mountains, Texas | 0.68 | 0.78 | **18** | 17 | 10 | 7 | 15 | 8 |
| Davis Mountains, Texas | 0.79 | 0.81 | 0.72 | **29** | 21 | 10 | 21 | 15 |
| Northwestern Chihuahua, New Mexico | 0.67 | 0.55 | 0.43 | 0.74 | **28** | 8 | 18 | 12 |
| Sacramento Mountains, New Mexico | 0.53 | 0.37 | 0.37 | 0.41 | 0.33 | **20** | 10 | 7 |
| Tularosa Basin, New Mexico | 0.86 | 0.64 | 0.67 | 0.75 | 0.65 | 0.43 | **27** | 14 |
| Lubbock County, Texas | 0.57 | 0.45 | 0.46 | 0.65 | 0.53 | 0.38 | 0.64 | **17** |

TABLE 5. Species of mammals occurring in the Guadalupe Mountains National Park, Texas, listed according to faunal units as described by Hoffmann and Jones (1970:364–365).

| | |
|---|---|
| Southwest species (26) | |
| *Myotis californicus* | *Perognathus penicillatus* |
| *Myotis thysanodes* | *Dipodomys merriami* |
| *Myotis velifer* | *Dipodomys spectabilis* |
| *Pipistrellus hesperus* | *Reithrodontomys megalotis* |
| *Antrozous pallidus* | *Peromyscus boylii* |
| *Sylvilagus audubonii* | *Peromyscus difficilis* |
| *Lepus californicus* | *Peromyscus eremicus* |
| *Ammospermophilus interpres* | *Peromyscus pectoralis* |
| *Spermophilus spilosoma* | *Peromyscus truei* |
| *Spermophilus variegatus* | *Onychomys torridus* |
| *Pappogeomys castanops* | *Neotoma albigula* |
| *Perognathus flavus* | *Bassariscus astutus* |
| *Perognathus intermedius* | *Conepatus mesoleucus* |
| Montane species (7) | |
| *Myotis volans* | *Neotoma mexicana* |
| *Plecotus townsendii* | *Microtus mexicanus* |
| *Eutamias canipes* | *Ovis canadensis* |
| *Thomomys bottae* | |
| Steppe species (4) | |
| *Cynomys ludovicianus* | *Dipodomys ordii* |
| *Perognathus hispidus* | *Neotoma micropus* |
| Southern species (3) | |
| *Tadarida brasiliensis* | *Sigmodon hispidus* |
| *Tadarida macrotis* | |
| Deciduous forest species (2) | |
| *Sylvilagus floridanus* | *Peromyscus leucopus* |
| Widespread species (23) | |
| *Myotis leibii* | *Mustela frenata* |
| *Eptesicus fuscus* | *Spilogale putorius* |
| *Lasiurus cinereus* | *Mephitis mephitis* |
| *Lasionycteris noctivagans* | *Taxidea taxus* |
| *Peromyscus maniculatus* | *Felis concolor* |
| *Erethizon dorsatum* | *Felis rufus* |
| *Canis latrans* | *Odocoileus hemionus* |
| *Canis lupus* | *Odocoileus virginianus* |
| *Urocyon cinereoargenteus* | *Cervus elaphus* |
| *Ursus americanus* | *Antilocapra americana* |
| *Ursus arctos* | *Bison bison* |
| *Procyon lotor* | |

We also compared these same geographic areas using only their rodent faunas. Rodents may be somewhat better indicators of faunal resemblance

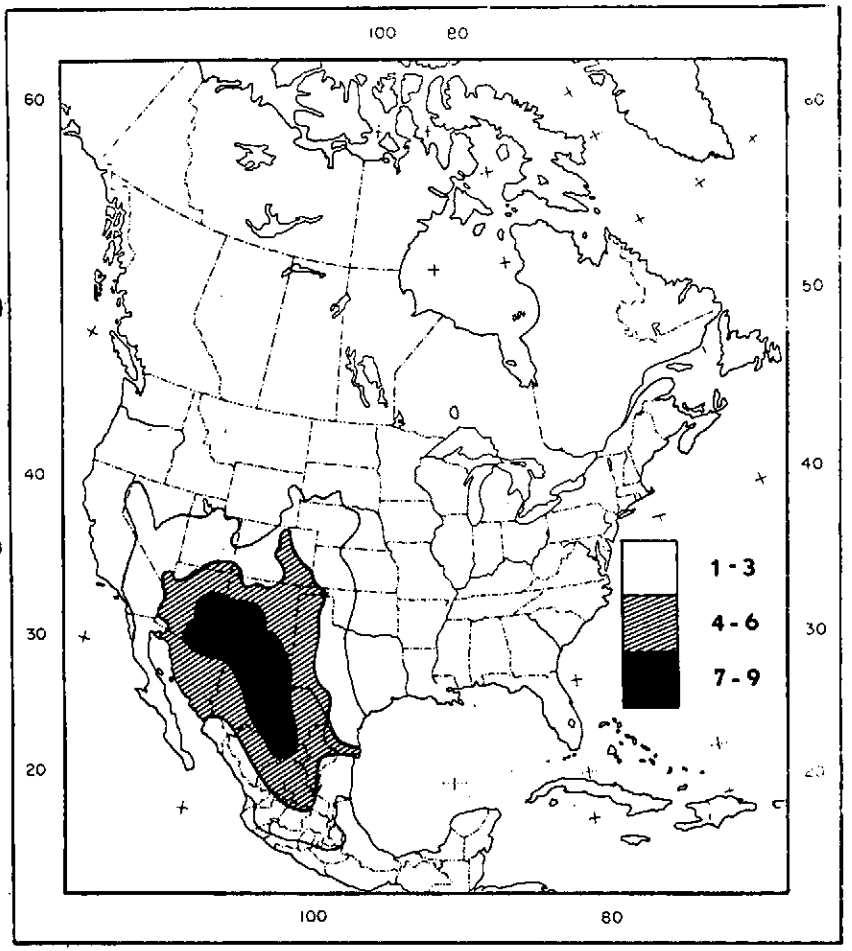


**Fig. 11.** Superimposed geographic distributions of sciurid, heteromyid, and geomyid rodents with affinities to the Southwest that occur in the Guadalupe Mountains National Park.

because they are less vagile, are highly affected by the environment, and generally do not have widespread geographic ranges. This changes the relationships among the areas slightly. The rodent fauna of the Guadalupe Mountains National Park shows the highest similarity to the rodent fauna of the Tularosa Basin (Table 4). The Tularosa Basin is a desert area lying to the northwest of the lowland areas of the western portion of the park. Similarity remains high with the Davis Mountains.

Intermediate similarity values were obtained between the rodent faunas of the Big Bend National Park, Sierra Vieja Mountains, and northwestern

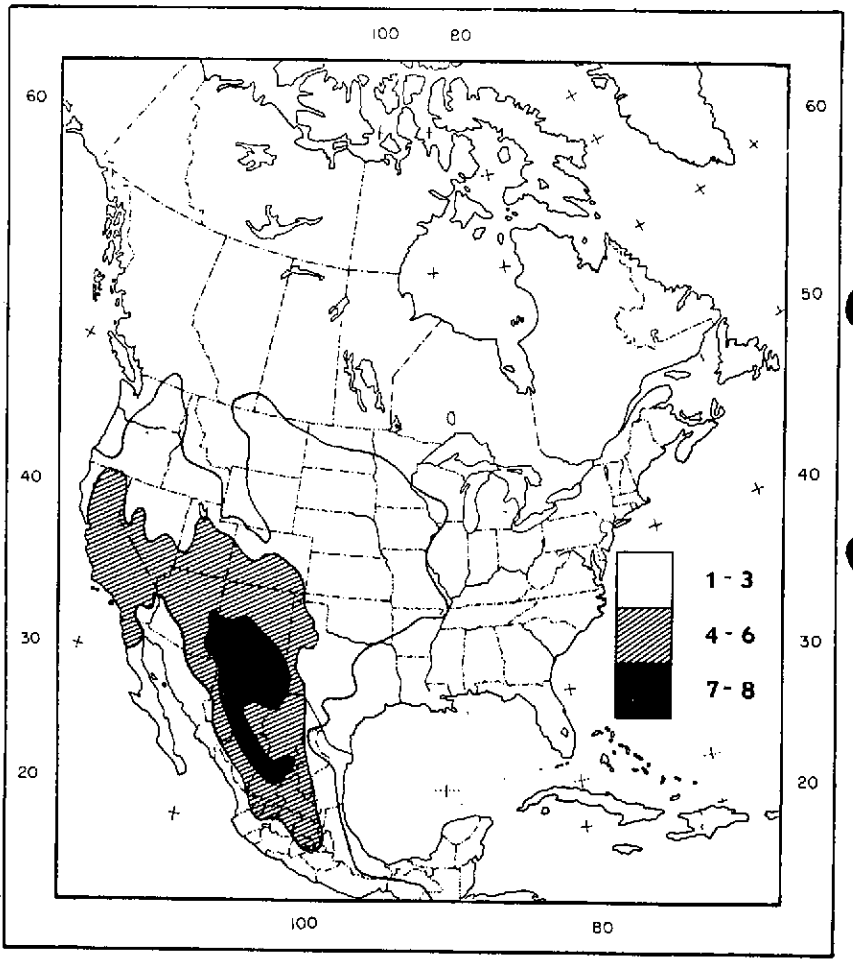


**Fig. 12.** Superimposed geographic distributions of cricetid rodents with affinities to the Southwest that occur in the Guadalupe Mountains National Park.

Chihuahua. These more southern areas lack montane and grassland forms such as *Microtus mexicanus* and *Eutamias canipes* that are present in the park and the Guadalupe Mountains National Park lacks southern arid-adapted species such as *Perognathus nelsoni*. The lowest similarity coefficients were obtained with the Sacramento Mountains, which lacks the desert species, and Lubbock County, which lacks the desert and montane species.

Clustering of these similarity values for the rodent fauna (Fig. 10) shows the Guadalupe Mountains closely clustered with the Tularosa Basin and in a major cluster with the three Trans-Pecos mountain ranges (Big Bend National Park, Davis Mountains, and Sierra Vieja Mountains). This cluster

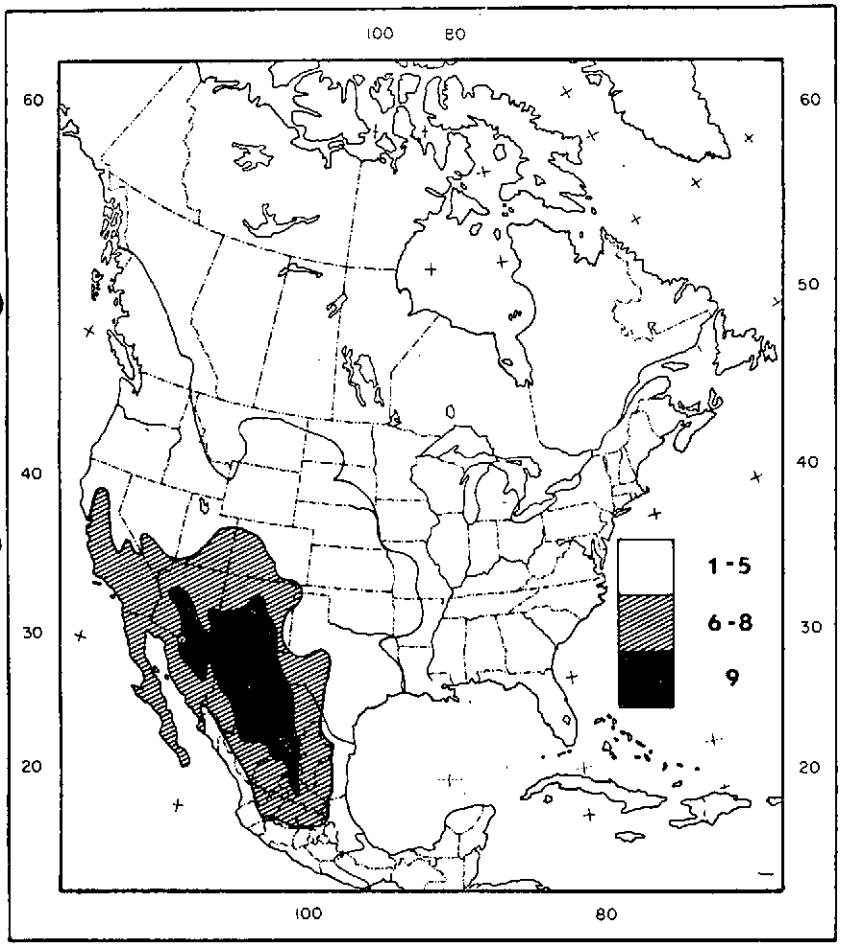


**Fig. 13.** Superimposed geographic distributions of chiropterans, lagomorphs, and carnivores with affinities to the Southwest that occur in the Guadalupe Mountains National Park.

is progressively further from rodent faunas of the other three areas—northwestern Chihuahua, Lubbock County, and Sacramento Mountains.

The Guadalupe Mountains National Park's rodent fauna is dominated by desert-adapted species; however, it does contain some unique species. The total rodent fauna shows a rather distant relationship to a true grassland rodent fauna and even less with a true montane rodent fauna.

The 65 species of mammals native to the Guadalupe Mountains National Park discussed in this account are from six faunal units (Table 5) as described by Hoffmann and Jones (1970:364–365). The faunal units represented are

Southwest (26 species), Montane (7), Steppe (4), South (3), Deciduous Forest (2), and Widespread Species (23). Widespread Species are those with broad geographic ranges and are of little value in determining the relationships of a fauna.

Figures 11–13 show the superimposed geographic ranges of the species believed to have Southwestern affinities. The sciurid, heteromyid, and geomyid rodents occurring in the park have a center of distribution in the Chihuahuan and eastern portion of the Sonoran deserts. The cricetid rodents of the park are centered basically on the Chihuahuan Desert and the

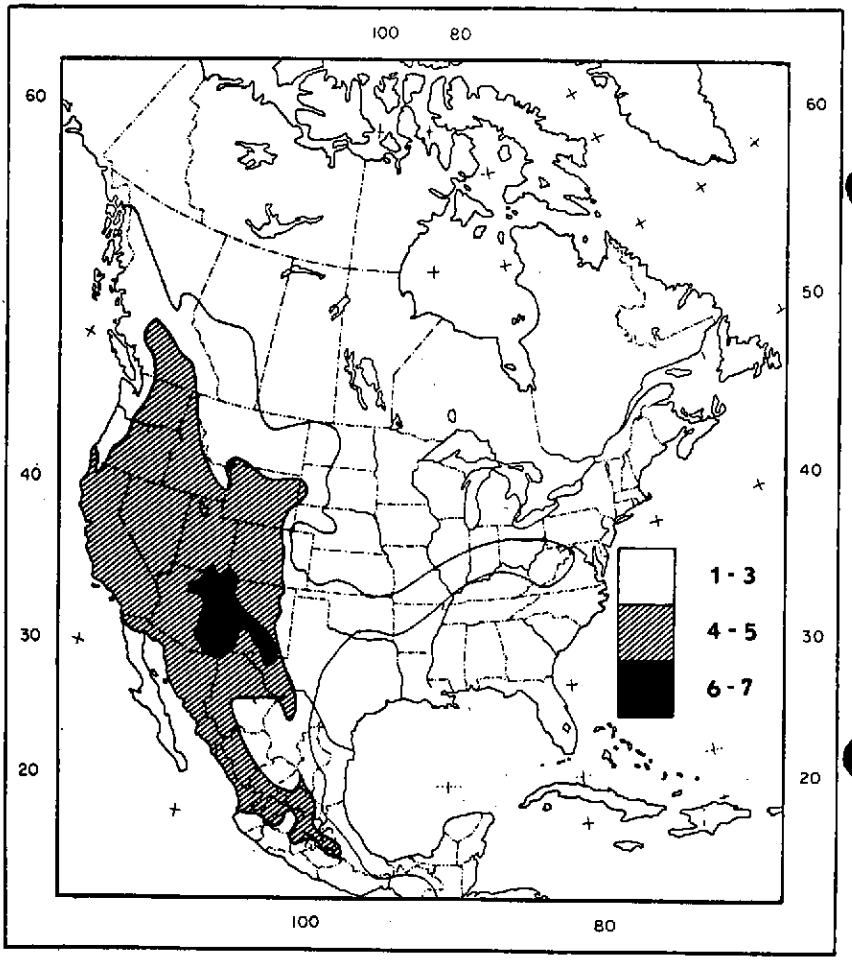


**Fig. 14.** Superimposed geographic distributions of mammals with montane affinities that occur in the Guadalupe Mountains National Park.

nonrodent species center on the Chihuahuan and eastern Sonoran deserts. The seven montane species shown in Fig. 14 have a center of distribution that includes the southern Rocky Mountains and southwestern desert ranges. Although these are animals from high elevations, they represent primarily the southwestern extension of this faunal unit. The four Steppe species from the park (Fig. 15) have a distributional center on the southern Great Plains and northern Chihuahuan Desert. In the desert regions, these species are occurring basically in desert grasslands as we have seen in the park.

The species of mammals from the South are basically tropical and sub-

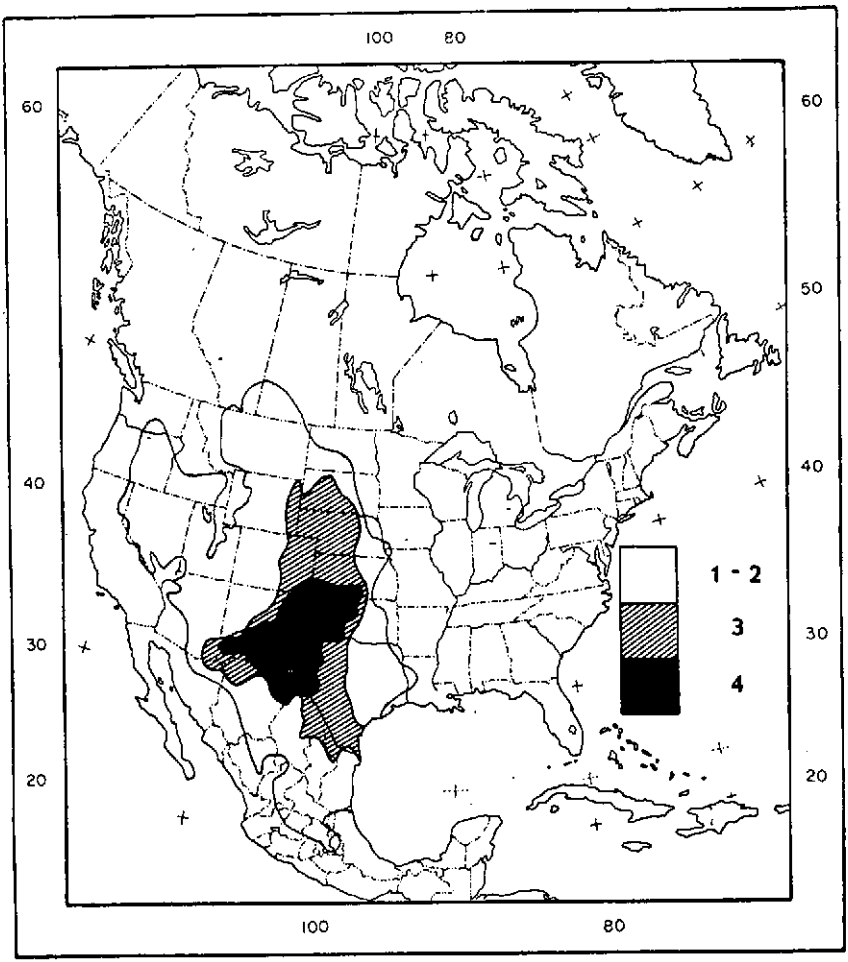


**Fig. 15.** Superimposed geographic distributions of mammals with Steppe affinities that occur in the Guadalupe Mountains National Park.

tropical in distribution. The two species of *Tadarida* are migratory and occur in the park only during the summer months; they overwinter in central Mexico or farther south. The hispid cotton rat is a species that is still expanding its geographic range northward. The two species with affinities to the deciduous forest (*Sylvilagus floridanus* and *Peromyscus leucopus*) have relatively wide ranges but almost always occur in forested areas.

The mammalian fauna of Guadalupe Mountains National Park is predominately Southwestern in affinities, with the Chihuahuan Desert forms being the chief component. The montane faunal unit, although third in number of species (seven), contains relatively few of the total mammalian species in the park. However, it was for the preservation of this unique faunal component, which occupies a mountaintop island, for which the Guadalupe Mountains National Park was established.

**Recommendations**

This survey must be considered as a starting point, which supplies baseline data, and is not an end in itself. With this in mind, we have submitted the following recommendations to the National Park Service for future work and development of the park.

1. An inventory of the larger mammals in the park should be undertaken. These animals (such as the elk, mule deer, bear, coyote, bobcat, mountain lion, and fox) have an important role in the ecosystem. It is essential to the success of resource management in the park that more information is gathered concerning these animals.

2. It is essential that the status of the elk herd be fully investigated. Knowledge of their food habits, age structure of the herd, reproductive success, herd movements, and water stress is needed.

3. A program of continuous monitoring of mammalian populations with scheduled periodic censuses should be established. A combination of grid trapping supplemented with general trapping with live traps is recommended for detecting population trends in small mammals. For monitoring the larger mammals a combination of aerial census, field observations, and fecal pellet group analysis could be used. The following sites are recommended for periodic censusing: Upper Dog Canyon Ranger Station; The Bowl; Nipple Hill; Pratt Lodge—McKittrick Canyon; entrance to Williams Ranch Road; Lewis Well; Crossroads at the north end of the Patterson Hills.

4. Special efforts must be made during census procedures to monitor the status of the species that are rare in the park: *Microtus mexicanus guadalupensis*; *Sylvilagus floridanus robustus*; *Thomomys bottae guadalupensis*; *Eutamias canipes canipes*; *Ammospermophilus interpres*. Careful monitoring of these mammals may prevent their loss from the park.

5. The grid now established in Upper Dog Canyon should be made permanent. Additional permanent population grids should be established at the following sites: The Bowl; between Nipple Hill and Choza Spring or Pine Springs Canyon; Williams Ranch House; Lewis Well. Periodic live trapping

on these grids would yield much valuable data and detect population trends.

6. The following areas are considered to be the most biologically significant from the standpoint of mammals in Guadalupe Mountains National Park: Upper Dog Canyon; The Bowl; Nipple Hill area; Lewis Well; McKittrick Canyon; every spring and waterhole in the park.

7. The zones of contact between *Neotoma albigula* and *N. mexicana* in Upper Dog Canyon and between *N. albigula* and *N. micropus* north of the Patterson Hills should be monitored periodically to note any shifts in the zones. Such shifts may indicate changing environmental conditions.

8. Data from periodic censuses should be used to test the computer model under development for remote sensing of the park. Remote sensing should prove especially useful in the monitoring of vole habitat.

9. A special effort should be made to determine if the following mammals occur within the park boundaries: *Notiosorex crawfordi*; *Myotis evotis*; *Euderma maculatum*; *Lasiurus borealis*; *Spermophilus mexicanus*; *Tamiasciurus hudsonicus*; *Onychomys leucogaster*; *Vulpes macrotis*; *Dicotyles tajacu*.

10. High priority should be given to repairing or rebuilding the boundary fences on the south and west sides of the park. During the mammal survey, a large number of cattle have been observed within the park boundaries. The number of trespassing cattle has increased in the last two years and they have recently been observed at the west base of the Guadalupe escarpment. This area of the park recovers from grazing very slowly in the total absence of livestock; therefore, it is imperative that the fences be repaired and the cattle removed.

11. One of the real joys for tourists, especially children, is seeing deer and other wildlife at Pine Springs Campground and Upper Dog Canyon campsite. Several times we have observed unleashed dogs chasing deer and other mammals away. Every effort should be made to enforce the existing leash law at the park. A little thoughtfulness on the part of pet owners will allow everyone to share the experience of viewing some of the park's wildlife. This is not a criticism of the current park personnel as we have observed them enforcing the leash laws. Perhaps, pets should be excluded from the park. If people want to take their pets on vacation, they can stay at private campgrounds and leave their pets there while visiting the National Park.

12. Most of the endangered species that occur in Guadalupe Mountains National Park probably occur in Carlsbad Caverns National Park as well. We would strongly recommend that a mammal survey be conducted in Carlsbad Caverns National Park. This research would provide valuable information which should be included in the final environmental statement for the master plan proposed for Carlsbad Caverns National Park. If the endangered species are present in Carlsbad Caverns National Park, a management program consistent in both parks could be developed which would increase the possibilities of preserving the species for future generations.

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# *Demographic Patterns of Small Mammals: A Possible Use in Impact Assessment*

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Valuable inventory studies of the flora, fauna, and other related factors have been initiated in the Guadalupe Mountains National Park in the past few years. The aim of one of these has been to establish intensive study sites to monitor demographic patterns in small mammals. The assessment of these patterns may prove helpful in planning future public use of various areas within the park. When specific areas have been opened to visitor traffic, a system of monitoring the effects of human impact in these areas should be continued.

Changes in vegetational composition as a result of impact have usually been assayed before and after human use. Also common are comparative studies of floral elements of an area open to human traffic with those of a nearby or similar area with restricted visitation (Whitson 1974). Most assessment efforts have been restricted to vegetational analyses because floristic structure is one of the most important and readily studied elements in a local ecosystem; however, there is no reason to restrict inventories to plants for impact use. Demographic patterns of small mammals may be important in the determination of the effects of human use upon a given area.

Because of the close ecological relationship between small mammals and the floral components of an ecosystem, we suspect that human use will affect the structure and function of small mammal populations. To test this hypothesis, dynamics of both the plant and animal elements of an area must be measured before and after the disturbance. We are presently engaged in gathering pre-use, baseline data. In the following, we will discuss the techniques employed in measuring different parameters of small mammal populations, demographic data collected to date, and sampling strategies for future censuses.

## MATERIALS AND METHODS

Three live-trapping grids were established in different localities in 1974 and 1975. Each grid was designed in a fashion similar to that prescribed by the International Biological Program (French 1971); stations were located at 7.5-m intervals in 12 rows by 12 columns, resulting in a grid of 144 stations, covering 0.81 ha. Each station was marked by a 1-m wooden stake painted with the row and column number for location identification. The three study areas are located at the following places within the park.

**Upper Dog Canyon.**—The Upper Dog Canyon study site was established in May 1974. The grid is located in a grassy meadow, approximately one-fourth mile north of the ranger's cabin (elevation 1890 m). Dominant vegetation of the grid includes *Stipa tenuissima, Muhlenbergia repens, Juniperus deppeana,* and *Opuntia* sp. (Fig. 1). Access to Dog Canyon is presently limited to researchers, park personnel, and backpackers. Trapping data were collected in 1974 and 1975.

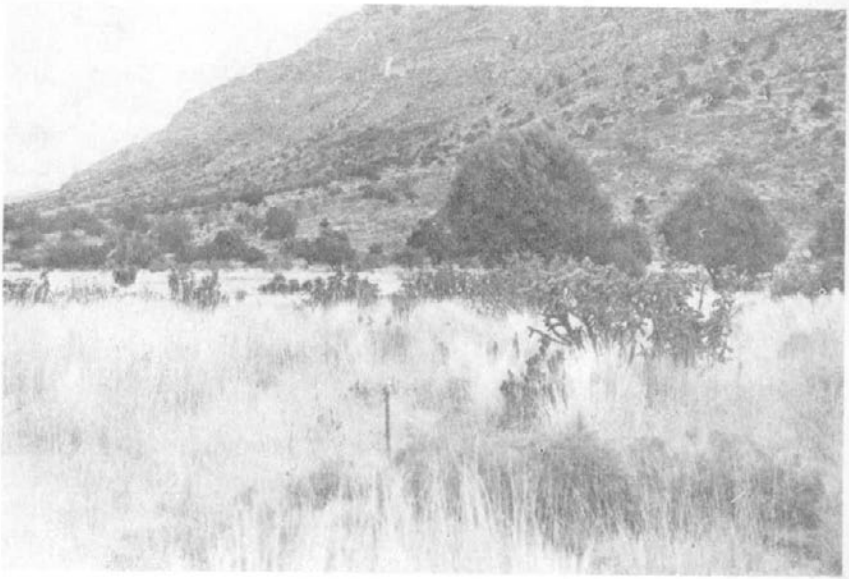

FIG. 1. Upper Dog Canyon study area.

**Pine Springs.**—The Pine Springs study site, established in May 1975, is located just north of the Houser House (elevation 1671 m). This location was chosen because it is typical of the desert-grassland vegetation of the lower elevations (Fig. 2). Most common grasses found on the study site are *Bouteloua curtipendula, B. gracilis, Lycurus phleoides, Muhlenbergia setifolia, Artistida glauca,* and *Stipa neomexicana.* Common perennials

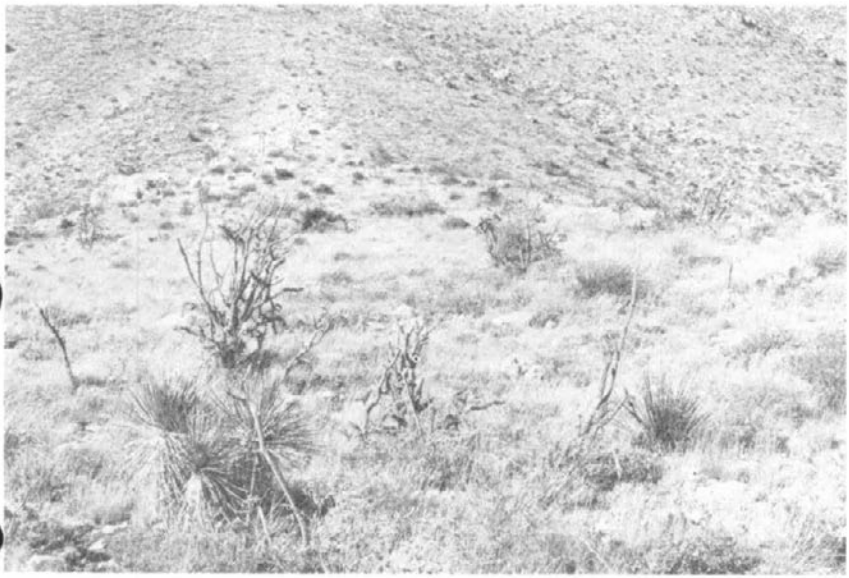

FIG. 2. Pine Springs study area.

include *Parthenium incanum, Opuntia imbricata*, and *Dasyliron* sp. (Northington and Burgess 1977). Presently, this area receives minimal human traffic, but increases are expected because of close proximity to the Bear Canyon Trail.

**Williams Ranch.**—The Williams Ranch site, established in May 1975, is on the west side of the Guadalupes at an elevation of 1318 m. The grid is approximately one-fourth mile inside the entrance gate and is bisected by a dirt road 7 m wide. This area is typical desert-scrub habitat dominated by *Larrea tridentata, Prosopis glandulosa, Acacia neovericosa, Flourensia cernua,* and *Atriplex canescens* (Fig. 3). In association with these microphyllous shrubs are the grasses, *Bouteloua eripoda, Sporobolus airoides*, and *Erioneuron pulchellum* (Northington and Burgess 1977). This area is accessible to Park visitors, on a limited basis, by a narrow dirt road. As the Park grows in popularity, increased visitor traffic is anticipated. This site should provide valuable data on the effects of increased road usage on small mammal populations.

All mammal trapping was conducted in late spring and summer, and each trapping period was for 5 consecutive days. Sherman live traps, baited with rolled oats, were used throughout the study. Traps were set (one per grid station) in the late afternoon and examined early the following morning. In a few instances, traps were examined in the middle of the night to minimize the risk of killing animals in unusually cold weather. The following were recorded for each capture: station number; species and number of each (all

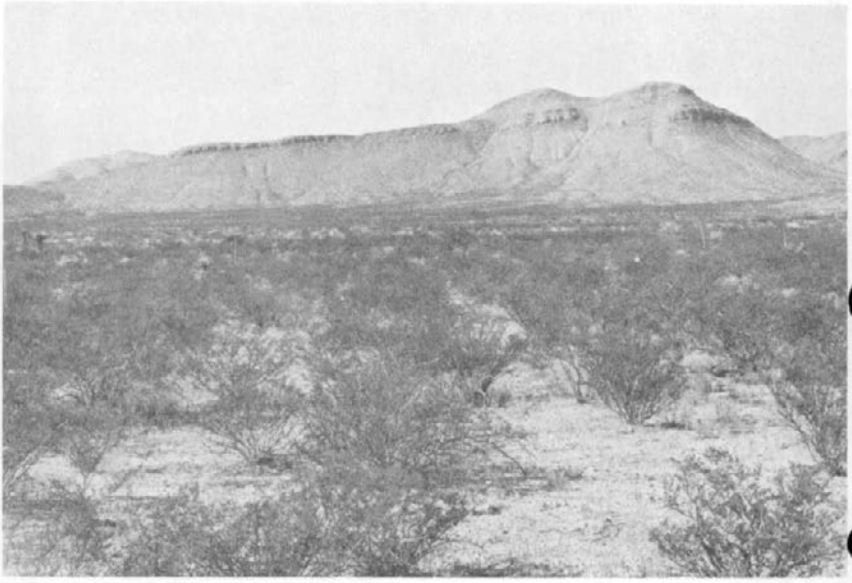

FIG. 3. Williams Ranch study area.

mammals were given a toe clip formula); sex; reproductive condition (testes scrotal or abdominal in males, vulva inactive, turgid, cornified, or pregnant in females); age; physical condition. These data were recorded on a standardized sheet developed by the International Biological Program (IBP) (form NREL–10). After each census period, the data were transferred to computer cards for storage and future analysis.

Home ranges were calculated using the exclusive boundary strip method (Stickel 1954). This procedure was chosen because the home-range estimates produced were conservative. Also, the technique did not require a large number of recaptures per individual. Animals with three or more captures were used in the analysis. Density estimates were determined using the minimum number known alive technique (Zippin 1958). A detailed description of techniques employed in this study will appear in a later paper.

## RESULTS AND DISCUSSION

Results reported herein are preliminary. One year's sampling data have been gathered for the Pine Springs and Williams Ranch grids, whereas data for 2 years have been collected for the Upper Dog Canyon grid. Year-to-year comparisons cannot be attempted with such minimal information.

### Upper Dog Canyon

Six species of mammals were caught in the Upper Dog Canyon study area in 1974. Density estimates for 1974 in number of animals per hectare are as

TABLE 1. Individuals, number of captures (in parentheses), and home ranges of rodents caught in the study areas. Home ranges are given only for those species with adequate number of recaptures.

| Locality and species | Number of individuals | Home ranges ($m_2$) |
|---|---|---|
| Pine Springs | | |
| *Perognathus flavus* | 3(4) | |
| *Peromyscus maniculatus* | 6(17) | 416 |
| *Peromyscus pectoralis* | 12(30) | 499 |
| *Reithrodontomys megalotis* | 1(1) | |
| *Sigmodon hispidus* | 6(16) | 262 |
| *Neotoma micropus* | 1(1) | |
| Williams Ranch | | |
| *Perognathus penicillatus* | 11(20) | 469 |
| *Perognathus intermedius* | 4(12) | 732 |
| *Dipodomys merriami* | 12(44) | 573 |
| *Dipodomys spectabilis* | 3(22) | 753 |
| *Dipodomys ordii* | 2(2) | |
| *Peromyscus maniculatus* | 10(20) | 547 |
| *Peromyscus eremicus* | 7(10) | |
| *Onychomys torridus* | 7(27) | 1203 |
| *Neotoma micropus* | 15(31) | 258 |
| *Spermophilus spilosoma* | 5(6) | |
| *Spermophilus mexicanus* | 1(1) | |
| Upper Dog Canyon, 1974 | | |
| *Peromyscus* sp. | 19(51) | 286 |
| *Reithrodontomys megalotis* | 30(46) | 511 |
| *Sigmodon hispidus* | 34(81) | 893 |
| *Neotoma albigula* | 17(62) | 217 |
| *Microtus mexicanus* | 1(1) | |
| Upper Dog Canyon, 1975 | | |
| *Peromyscus boylii* | 6(33) | 987 |
| *Peromyscus pectoralis* | 5(22) | 382 |
| *Reithrodontomys megalotis* | 29(46) | 371 |
| *Sigmodon hispidus* | 11(53) | 1347 |
| *Neotoma albigula* | 5(15) | 262 |
| *Microtus mexicanus* | 8(10) | 169 |

follows: all rodents, 103.0; *Microtus mexicanus*, 1.2; *Neotoma albigula*, 23.5; *Sigmodon hispidus*, 42.0; *Reithrodontomys megalotis*, 37.0; *Peromyscus* sp., 23.5. *Peromyscus* species identification was not made in the 1974 sampling. Recent inspection of museum specimens suggests *P. boylii* and *P. pectoralis* were the species caught on the grid. See Genoways et al. (1977) for a discussion of the *Peromyscus* of Upper Dog Canyon. Home-range data are given in Table 1.

Reproductive data suggest breeding occurred throughout the summer.

Seventy-one percent of the rodents were sexually active in the June census, 77%, in July, and 71%, in August.

In 1975, six species of small mammals were caught regularly (Table 1). *Sigmodon hispidus* and *Reithrodontomys megalotis* accounted for 56% of the total captures and were likely the dominant rodents of the study grid. In number of animals per hectare, the following density estimates for 1975 were calculated: all rodents, 81.5; *Microtus mexicanus*, 9.9; *Peromyscus boylii*, 8.6; *P. pectoralis*, 6.2; *Reithrodontomys megalotis*, 35.8; *Sigmodon hispidus*, 14.8; *Neotoma albigula*, 6.2.

The average home ranges of all taxa caught are shown in Table 1. *Microtus* and *Neotoma* had the smallest home ranges. Because of the few captures, the *Microtus* estimate may not reflect a true home-range size. The small home range of *Neotoma* suggests they confine their movements to the area of their nest site.

The reproductive data indicate rodents in the Upper Dog Canyon grid reproduced later in the year when compared with the other two study areas (Fig. 4). This probably results because principal growth of vegetation (primarily grasses) occurs toward the end of summer. In the lower elevation study areas, primary production (herbs and shrubs) begins in early to middle summer. Another possible explanation of this latent breeding season observed in Upper Dog Canyon may relate to rainfall patterns observed in the Guadalupes in 1975. Williams Ranch and Pine Springs received summer

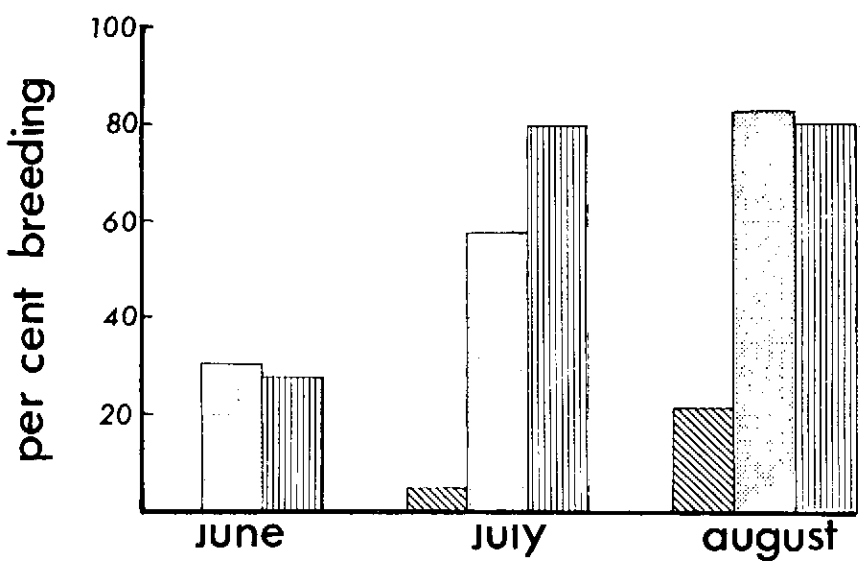


FIG. 4. Reproductive data for small mammals caught in 1975. Diagonal bars represent Upper Dog Canyon grid, dots represent Williams Ranch grid, and vertical bars represent Pine Springs grid.

rains earlier than did Upper Dog Canyon. The desert-adapted annual vegetation of the lower grids responds in growth more quickly to precipitation than grasses (Tony L. Burgess, pers. comm.).

There is a high rate of population turnover in the Upper Dog Canyon grid, based on the number of animals caught both sampling years. One *Sigmodon*, two *Neotoma*, and one *Peromyscus boylii* were caught both years. The *Microtus* population increased significantly during the second sampling period. In 1974, only one individual was captured, whereas eight were captured in 1975. *Microtus mexicanus* has a distribution restricted to grassy meadows of the higher elevations. Efforts should be made to protect the few areas of favorable habitat of this endemic vole.

**Pine Springs**

Of the three study areas, Pine Springs had the lowest population density. In number of animals per hectare, estimated densities in 1975 were as follows: all rodents, 35.0; *Peromyscus maniculatus*, 7.5; *P. pectoralis*, 15.0; *Neotoma micropus*, 1.2; *Perognathus flavus*, 3.8; *Reithrodontomys megalotis*, 1.2; *Sigmodon hispidus*, 7.5. Home ranges of *Peromyscus* and *Sigmodon* are shown in Table 1. Home ranges were not calculated for *Perognathus, Reithrodontomys*, and *Neotoma* because of a lack of sufficient recapture data. Reproductive data are given in Fig. 4.

**Williams Ranch**

This area had the highest density and greatest rodent diversity of the three study areas. In number of animals per hectare, estimated population densities in 1975 were as follows: all rodents, 95.1; *Dipodomys merriami*, 16.0; *D. ordii*, 2.5; *D. spectabilis*, 3.7; *Neotoma micropus*, 18.5; *Onychomys torridus*, 8.6; *Peromyscus eremicus*, 8.6; *P. maniculatus*, 8.1; *Perognathus intermedius*, 4.9; *P. penicillatus*, 11.1; *Spermophilus spilosoma*, 6.2; and *S. mexicanus*, 1.2.

Sufficient recapture data permit the estimate of home ranges for 7 of the 11 species (Table 1). *Onychomys* had the largest home range of all the rodents. This may result from the wide-ranging foraging habits of this carnivorous rodent. The remaining species are herbivores or granivores and had similar home-range sizes—about half that of *Onychomys*. *Neotoma micropus* had an extremely small home range as a result of restrictive movements about the vicinity of the nest site. Reproductive data are given in Fig. 4.

## FUTURE SAMPLING IN THE GUADALUPE MOUNTAINS

Small mammal populations undergo cyclic shifts in numbers and reproductive rates (Krebs et al. 1973). These cycles are governed by extrinsic forces such as food availability, cover, and home site availability, as well as intrinsic forces such as behavioral patterns, density, and species diversity. A population must be sampled over a long period of time to ascertain the

magnitude of cyclic oscillations. It is for this reason that data are being collected now in relatively undisturbed study areas. When these areas are opened for heavy visitor use, pre-use baseline information will be available to compare with post-impact demographic data. It is imperative that the pre-use data include the range of amplitudes in population densities throughout the seasons. This is necessary in order to minimize the possibility of confusing impact of human use with normal oscillation phenomena. Vegetational components of ecosystems are generally affected first by perturbations. This, in turn, influences rodent population parameters. Care must be exercised in assaying visitor impact on the small mammals without first referring to data on the vegetational components. For this reason, collection of quantitative vegetational structure data coupled with demographic data is needed in the future.

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# *Population Size of* Tadarida brasiliensis *at Carlsbad Caverns in 1973*

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The evening outflight of the summer colony of *Tadarida brasiliensis* (Mexican free-tailed bat) from Carlsbad Cavern, Eddy County, New Mexico, has been an important drawing card for tourism to Carlsbad Caverns National Park. In recent years National Park Service personnel have reported a reduction in the density of the outflight, the area of the roost occupied by bats, and the noise level in the roost area (National Park Service Personnel, pers. comm.). A population size estimate of 66,700 bats made 16 June 1957 by Constantine (1967) compares poorly with an estimate of slightly more than 8,700,000 estimated by Allison (1937) on 16 June 1936. Since 1955, National Park Service records report several short periods of bat mortality lasting a few days and involving a few to an estimated several thousand bats (Constantine 1967; National Park Service Personnel, pers. comm.). During a visit by one of the authors (Altenbach) in September 1971, several thousand infant bats were found dead on the floor beneath the roost area. The condition of the bats suggested they had all died that summer and most were less than a few days old at the time of death.

Concern about the decline in the summer *Tadarida* population prompted the National Park Service to support a detailed study of the bat population at Carlsbad Cavern. Initiated in the spring of 1973, this study was to determine (1) the extent of the population decline; (2) factors contributing to the decline; and (3) the general dynamics of the population each season for several seasons. An accurate estimation of the size of the *Tadarida* population is essential for each of these objectives.

Humphrey (1971) pointed out that techniques of evening flight counts which have provided accurate estimates of population size in small bat colonies (Moffat 1905; Venables 1943; Greenhall and Stell 1960; Sluiter and VanHeerdt 1966; Baker and Ward 1967; Stebbings 1968; Humphrey and

Cope 1968; Watkins 1970) are of little value in estimating size of large populations of *Tadarida*. Humphrey (1971) also pointed out that population estimates of *Tadarida* by visual inspection of roosting clusters, evening flight, or both (Davis et al. 1962; Perry 1965; Constantine 1967; Cockrum 1969; Twente 1956) "are probably in the correct order of magnitude but otherwise of questionable accuracy."

In the summer of 1973 the entire *Tadarida* population at Carlsbad Cavern roosted on the ceiling of an elongated dome near the east end of the portion of the cavern known as Bat Cave. We considered a careful reapplication of the technique of multiplying the number of bats per unit area of roost surface by the total area of occupied roost surface that Constantine (1967) had applied at this roost several years before and that other investigators had applied elsewhere. However, the ceiling of the roost, which is highly irregular and averages roughly 80 ft above the floor, is inaccessible. From below, the exact area of the roost cannot be calculated. Rock-climbing techniques that could provide access to the roost area are not practical because of the decomposed nature of the limestone and the adherence of large mats of damp guano to the rock surface. We also agreed that the disturbance of the bat colony by an application of this technique was not justified even if it were feasible. However, the shape and relative size of the cluster of roosting bats could be noted quickly and was useful in determining movements of the bats in the roosting area and large changes in population size.

We also considered a capture-recapture method that had been used at Carlsbad Cavern by Constantine (1967) and at Eagle Creek Cave, Greenlee County, Arizona, by Cockrum (1969, pers. comm.). This technique employed a bat trap, developed by Constantine (1958), which was set in the cavern entrance and collected bats during the outflight. Bats caught on one night were marked by banding and released. The ratio of marked bats to unmarked bats caught on a subsequent night was used to estimate the total bat population. We chose not to use this technique because we could not make the necessary assumption that a bat captured and marked had an equal chance of being recaptured. We also felt that the placement of a bat trap in the cavern entrance and resultant disturbance of large numbers of bats would not be justified.

Allison (1937) estimated the size of the Carlsbad population of *Tadarida* on 16 June 1936 by observing the column of bats as they flew from the mouth of the cavern. He estimated that during the "full force" of the outflight the cross-sectional area of the column was 314.16 $ft^2$ (20 ft in diameter), that each cubic foot of the column contained one bat, and that the airspeed of the bats was 29 ft/sec. Thus, 29 linear ft passed his observation point each second. The evening of his observation the "full force" of the outflight lasted from 7:03 to 7:17 p.m. From 7:17 to 7:21 p.m. he estimated bats left the cavern at one-half the "full force" rate. By multiplying the bats per second value by total seconds for each time period and adding the totals he estimated

8,741,760 *Tadarida* left the cavern that evening. He did not report whether any bats remained in the roost after the outflight.

A more conservative estimate of 3 million had been made by Bailey (1928) but in personal communication with Allison (1937) Bailey accepted the 8 million figure as being more nearly correct. Again by personal communication with Allison (1937), Bailey suggested that an accurate estimation of the population size would require still and motion picture photography of the outflight.

The first report of the application of a photographic *Tadarida* population estimation technique was that by Humphrey (1971) who took one photograph every 60 sec of the outflight column from Vickery I Cave, Major County, Oklahoma. The bats were photographed while in a confined column shortly after leaving the cave and before dispersing to feed. The number of bats in each photograph, the speed of the column, and the duration of the outflight were used to estimate the total number of bats that left the cave each evening.

The application of a photographic technique at Carlsbad Cavern in 1973 was more complicated because the column of bats was very erratic once it passed the cave mouth, and was of such low density, in contrast to the description of Allison (1937), that scattered bats covered an area far too large for photographs. Careful observations of the outflight for a period of several weeks revealed that the only place the column of bats could be photographed was against the ceiling of the first undercut in the mouth of the cave. All the bats left the cave through a restricted space beneath this portion of the ceiling.

## METHODS

On the evening of 1 September 1973, a 35-mm camera with a 50 watt-second electronic flash and a Miliken 16-mm high-speed motion picture camera with a 650-watt movie light were set up on the trail 45 ft beneath the critical area of cave ceiling and focused on a point about 3 ft beneath the ceiling. Still photographs were taken at 30-sec intervals during the first 44.5 min of the outflight and at 1-min intervals thereafter (Table 1). Illumination was provided by the electronic flash unit and the film was exposed at an ASA rating of 1000. Five second long high-speed motion picture runs at 200 frames per sec were taken at 5-min intervals during the first 45 min of the outflight, using Kodak Four-X Reversal Film.

Glossy, 8 × 10 in. prints were made from the 35-mm negatives, and bats were counted and their direction of flight recorded. A line parallel to (*Y*-axis line) and another perpendicular to (*X*-axis line) a line drawn across the mouth of the cave were superimposed on each photograph (Fig. 1).

The motion pictures of the outflight showed that there was a small area of space, hereafter called the "exit space," immediately inside the lip of the undercut through which all the bats left the cave (Fig. 1). However, only bats

TABLE 1. Data from the photographic population size estimation of *Tadarida brasiliensis* at Carlsbad Cavern.

| $n$ | $x$ | $N_x$ | $T_n$ | $n$ | $x$ | $N_x$ | $T_n$ | $n$ | $x$ | $N_x$ | $T_n$ |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 7:24 | 10 | | | 7:43 | 26 | | | 8:02 | 9 | |
| 1 | 7:24:30 | 5 | 0.35 | | 7:43:30 | 22 | | | 8:02:30 | 9 | |
| | 7:25 | 1 | | 5 | 7:44 | 20 | 0.30 | | 8:03 | 32 | |
| | 7:25:30 | 34 | | | 7:44:30 | 20 | | | 8:03:30 | 18 | |
| | 7:26 | 27 | | | 7:45 | 27 | | 9 | 8:04 | 14 | 0.30 |
| | 7:26:30 | 16 | | | 7:45:30 | 7 | | | 8:04:30 | 27 | |
| | 7:27 | 17 | | | 7:46 | 25 | | | 8:05 | 13 | |
| | 7:27:30 | 14 | | | 7:46:30 | 12 | | | 8:05:30 | 16 | |
| | 7:28 | 19 | | | 7:47 | 22 | | | 8:06 | 17 | |
| | 7:28:30 | 45 | | | 7:47:30 | 21 | | | 8:06:30 | 17 | |
| 2 | 7:29 | 47 | 0.27 | | 7:48 | 24 | | | 8:07 | 7 | |
| | 7:29:30 | 47 | | | 7:48:30 | 22 | | | 8:07:30 | 18 | |
| | 7:30 | 16 | | 6 | 7:49 | 28 | 0.29 | | 8:08 | 16 | |
| | 7:30:30 | 59 | | | 7:49:30 | 6 | | | 8:08:30 | 2 | |
| | 7:31 | 6 | | | 7:50 | 26 | | | 8:09 | 11 | |
| | 7:31:30 | 32 | | | 7:50:30 | 17 | | | 8:10 | 11 | |
| | 7:32 | 17 | | | 7:51 | 17 | | 10 | 8:11 | 16 | 0.27 |
| | 7:32:30 | 39 | | | 7:51:30 | 27 | | | 8:12 | 22 | |
| | 7:33 | 35 | | | 7:52 | 19 | | | 8:13 | 1 | |
| | 7:33:30 | 33 | | | 7:52:30 | 22 | | | 8:14 | 9 | |
| 3 | 7:34 | 65 | 0.30 | | 7:53 | 21 | | | 8:15 | 10 | |
| | 7:34:30 | 24 | | | 7:53:30 | 24 | | | 8:16 | 4 | |
| | 7:35 | 30 | | 7 | 7:54 | 13 | 0.29 | | 8:17 | 0 | |
| | 7:35:30 | 31 | | | 7:54:30 | 17 | | | 8:18 | 6 | |
| | 7:36 | 38 | | | 7:55 | 17 | | | 8:19 | 5 | |
| | 7:36:30 | 46 | | | 7:55:30 | 16 | | | 8:20 | 5 | |
| | 7:37 | 21 | | | 7:56 | 13 | | | 8:21 | 4 | |
| | 7:37:30 | 25 | | | 7:56:30 | 14 | | | 8:22 | 3 | |
| | 7:38 | 42 | | | 7:57 | 18 | | | 8:23 | 0 | |
| | 7:38:30 | 21 | | | 7:57:30 | 19 | | | 8:24 | 1 | |
| 4 | 7:39 | 30 | 0.31 | | 7:58 | 20 | | | 8:25 | 0 | |
| | 7:39:30 | 13 | | | 7:58:30 | 20 | | | | | |
| | 7:40 | 11 | | 8 | 7:59 | 12 | 0.30 | | | | |
| | 7:40:30 | 5 | | | 7:59:30 | 33 | | | | | |
| | 7:41 | 12 | | | 8:00 | 9 | | | | | |
| | 7:41:30 | 19 | | | 8:00:30 | 13 | | | | | |
| | 7:42 | 20 | | | 8:01 | 9 | | | | | |
| | 7:42:30 | 23 | | | 8:01:30 | 12 | | | | | |

$x$ = time of still photograph (MDST);
$N_x$ = number of bats leaving cave in photograph at time $x$;
$n$ = motion picture run number;
$T_n$ = replacement time (in seconds) used as an estimator within time period enclosed in brackets.

oriented with the long-body axis inclined outward from a $Y$-axis line in a photograph (Fig. 1) seemed committed to exit from the cave. Bats with long-body axis parallel to or inclined inward from a $Y$-axis line (Fig. 1) seemed

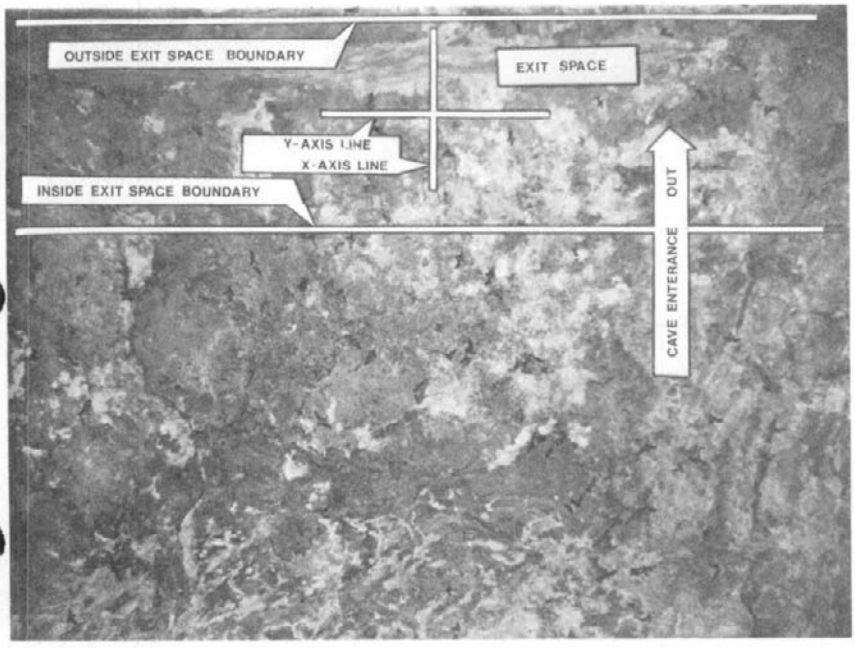


**Fig. 1.** Photograph of the ceiling of the entrance area of Carlsbad Cavern, showing areas used in the photographic population estimation technique.

committed to fly back into the cave mouth. The motion picture data showed that less than 0.1 percent of the bats in the exit space failed to behave in this manner. The motion pictures also showed that a few bats, which had apparently left the cave, flew back into the cave through the exit space. This number of in-flying bats was less than 1 percent of the number of out-flying bats and was accounted for by subtracting the number of bats in the exit space with their long-body axis oriented directly into the cave from the number of out-flying bats. Thus a number of out-flying bats in a still photograph taken at instant $X$ was computed ($N_x$).

Bats moving through the exit space parallel to the $X$-axis line (Fig. 1) crossed the space in 0.20 sec. Those moving through the exit space at greater angles from the $X$-axis line or in arcs took more time to cross the space. By projecting the films repeatedly and timing the flight of individual bats across the exit space, an average time period ($T_n$) for bats to cross the exit space was computed for each motion-picture sequence. This time period was considered the time (replacement time) required for the out-flying bats photographed in the exit space at one instant to be replaced by a new group of bats. Each $T_n$ value was used as the replacement time for out-flying bats over a time period for which $T_n$ is the estimator (Table 1). For example, during each of the time periods before and after the motion picture run at 7:29 p.m.

(the periods with the instants 7:27–7:31:30 as their midpoints), a group of bats in the exit space was assumed to be replaced by another group of bats every 0.27 sec (Table 1).

Each photograph was used to estimate the number of bats leaving the cave during a time period ($P_x$) which had the instant of the photograph as its midpoint. The photograph of 7:24, which is an estimator of only the 15-sec period preceding it and the 30-sec period following it, and the photograph of 8:09, which is an estimator of the 15-sec period preceding it and the 30-sec period following it, are the only exceptions (Table 1). A $T_n$ value was divided into each of the time periods ($Px$ values for which it was an estimator, to calculate the number of replacements of out-flying bats, $R_x$) in the exit space during each of those time periods. Each $R_x$ value was multiplied by the appropriate $N_x$ value to produce an estimate of the number of bats that left the cavern during each time period. This procedure is summarized as follows: $P_x / T_n = R_x$ and $R_x(N_x) = E_x$;
where

$P_x$ = time period for which photograph at time $X$ is an estimator;
$T_n$ = average time for bats to cross exit space during the time period for which motion-picture run is an estimator (replacement time);
$R_x$ = number of replacements of bats in the exit space during time period $P_x$;
$N_x$ = number of bats leaving the cavern in photograph at time $X$;
$E_x$ = estimate of the total number of bats leaving the cavern during the time period $P_x$.

Table 1 shows the time each still photograph was taken ($x$), the $N_x$ value for each still photograph, the time of each motion-picture run ($n$), and the time period for which it is an estimator. By adding each of the $E_x$ values, we produced an estimate of the total bats that left the cavern the evening of 1 September 1973.

## RESULTS AND DISCUSSION

The total number of bats that left the cave the evening of 1 September 1973 was calculated to be 218,153. No bats were seen in the roost area immediately after the outflight. *Tadarida* born at Carlsbad Cavern in 1973 began flying an average of 39 days after birth. This period is similar to those reported by Davis et al. (1962) for Texas *Tadarida* colonies and by Constantine (1967) for Carlsbad Cavern during the 1957 season. The first outflight sample in which all of the nonbarren females were postpartum was that of 14 July (Fig. 2). In the sample of 6 July, 95% of the nonbarren females were postpartum. Thus, by 14 August, 95% of the surviving young of the year should have been flying, and by 22 August, 9 days before our population estimation, all of the 1973 young should have been flying (Fig. 2). The size and position of the cluster of roosting bats were carefully observed over the period of 12 days preceding 1 September. We could detect no changes

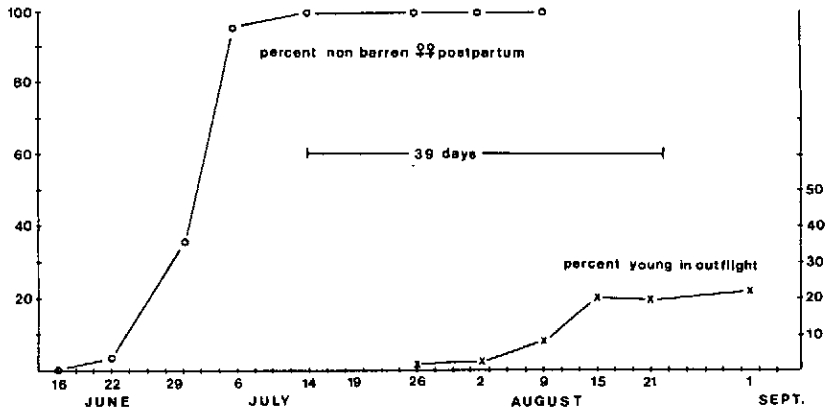


**Fig. 2.** Data from bats captured during the outflights from Carlsbad Cavern during June, July, August, and September 1973. The graph on the left is the percent of nonbarren females in the population which were postpartum.

in the relative size of the cluster during this time. The duration and the density of the outflight also remained about the same during this period. Thus we assumed no immigration or emigration during the 12-day period preceding our population estimation procedure. We feel our estimate is more accurate than any made heretofore and represents a relatively stable population of adult males, barren females, nonbarren postpartum females, and all surviving young of the year. Data on sex and age composition of the population during, before, and after 1 September 1973 have been assembled and are the subject of another report.

This technique for population size estimation was not used again during 1973. However, it was used during the summer of 1974 and will be used at monthly intervals during the summer of 1975 and 1976. We feel confident that we have a useful and valid means of estimating the size of large *Tadarida* populations with minimal disturbance of the bats. This technique should be applicable at any *Tadarida* colony and facilitate additional population studies on this bat.

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# *Coexistence of Two Species of Kangaroo Rats (Genus* Dipodomys*) in the Guadalupe Mountains National Park, Texas*

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Several species of heteromyid rodents are often found in coexistence in the deserts of North America (Hawbecker 1951; Reynolds 1958; Chew and Butterworth 1964; Brown 1973; Rosenzweig 1973; Reichman 1975). Six species of heteromyid rodents, *Dipodomys ordii, D. merriami, D. spectabilis, Perognathus penicillatus, P. flavus*, and *P. intermedius*, have been found in the western portion of the Guadalupe Mountains National Park, Texas. These rodents have broadly similar ecological needs. They are basically granivorous, nocturnal, and burrowing. Whenever species with similar ecological needs are found in sympatry, the possibility of interspecific competition arises. The widespread coexistence of different species of heteromyid rodents suggests that these animals have evolved with mechanisms which reduce competitive elimination. Models that explain the coexistence of similar and dissimilar sympatric species by habitat selection and resource allocation have been constructed by MacArthur and Levins (1964). Several workers have applied these models to coexistence in heteromyid rodent populations. Rosenzweig (1973) has shown habitat selection to be an important factor in the coexistence of *Dipodomys* and *Perognathus*. Seed size has been proposed as a mechanism of resource allocation among heteromyids (Brown and Lieberman 1973). Recently, Reichman (1975) reported that *Dipodomys* and *Perognathus* specialize on different proportions of the same food resources.

A prerequisite to understanding allocation of food resources in areas of sympatry is a knowledge of the animals' diets. The primary purpose of this study was to determine the diets of two species of kangaroo rats, *Dipodomys merriami* and *D. ordii*, through microscopic analysis of stomach contents, to examine dietary overlap in various seasons and habitats, and to evaluate these data in light of models for coexistence. These two species of

*Dipodomys* were chosen for study because they are relatively abundant in the area and, although easy to distinguish in the field, they are of similar size and morphology. The food habits of heteromyids have generally been determined by examination of cheek-pouch contents (Reynolds 1958; Dunham 1968; Gaby 1972; Chapman 1972). These workers have assumed that cheek-pouch contents are an accurate indicator of the actual diet of the rodent. Thus, a second objective of this study was to compare cheek-pouch contents and stomach contents in these two rodents.

The western portion of the Guadalupe Mountains National Park was not included within the proposed Wilderness Area of the 1974 Master Plan for the park (U.S. Department of Interior 1974). According to this document, this area may be transversed by roads. Thus it is presently in a state of transition; in the past it has been heavily grazed, in the future it may face human impact of a different nature. Because interspecific relationships are often of a very tenuous nature, any alteration in habitat may favor one species over the other. A further purpose of this study was to provide the baseline data from which these two kangaroo rats may be used as biological indicators of the changing range conditions and the degree of human impact in this area of the national park.

## DESCRIPTION OF THE STUDY AREA

The study is located in the western portion of the Guadalupe Mountains National Park, Texas. It is characterized by bajadas extending westward from the sheer limestone escarpment that forms the western edge of the Guadalupe Mountains. Elevation ranges from 1430 m at the base of the escarpment to 1120 m on the western boundary.

This area includes a combination of features from the grassland and desert scrub formations (Warnock undated; Burgess and Northington 1977). The western boundary of the park is in close proximity to an extensive salt flat. *Atriplex canescens* (four-wing-saltbush) and *Sporobolus airoides* (alkali sacaton) are the dominants on these saline soils. Beyond these soils, *Atriplex* gives way abruptly to *Larrea tridentata* (creosote bush) which is the major dominant of the area. On the lower portions of the bajada, *Larrea* is found in association with *Prosopis glandulosa* var. *torreyana* (honey mesquite), whereas nearer the escarpment its associates include *Bouteloua eriopoda* (black grama) and *Erioneuron pulchellum* (fluffgrass). Throughout the area various species of *Yucca* (Spanish bayonet) and *Opuntia* (prickly pear) are present.

The temperatures for the area ranged from an average low of -2.4° C in December 1974 to an average high of 27.2° C in June 1974 (U.S. Department of Commerce 1974). Precipitation was relatively low, 137.9 mm during the 10 months prior to the the study. The first 5 months of the study (February through June 1974) were also dry, with 17.2 mm of precipitation. The area received 329.6 mm of rain from July 1974 through January 1975 and 102.4 mm of snow in December 1974 and January 1975.

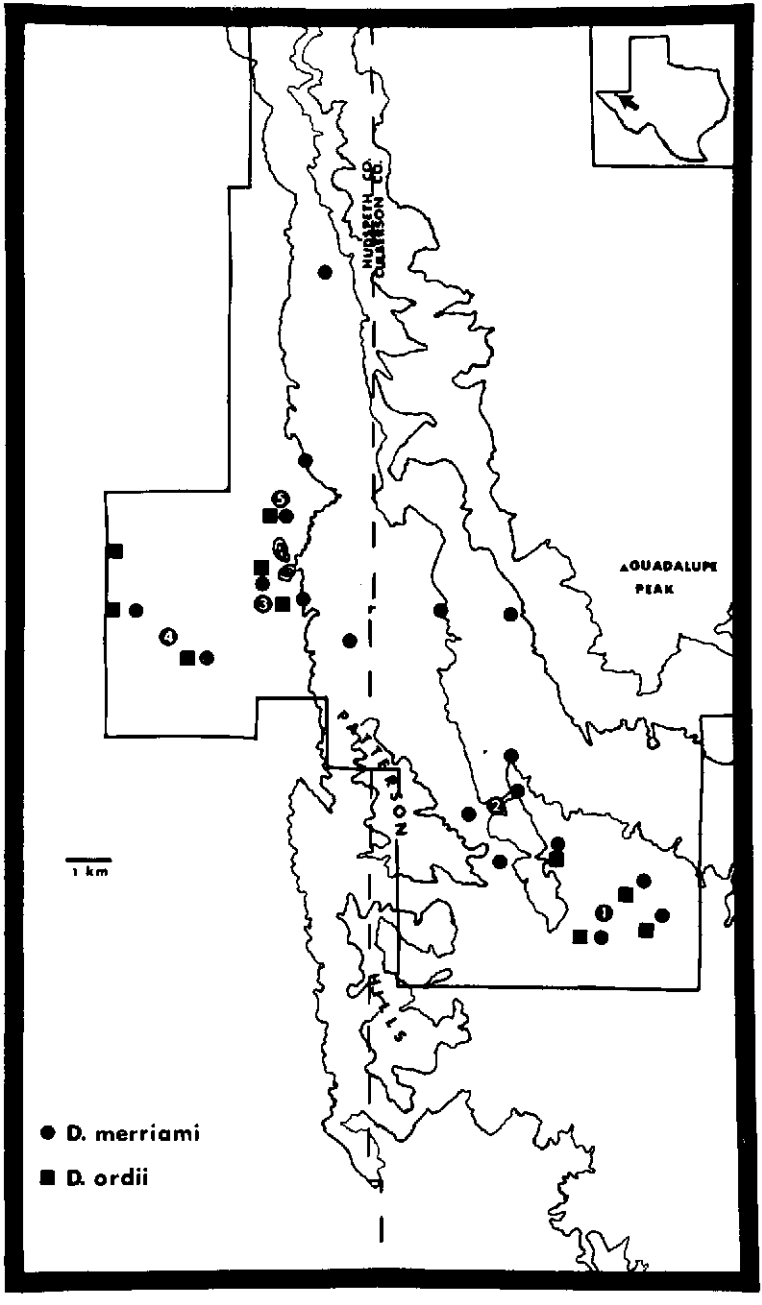


Fig. 1. Distribution of the two species of *Dipodomys* in the western portion of the Guadalupe Mountains National Park, Texas. The numbers denote the five main trapping localities of this study.

## METHODS AND MATERIALS

The populations were sampled a minimum of once a month from February 1974 through January 1975, with a total of 5728 trap-nights. Museum Special snap traps and Victor rat traps were placed at 4-m intervals along a transect.

Initially, trapping was conducted to determine the distribution of *Dipodomys merriami* and *D. ordii* within the western portion of the park. Once distribution patterns were established, trapping was limited to five main areas (Fig. 1).

Rodents were either prepared in the field or frozen on dry ice and prepared in the laboratory. Stomachs were removed, their contents air dried, and cheek-pouch contents were collected. Stomach contents of 276 *D. merriami* and 58 *D. ordii* were examined for dietary analysis. Even though population data were not collected, field observations suggest that these numbers probably reflect the relative densities of the two species in the area.

Stomach contents were prepared using the procedures outlined by Baumgartner and Martin (1939), Dusi (1949), Hansen and Flinders (1969), and Hansson (1970). Contents were washed over a 200-mesh screen sieve and thoroughly mixed. Randomly selected aliquots of the contents of each stomach were placed on two microscope slides and cleared with several drops of Hertwig's solution (Baumgartner and Martin 1939). The Hertwig's solution was evaporated by boiling, and the material was spread evenly over the slide. Hoyer's solution was added as the mounting medium and the slides were dried at 55°C for 48 hours.

A reference collection was made of the plants in the area. Plants were collected, dried, and ground, using either a Waring blender or a Wiley Mill. Reference material was prepared on microscope slides in the same manner as the stomach contents, with the exception that Permount was used as the mounting medium.

Ten nonoverlapping microscope fields (100×) were examined from each of the two slides made from the contents of each rodent's stomach. The presence of each food item in each microscope field was recorded. Percent frequency for each food item was determined as the number of times it appeared in a field expressed as a percentage of the total number of fields examined (Flinders and Hansen 1972).

Percent frequency can be converted to particle density per field (Fracker and Brischle 1940), and relative density can then be used to estimate percent dry weight of food items in diets (Sparks and Malechek 1968). Sparks and Malechek (1968) based their estimation of percent dry weight on samples containing known amounts of grasses and forbs that had been artificially mixed prior to analysis. Many workers in diet studies have successfully used this procedure (Ueckert and Hansen 1971; Flinders and Hansen 1972); however, these studies have dealt primarily with animals whose diets were basically green vegetation, i.e., leaf and stem material. Unlike green vegetation, different seed types vary considerably in size and specific weight

Because kangaroo rats are primarily granivorous, this procedure was not used in this study, and the data are based on percent frequency.

Kulzynski's Similarity Index (from Oosting 1956) was used to indicate the similarity of diets between interspecific and intraspecific samples as to sex, time, and locality. This expression is calculated by the formula:

$$2 \sum_{i=1}^{s} (w_i)\,(100) \Big/ \sum_{i=1}^{s} a_i + b_i,$$

where $a_i$ represents the mean percentage of food item $i$ in the diet of group $X$, $b_i$ represents the mean percentage of food item $i$ in group $Y$, and $w_i$ represents $a_i$ if $a_i \leq b_i$ and $b_i$ if $b_i \leq a_i$.

Cheek-pouch contents were used as a separate indicator of these animals' diet. The dry-weight composition of the cheek pouches was determined as the weight of one type of food item per total weight of all food items. Seeds found in the cheek pouches were identified by comparison with a reference collection of seeds from the study area. Cheek-pouch contents of 192 *D. merriami* and 9 *D. ordii* were examined.

The number of food items appearing in each animal's stomach and cheek pouch was recorded. The mean number of food items per stomach and per cheek pouch was determined for each species during the different months of the year. The BMD, 07V computer program was used to perform an analysis of variance on these data and to separate the means into homogeneous subsets using the Student-Newman-Keuls test (Sokal and Rohlf 1969).

## RESULTS

### Distribution

The trapping revealed an almost continual distribution of *Dipodomys merriami* throughout the entire study area and a scattered distribution of *D. ordii* (Fig. 1). The only location from which *D. merriami* was not collected was the white gypsiferous sand dunes on the western boundary of the park. *Dipodomys ordii* was collected at the lower elevations near the southern entrance to the park (1230 to 1340 m), the area north of the Patterson Hills (1220 m), and the westernmost portion of the park (1230 to 1350 m). For a complete account of all specimens collected and locality descriptions, see Genoways et. al. (1977).

During the study, *Dipodomys spectabilis* was collected for the first time from the Guadalupe Mountains National Park. Although trapping success for this larger kangaroo rat has been low, field observations of active burrows suggest that the distribution of *D. spectabilis* is also continuous throughout the western portion of the park.

In addition to kangaroo rats, three other heteromyid rodents, *Perognathus penicillatus, P. intermedius*, and *P. flavus*, have been collected from this area. These smaller heteromyids also have a continuous distribu-

tion in this area. The diets of these pocket mice are being analyzed and will be reported at a later date.

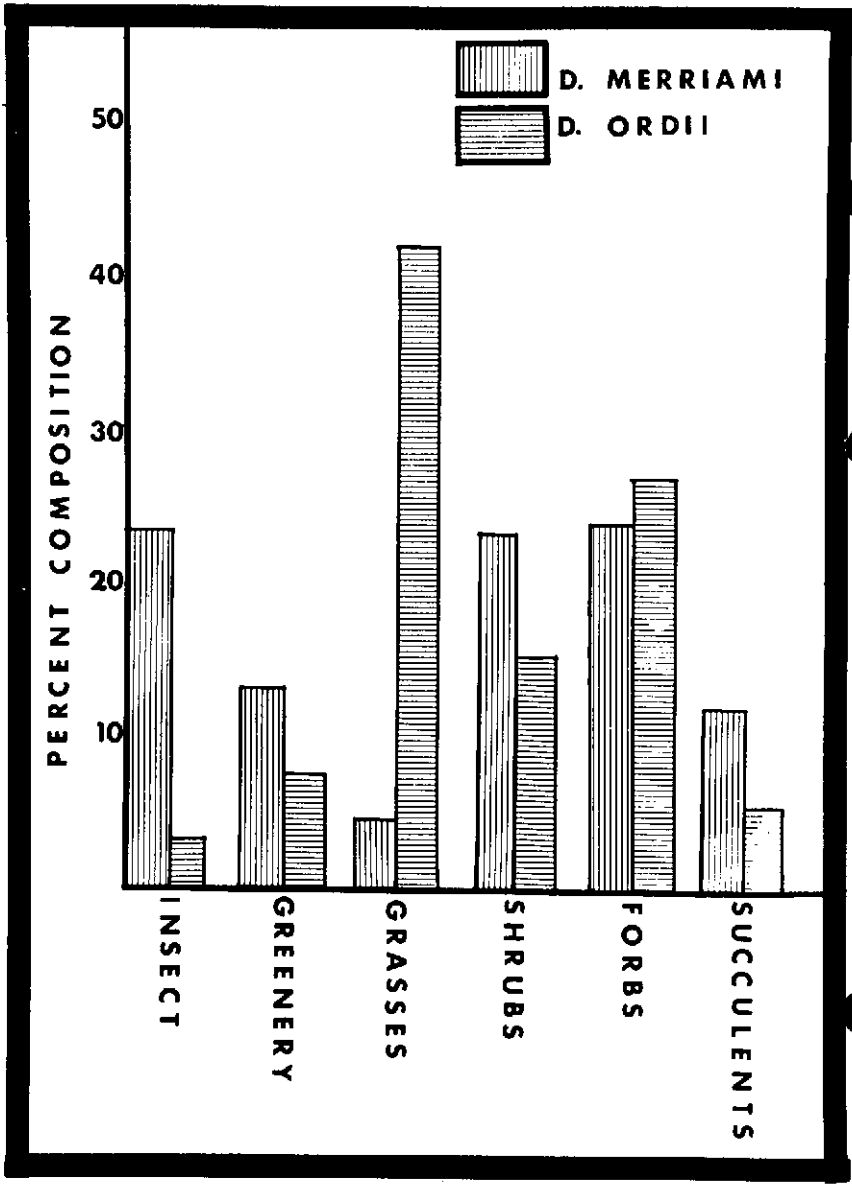


**Fig. 2.** Mean percent composition based on relative frequency of major food items in the annual diets of *Dipodomys merriami* and *D. ordii* as determined from stomach analyses. Greenery refers to leaf and stem material. Grasses, shrubs, forbs, and succulents refer to seeds of these plant types.

**Diet**

Seeds were the most important food item for both *Dipodomys merriami* and *D. ordii*. In addition, insects and green vegetation were important in the diets of both species.

Seeds made up 63.6% of the diet of *D. merriami*, with shrub seeds constituting 23%, forb seeds, 24.1%, grass seeds, 4.5%, and succulent plant seeds, 12% of the total diet (Fig. 2). The diet of *D. merriami* varied seasonally (Fig. 3). Seeds, insects, and green vegetation were present in the diet throughout the year; however, during the late summer and autumn,

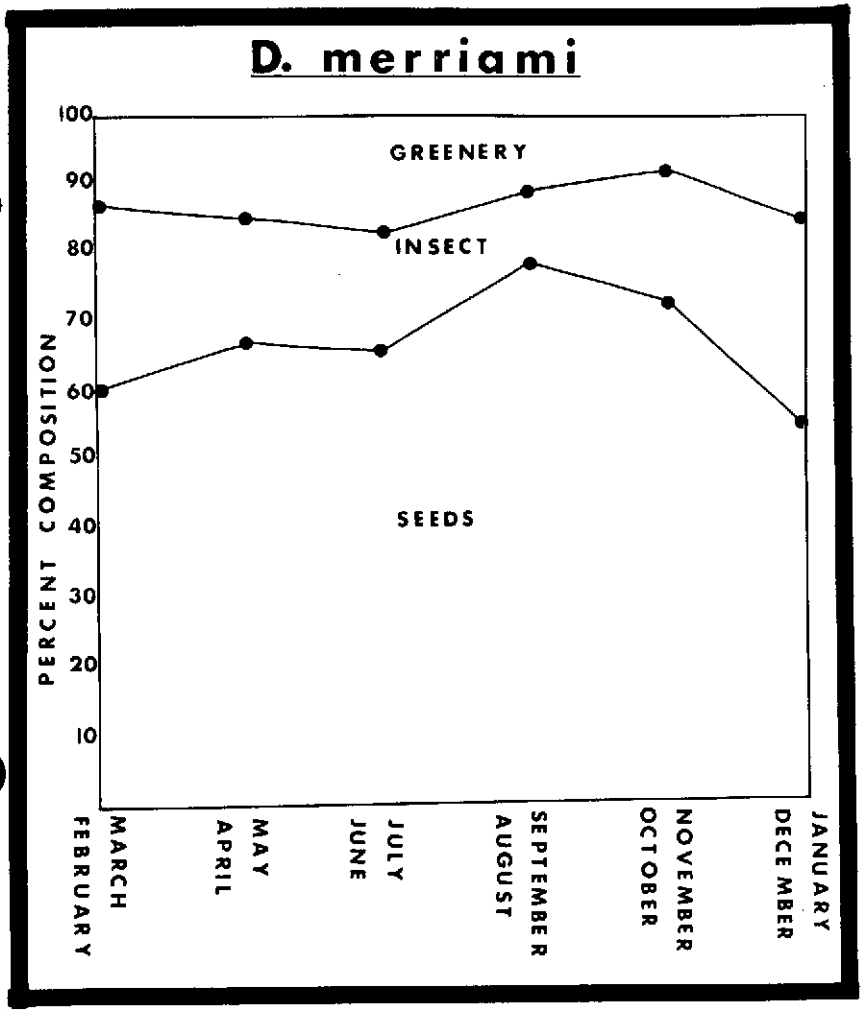


Fig. 3. Seasonal variation of the three main food items in the diet of *Dipodomys merriami*, as determined from microscopic examination of stomach contents.

both insects and green vegetation were less important. Green vegetation was most important during mid-summer. Insects were eaten in greatest quantities during the winter months. The seasonal variation of the four seed types is shown in Fig. 4. The high percentage of succulent plant seeds during April and May reflects the importance of *Dasylirion* (sotol) seeds in the diet at this time. Shrub seeds became more important in the diet during mid-summer, corresponding to the seed-setting of both *Prosopis* and *Larrea*. During the autumn, forb seeds became very important, with *Euphorbia* seeds the major component of the diet.

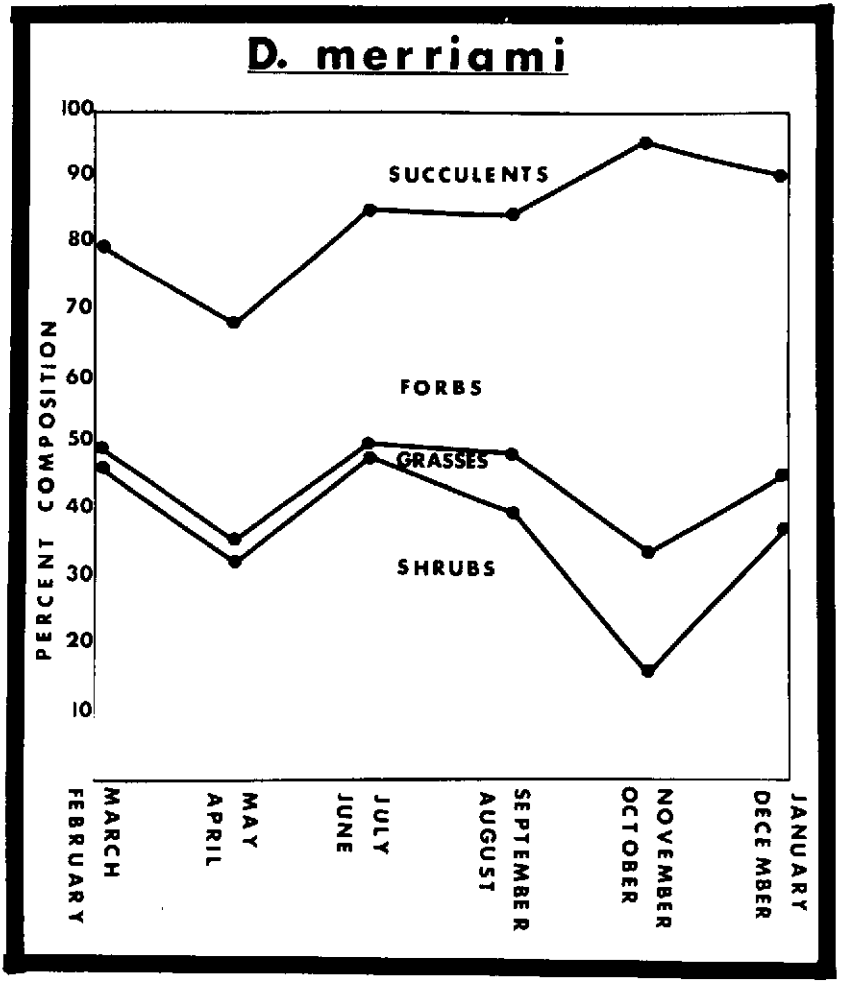


Fig. 4. Seasonal variation of the four major seed types in the diet of *Dipodomys merriami*, as determined from microscopic analysis of stomach contents.

Of the 33 food items identified in the diet of *D. merriami*, 16 items made up over 1% (Table 1). The most important food items included *Larrea*, insects, *Euphorbia*, green vegetation, *Opuntia*, *Prosopis*, and *Lepidium* (peppergrass).

Seeds were more important in the diet of *D. ordii*, making up 89.5% of the total diet. Shrub seeds constituted 15.5%, forb seeds, 27%, grass seeds, 41%, and succulent plant seeds 6% (Fig 2). The seasonal variation of the three main food types is shown in Fig. 5. Seeds were the major component

TABLE 1. Percent composition of food items in the mean annual diets of *Dipodomys merriami* and *D. ordii* as determined from stomach analyses.

| Food item | Common name | *D. merriami* | *D. ordii* |
|---|---|---|---|
| *Larrea* | Creosote bush | 14.2 | 5.1 |
| Insects | | 23.5 | 3.1 |
| *Prosopis* | Mesquite | 4.2 | 4.1 |
| Greenery | | 12.9 | 7.5 |
| *Bouteloua* | Grama grass | 3.1 | 17.8 |
| *Lesquerella* | Bladder-pod | Tr | 1.1 |
| *Lepidium* | Peppergrass | 4.6 | Tr |
| *Yucca* | Spanish bayonet | 3.7 | 1.7 |
| *Flourensia* | Tarbush | 1.7 | Tr |
| *Sporobolus* | Dropseed | 1.4 | 17.0 |
| *Atriplex* | Saltbush | 2.4 | 6.4 |
| *Euphorbia* | Spurge | 10.2 | 2.0 |
| *Croton* | Rosval | Tr | 4.6 |
| *Opuntia* | Prickly pear | 4.0 | 3.0 |
| *Gutierrezia* | Snakeweed | 1.5 | 1.0 |
| *Dyssodia* | Dogweed | 2.2 | Tr |
| *Chilopsis* | Desert willow | Tr | 1.6 |
| *Nerisyrenia* | | Tr | 8.8 |
| *Dasylirion* | Sotol | 4.1 | Tr |
| *Pectis* | | 1.5 | Tr |
| *Tridens* | Slim Tridens | Tr | 1.1 |
| *Oenothera* | Evening primrose | Tr | 3.1 |
| *Kallstroemia* | | Tr | 2.4 |
| *Erioneuron* | Fluffgrass | Tr | 1.4 |
| *Sphaeralcea* | Globe mallow | Tr | 1.1 |
| *Fallugia* | Apache-plume | Tr | 1.9 |
| *Erodium* | Alfilerillo | Tr | Tr |
| *Tetraclea* | | Tr | Tr |
| *Coldenia* | | Tr | Tr |
| *Poliominthia* | Rosemary mint | A | Tr |
| *Bahia* | | Tr | Tr |
| *Tidestomia* | | Tr | Tr |
| *Krameria* | Range ratany | Tr | Tr |
| *Fouquieria* | Ocotillo | Tr | Tr |

Tr = a trace, or less than 1%; A = absence from the diet.

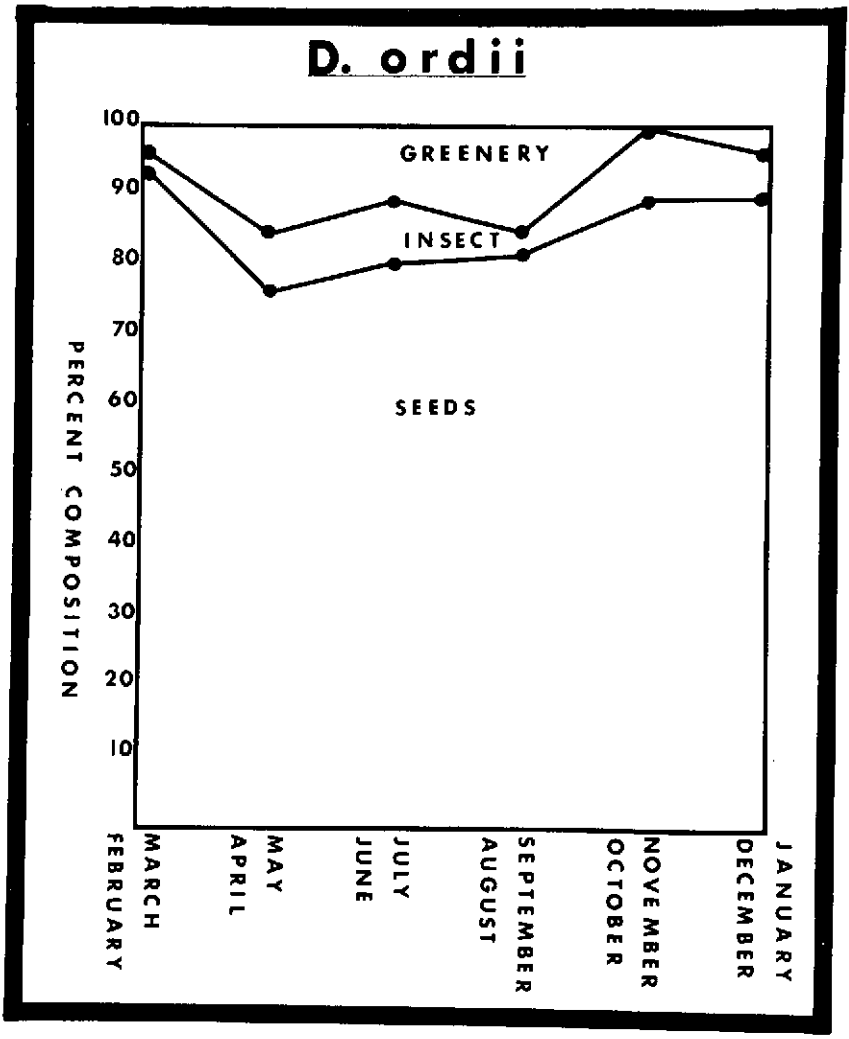


**Fig. 5.** Seasonal variation of the three main food items in the diet of *Dipodomys ordii*, as determined from microscopic analysis of stomach contents.

throughout the year, whereas green vegetation was most important during the spring and late summer. Insects were relatively constant throughout the year, becoming less important during the late summer and, unlike *D. merriami*, during the winter.

The seasonal variation of the four seed types is shown in Fig. 6. Succulent plant seeds were present in the diet with relatively constant precentages throughout the year. The increased importance of forb seeds during the

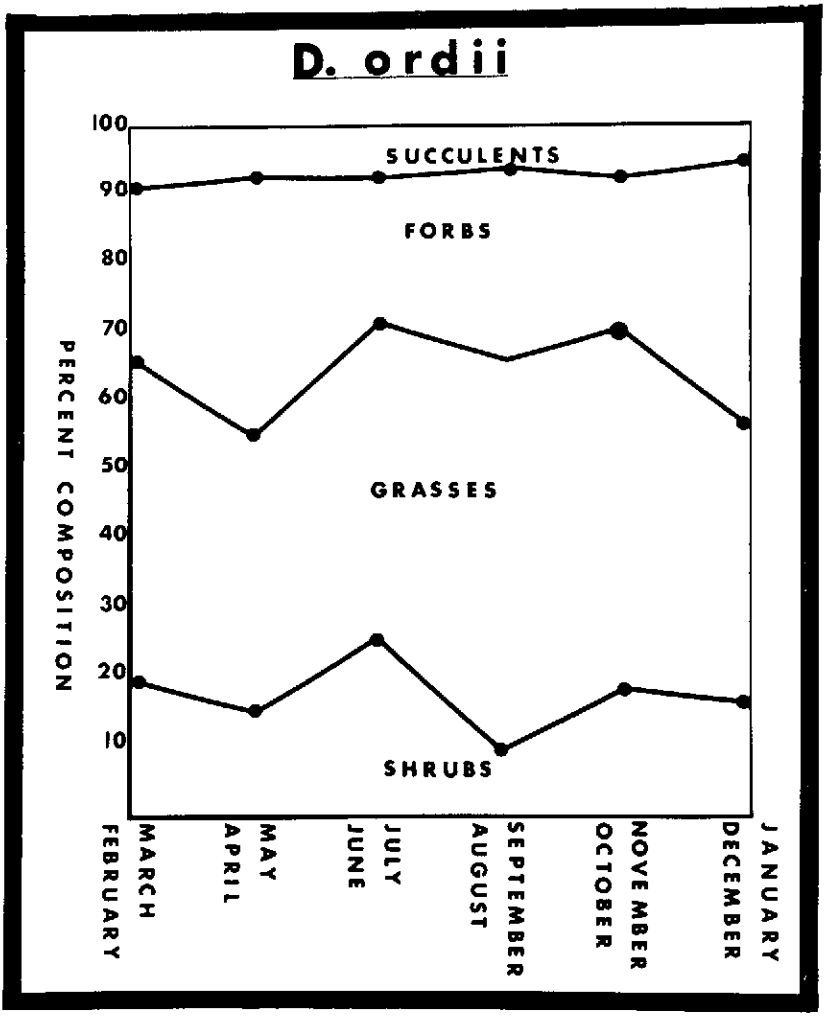


Fig. 6. Seasonal variation of the four major seed types in the diet of *Dipodomys ordii*, as determined from microscopic analysis of stomach contents.

spring reflects the amount of *Lepidium* eaten at this time. As in the diet of *D. merriami*, shrub seeds became more important during mid-summer. Grass seeds were eaten in greater quantities during the late summer and autumn.

Twenty of the 34 food items identified in the diet of *D. ordii* contributed over 1% of the diet (Table 1). *Larrea, Bouteloua*, green vegetation, *Sporobolus, Atriplex*, and *Nerisyrenia* were the major components of the diet.

**Comparison of Cheek-Pouch and Stomach Contents**

If cheek-pouch contents rather than stomach contents are used to describe the diet, the picture is considerably different. Seeds made up 99.2% of the diet of *D. merriami*, based upon cheek-pouch contents. Only one insect was found in the cheek pouches of the 276 specimens examined (Fig. 7).

The most important seeds found in the cheek pouches were *Larrea, Prosopis, Opuntia*, and *Euphorbia*. Although these seeds were also important in the stomach contents, they appeared in different proportions in the cheek pouches (Fig. 7). For example, *Larrea* seeds constituted 14.2% of the diet as determined from stomach contents, but made up 37.2% of the diet as determined from cheek-pouch contents. Some seeds, such as *Lepidium*, were relatively important in the stomach contents but insignificant in the cheek-pouch contents (Fig. 7). Conversely, other seeds, such as *Chilopsis*,

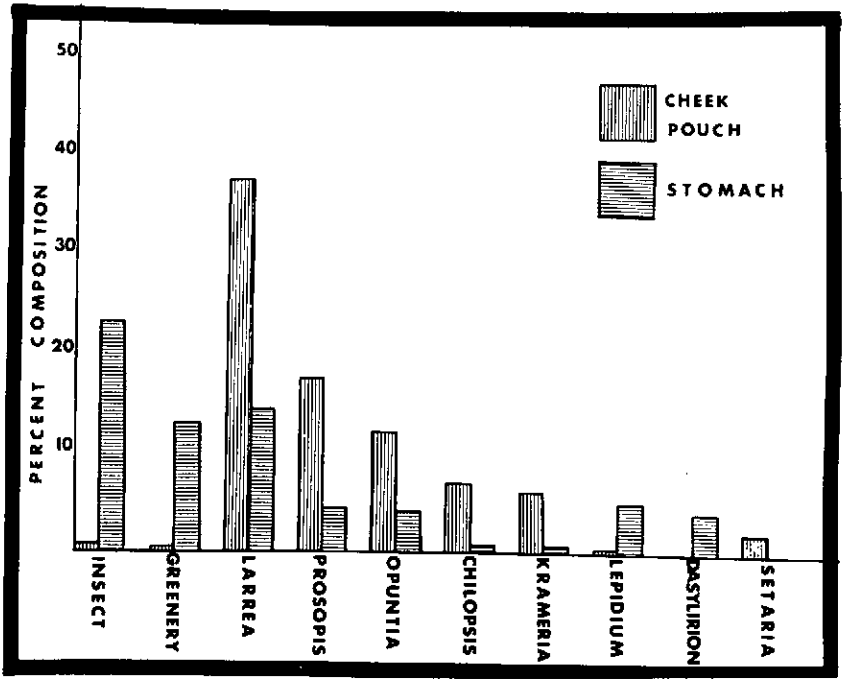


Fig. 7. Comparison of the contribution of 10 food items in the diet of *Dipodomys merriami* as determined by examination of cheek-pouch contents to the contribution of these foods as determined by examination of stomach contents. Percent composition was determined on a dry weight basis in cheek-pouch samples and on a relative frequency basis in stomach samples.

appeared in the stomach contents with a percentage less than one, whereas they constituted 6.8% of the diet as determined by cheek-pouch contents. The importance of four food items including insects, greenery, *Lepidium*, and *Dasylirion* were grossly underestimated by cheek-pouch examination, whereas six foods including *Larrea, Prosopis, Opuntia, Chilopsis, Krameria*, and *Setaria* were greatly overestimated by cheek-pouch examination.

These trends also appeared in the comparison of cheek-pouch contents with stomach contents of *D. ordii*; however, only 15% (nine) of the cheek pouches of *D. ordii* contained food items. This small sample size was considered inadequate to determine percent composition.

## Variation in Number of Food Items in Diets

The mean numbers of food items per stomach were 4.8 ± 0.8 (standard deviation) for *Dipodomys merriami* and 5.6 ± 1.0 for *D. ordii* for the entire year. Analysis of variance revealed significant ($P \leq 0.05$) seasonal difference between the mean numbers of food items.

TABLE 2. The mean number of food items appearing per stomach contents of *Dipodomys ordii* during the different seasons.

| Season | Mean number of food items |
|---|---|
| February 1974 | 6.4 ± 1.2 |
| May–June 1974 | 5.2 ± 1.0 |
| August 1974 | 4.1 ± 1.0 |
| January 1975 | 6.7 ± 1.2 |

For *D. ordii*, months represented with a sufficient sample size were separated into two homogeneous subsets:—(1) February 1974 and January 1975, and (2) May–June and August 1974. The mean number of food items per stomach for the first subset was 6.1 ± 0.6 and was 4.5 ± 0.6 for the second subset (Table 2).

The means number of items per *D. merriami* stomachs varied seasonally (Table 3). February, March, April, December 1974, and January 1975 fell into one homogeneous subset with a mean number of items of 5.5 ± 0.7. A second subset included May, June, August, September, October, and November 1974 with a mean of 4.0 ± 0.6 food items per stomach.

The overall average number of food items per cheek-pouch was 1.4 ± 0.2 for *D. merriami* (Table 3). The mean number of food items in cheek pouches did not vary significantly during the different months of the year ($P \leq 0.05$).

TABLE 3. The mean number of food items appearing per stomach and cheek pouch contents of *Dipodomys merriami* during the different seasons.

| Season | Mean number of food items | |
|---|---|---|
| | Stomach contents | Cheek-pouch contents |
| February 1974 | 6.0 ± 1.1 | 1.6 ± 0.7 |
| March 1974 | 5.2 ± 1.2 | 1.3 ± 0.6 |
| April 1974 | 5.2 ± 0.9 | 1.8 ± 0.9 |
| May 1974 | 5.5 ± 1.2 | 1.3 ± 0.4 |
| June 1974 | 5.1 ± 1.0 | 1.7 ± 0.8 |
| August 1974 | | 1.4 ± 0.6 |
| Area no. 3 | 4.0 ± 0.6 | |
| Area no. 2 | 3.5 ± 0.6 | |
| Area no. 1 | 3.6 ± 0.9 | |
| September 1974 | 3.1 ± 1.0 | 1.2 ± 0.4 |
| October 1974 | 3.9 ± 0.9 | 1.5 ± 0.5 |
| November 1974 | 4.1 ± 1.0 | 1.5 ± 0.8 |
| December 1974 | 5.0 ± 1.0 | 1.6 ± 0.8 |
| January 1975 | | 1.2 ± 0.5 |
| Area no. 3 | 5.9 ± 1.2 | |
| Area no. 5 | 7.0 ± 1.2 | |

## Interspecific Dietary Similarity

A comparison of the mean annual diets of *D. merriami* and *D. ordii* yielded a similarity index of 42 (Table 4), which indicates no serious dietary overlap. The diets of the two species overlapped on 33 food items (Table 1); however, a food consumed in fairly large proportions by one species was usually of minor importance in the diet of the other species.

TABLE 4. Interspecific similarity indices for mean annual diets of *Dipodomys merriami* and *D. ordii*, and for selected seasonal diets in two habitats.

| Comparison | Similarity index |
|---|---|
| Total year | 42 |
| Area no. 1 | |
| February 1974 | 36 |
| August 1974 | 55 |
| Area no. 5 | |
| January 1975 | 65 |

Interspecific dietary similarity varied both with season and location (Table 4). The similarity index for the diets of the two species for area no. 1 (Fig. 1), the southern entrance to the park, during February 1974 was 36.

This low similarity index reflects the fact that *D. merriami* consumed more insects than did *D. ordii*. Insects made up 28.7% of the diet of *D. merriami* and only 2.8% of the diet of *D. ordii*. *Bouteloua* seeds did not appear in the diet of *D. merriami* at this time, but they made up 34.7% of the diet of *D. ordii*.

During August 1974 at the same location, the similarity index between the diets of the two increased to 55. Insects remained more important in the diet of *D. merriami*, 25.3% as compared to 3.1% in *D. ordii*, and *Bouteloua* seeds were still more important to *D. ordii* (17%) than to *D. merriami* (1.3%). However, *Prosopis* seeds, which had not been of great importance in either kangaroo rat's diet during February, contributed 22.4% and 20.5% to the diets of *D. merriami* and *D. ordii*, respectively.

The similarity index for the two diets for a quartz sand–hill habitat (area no. 5; Fig. 1) during January 1975 was 65. Both species of rodents had more food items per stomach at this locality than at any other (Tables 2 and 3). These sand hills had 33 plant species, which is more than three times the number found on the surrounding creosote–bush flats (Burgess and Northington 1977).

**Intraspecific Dietary Similarity**

The intraspecific comparisons indicate no dietary difference between sexes in either species. The index of similarity between males and females was 90 for *D. merriami* (Table 5) and 89 for *D. ordii* (Table 6). The high similarity indexes for conspecific males and females indicate that the low interspecific similarities are probably not due to sampling error.

Intraspecific comparisons also suggest that both kangaroo rats shift their diets with respect to time of year and location (Tables 5 and 6). The diet of specimens of *D. merriami* collected from area no. 1 (Fig. 1), the southern entrance to the park, was compared for three different times of the year—February, August, and November 1974 (Table 5). The similarity index between February and August was 48 and that between February and November was 40. The diets during August and November showed little dietary overlap (similarity index = 28). During February, this kangaroo rat feeds on a small percentage of many different food items; however, during August and November, *D. merriami* selects larger quantities of fewer items. These selected items are different during August (*Prosopis*) than during November (*Euphorbia*).

At the same locality, the similarity index between February and August diets of *D. ordii* was 53 (Table 6). However, only one animal was collected from this area during November, making determination of the similarity index impossible.

Another locality (area no. 3; Fig. 1), the area to the north of the Patterson Hills, was compared during five different months—May, June, August, October 1974, and January 1975. This area is characterized by more open creosote flats, with less grass cover than the locality discussed above. The

TABLE 5. Intraspecific similarity indexes for the diet of *Dipodomys merriami*.

| Comparison | Similarity index |
|---|---|
| Males vs. females | 90 |
| Same Locality—Different Seasons | |
| Area no. 1 | |
| February vs. August | 48 |
| February vs. November | 40 |
| August vs. November | 28 |
| Area no. 3 | |
| May vs. June | 67 |
| May vs. August | 69 |
| May vs. October | 51 |
| May vs. January | 54 |
| June vs. August | 77 |
| June vs. October | 47 |
| June vs. January | 63 |
| August vs. October | 48 |
| August vs. January | 75 |
| October vs. January | 60 |
| Same season—Different localities | |
| August 1974 | |
| Area no. 1 vs. Area no. 3 | 62 |
| Area no. 1 vs. Area no. 2 | 55 |
| August 1974 | |
| Area no. 1 vs. Area no. 4 | 56 |
| Area no. 3 vs. Area no. 2 | 65 |
| Area no. 3 vs. Area no. 4 | 59 |
| Area no. 2 vs. Area no. 4 | 55 |
| Area no. 5 vs. Area no. 1 | 49 |
| Area no. 5 vs. Area no. 2 | 40 |
| Area no. 5 vs. Area no. 3 | 44 |
| Area no. 5 vs. Area no. 4 | 50 |
| January 1975 | |
| Area no. 5 vs. Area no. 3 | 12 |

similarity indexes were higher (40 to 77) throughout the year at this locality. The spring and summer months were more similar to each other and to a winter month than they were to an autumn month. However, the dietary overlap betweeen the autumn and winter months was also high.

The diet of *D. merriami* throughout various localities on the creosote–bush flats (areas no. 1, 2, 3, 4; Fig. 1) was similar (similarity index = 55 to 65) during August. However, when these localities were compared to the quartz sand hills (area no. 5; Fig. 1) during the same month, there was considerably less similarity (similarity index = 40 to 49) (Table 5). When a creosote–bush flat area (area no. 3; Fig. 1) was compared to the quartz sand hills (area no. 5; Fig. 1) during January 1975, there was even less dietary overlap (similarity index = 12). There was also very little similarity (similarity index =

TABLE 6. Intraspecific similarity indexes for the diet of *Dipodomys ordii*.

| Comparison | Similarity index |
|---|---|
| Males vs. females | 89 |
| Same locality—Different seasons | |
| Area no. 1 | |
| February vs. August | 53 |
| Area no. 5 | |
| August vs. January | 64 |
| Same season—Different locality | |
| August 1974 | |
| Area no. 3 vs. Area no. 1 | 59 |
| January 1975 | |
| Area no. 5 vs. Area no. 4 | 13 |

13) at this same time between the diet of *D. ordii* on the quartz sand hills (area no. 5; Fig. 1) and another creosote–bush flat location (area no. 4; Fig. 1) (Table 6).

## DISCUSSION

### Diet

The food habits of *Dipodomys merriami* and *D. ordii* are broadly similar. Both species are primarily granivorous but also eat insects and green vegetation. Of the 34 food items found in the diet of *D. ordii*, 33 also appeared in the diet of *D. merriami*. However, the proportions of these food items in the diet vary greatly between species. This finding gives support to the model of MacArthur and Levins (1964) that animals with similar diets will tend to specialize on specific proportions of the food resources. MacArthur in a later paper (MacArthur and Pianka 1966) suggested that this may occur because competitor animals will utilize fewer patches rather than reduce their diets. According to these authors, the high number of food items shared by these two species would suggest that the animals are foraging in different habitats, or patches. Rosenzweig (1973) has shown *D. merriami* to prefer open creosote–bush habitats with little cover. Field observations suggest that this is true, and that *D. ordii* may be utilizing areas with more cover.

The greatest dietary similarity between *D. merriami* and *D. ordii* occurred on the quartz sand hills. Although the percent cover in this habitat is approximately the same (21%) as the surrounding creosote–bush flats, the sand hills support three times as many species as the flats (Burgess and Northington 1977). This indicates that the diets of these two species may be more similar in areas of greater diversity. The diets of these two kangaroo rats on the creosote–bush flats were more similar during August than during February. Although quantitative data on the availability of seeds are not available, field notes of various workers in the area indicate that during 1974 the plants set seed from late spring through the autumn. This further

suggests that greater abundance may lead to more similarity between the diets of these two species. The tendency of these two kangaroo rats to concentrate on different proportions of the food resources during times of less abundance may be one mechanism allowing their coexistence.

Both *D. merriami* and *D. ordii* appear to be opportunistic feeders, able to shift their diets in response to varying habitat conditions. The lowest similarity indexes obtained from all inter- and intraspecific comparisons were those comparing the same species from different habitats. Intraspecific comparisons of the diets of *D. merriami* and *D. ordii* between the quartz sand hills (area no. 5; Fig. 1) and the creosote–bush flats (areas no. 3, 4; Fig. 1) yielded similarity indexes of 12 and 13, respectively. Thus, the diets of these two species may differ between regions and between years in the same area. Reichman (1975) has reported that *D. merriami* ate more seeds (78.4%) and less insects (15.5%) in a *Larrea*–dominated area of southern Arizona than has been reported here. However, there are most likely certain heteromyid food–habit trends that are common among all North American deserts.

**Variation in Number of Food Items in Diets**

Emlen (1966, 1968) has proposed that animals will be more selective and specialized in their diets when food is abundant and will become less selective and specialized as food items become scarce. Smigel and Rosenzweig (1974) have demonstrated, with radioactively labeled commercial seeds, that *D. merriami* and *Perognathus penicillatus* are more selective at higher seed densities.

The data presented here also support the model proposed by Emlen (1966, 1968). For both *D. merriami* and *D. ordii* the number of kinds of food items ingested (food niche breadth) was significantly less during the summer and autumn than during the winter and early spring. The food–habit data show that at certain times of the year one food item, for example, *Euphorbia* during November, will be utilized almost exclusively, whereas throughout the rest of the year, this item enters into the diet with much less frequency.

The comparison of the food items ingested by *D. merriami* among different months within one habitat reveals that a wide variety of food items were used during February. Although only one new food item appeared in the diet during August, seven items were not part of the diet. A similar situation occurred in November. Two food items appearing in the November diet had not been part of the February diet, whereas eight items appeared in February but not in November. These data further indicate that *D. merriami* is less discriminating in February and more selective in August and November.

**Comparison of Cheek-Pouch and Stomach Contents**

Many workers who have examined food habits of different species of *Dipodomys* have based their conclusions solely on the analysis of

cheek-pouch contents (Reynolds 1958; Dunham 1968; Chapman 1972; Gaby 1972). Gaby (1972) compared the diets, as determined by analysis of cheek-pouch contents, of *D. merriami* and *D. ordii* in southern New Mexico. Although the species of seeds eaten were generally similar to those found in this study, the proportions were different. Gaby reported neither green vegetation nor insects as important constituents of these kangaroo rats' diets.

Although cheek-pouch contents do give an indication of what the kangaroo rats are harvesting, the data presented in this paper demonstrate that cheek-pouch contents are unreliable indicators of relative proportions of foods in the diet. Percent composition of food items obtained from analysis of cheek-pouch contents varied greatly from that obtained from stomach analyses. The mean number of food items per cheek-pouch was lower and more uniform throughout the year than that of food items per stomach. The size of seeds in the cheek pouches were generally larger than those from the stomachs. Grass seeds were an exception, but they were usually found still on the spikelets.

Reichman (1975) has suggested that the items collected in heteromyid cheek pouches are for potential use rather than immediate ingestion. The findings of this study support this view. *Larrea* seeds were more than twice as important in the cheek-pouch contents than in the stomach contents. These seeds were present in the cheek pouches in equal dry weights throughout the year, but the frequency of *Larrea* seeds in the stomach contents fluctuated. *Larrea* is the dominant plant in the study area, making up almost all of the 21% total cover on the creosote-bush flats (Burgess and Northington 1977). The data suggest that the kangaroo rats are collecting the more abundant, more stable food sources for storage purposes, while immediately ingesting the less stable sources.

The high percentage of seeds and insignificance of insects and green vegetation in the cheek pouches (Fig. 7) further support the suggestion that the contents of cheek pouches are intended for storage purposes. Seeds are much better suited for storage in surface caches or burrows than are either insects or green vegetation. The higher percentage of larger seeds and lower percentage of smaller seeds in the cheek pouches as compared to stomach contents indicate that ease in handling different seed sizes may also be a factor determining what is placed in the cheek pouches or eaten immediately.

**Relation of *Dipodomys* to the Guadalupe Mountains National Park**

The western portion of the Guadalupe Mountains National Park was heavily grazed from the early 1900s up until the formation of the National Park in 1972. Warnock (undated) and Burgess and Northington (1977) point to grazing as a factor causing the increase of Chihuahuan Desert vegetation over grassland species. The question which immediately arises is, how will the vegetation respond to the termination of grazing in the area, and how will this affect the local animal populations? Reynolds (1950) studied the ecology

of *D. merriami* on the grazing lands of southern Arizona. By comparing the population densities of this kangaroo rat on grazed and ungrazed plots, he concluded that *D. merriami* favors grazed areas and avoids areas of dense perennial grasses. Rosenzweig (1973) also reported that *D. merriami* prefers open habitats. Thus the grazing practices in the western portion of the Guadalupe Mountains National Park may have favored *D. merriami*. If grasses were to become reestablished on the west side of the park, as Warnock (undated) suggests, this might cause a decrease in the *D. merriami* population. The high percentage of grass seeds in the diet of *D. ordii* suggests that an increase in grass cover may favor this species. Further monitoring of *Dipodomys* in this area will yield valuable information on the response of these animals to changing range conditions.

The activities of kangaroo rats also may have an effect on range conditions. Their habits of storing seeds in surface caches or burrows may effect the dispersal of plant species. Reynolds (1958) found that *D. merriami* has little effect on range conditions when the range is in good to excellent condition. Shrub seeds may be planted by the rodents, but under good range conditions their dispersal is slow. As range conditions deteriorate, he found numbers of *D. merriami* to increase and their presence to have an effect on range conditions. In advanced stages of range deterioration, Reynolds (1958) suggested that the activities of *D. merriami* may be sufficient to prevent range recovery even though cattle grazing is terminated.

The range conditions of the western portion of the Guadalupe Mountains National Park probably fall in this last category. Thus the activities of *D. merriami* in the area may have a negative effect on range recovery. The analysis of cheek-pouch contents has shown that *D. merriami* is probably storing the larger seeds of shrubs and succulent plants that are often indicators of poor range conditions. Under deteriorated range conditions, the storing activities of *D. merriami* have been found to aid in the dispersal of these plants (Reynolds 1958). The establishment of fenced-in plots to study the response of range vegetation (1) to no kangaroo rats; (2) to the presence of one species; and (3) to the presence of both species would yield critical information on the effect of these rodents on range conditions.

The 1974 Master Plan for the Guadalupe Mountains National Park (U.S. Department of Interior 1974) indicates that in the future the western portion of the park may be transversed by roads. The effects of roads on populations of small mammals is not well known. Oxley et al. (1974) found that roads through northern coniferous forests act as barriers to the dispersal of small mammals. The open spaces of the roads and their edges inhibited the movements of the animals. In the more open desert regions, this effect caused by roads probably is not an important factor. Roads may increase the food supply as a result of increased moisture from run-off of rain water. The increased supply of grasses along roadsides has caused an expansion of the ranges of some microtine rodents (Baker 1971). A paved road through the western portion of the Guadalupe Mountains National Park may alter the

vegetation adjacent to the road. An alteration of vegetation conditions may create changes in the distribution of rodent populations. For example, a road in this area may provide a corridor along which *D. ordii* could expand its distribution. If a road is built through this area, continued study of the rodent populations would provide a better understanding of the effects of roads on small mammals.

The average visitor to the Guadalupe Mountains National Park seldom sees the park's many mammals because these animals are elusive and primarily nocturnal. However, the careful observer can find an abundance of mammal signs in the area. One of the purposes of an interpretive program in the National Parks should be to help the visitor become a better and more appreciative observer. Kangaroo rats are well suited for use in interpretive programs. Although seldom seen, these animals construct conspicuous burrows under mesquite and creosote bushes. Their distinctive tracks are often seen in the sandy washes and by the surface caches they dig for seed storage. In addition, kangaroo rats are relatively easy to keep in captivity for display purposes. A combination of live kangaroo rats, with an explanation of their adaptations to desert habitats, and an exhibit explaining these rodents' signs could be an instructive part of the park's interpretive program.

The similarity indexes suggest that the diets of these two kangaroo rats are more similar with greater diversity and abundance of food resources. When food items become less diverse and abundant, the diets of the two species become less similar. The data suggest that in times of food scarcity the animals will concentrate on different food resources or on different proportions of the same resources. If future activities of man in the area were to create conditions of stress for these kangaroo rats, this stress would be reflected in their diets. Thus the diets of *Dipodomys merriami* and *D. ordii* could be used not only as biological indicators of the human impact on diversity and abundance of the habitat but also of human impact on these rodents populations.

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# *Ecological Distribution of Woodrats (Genus* Neotoma*) in Guadalupe Mountains National Park, Texas*

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The preservation of our national parks for the enjoyment and enlightenment of future generations depends on maintenance of human impact at levels which will not degrade natural assemblages of plants and animals. The slogan of the National Park Service, "parks are for the people," challenges us to develop management plans that will permit maximum use of the parks with minimal impact on the local ecosystems. A thorough understanding of interrelationships and ecological requirements of a park's flora and fauna is a prerequisite to solving this difficult problem. Once these relationships are known, methods of measuring human impact on the ecosystem must be developed and employed to monitor the condition of the ecosystem.

Although small mammals are an important part of the ecosystem, they have generally been overlooked in the development of resource management plans. Small mammal studies in our national parks have tended to be descriptive inventories without management implications. Some of the small mammalian species occurring in our national parks are endangered and should be actively managed to enhance their chances of survival. Small mammals also deserve careful study because of their role as prey for carnivores, because they may compete with other animals for food resources, and because of their impact, both positive and negative, on the flora of a park. A final consideration is utilization of small mammals as biological indicators of habitat conditions within a park.

Biological indicators are organisms, species, or communities which indicate the presence of certain environmental conditions. Plants have been widely used as indicators of habitat conditions and have proved useful as habitat management aids. Animals associated with these plants also can be utilized as habitat indicators. Human impact in a national park can be determined in part by monitoring changes in quantity and quality of different types of habitats and accompanying changes in density and distribution of associated animals.

The purpose of this research was to determine the distribution of woodrats in Guadalupe Mountains National Park, to quantify the size and components of representative woodrat houses, to analyze the habitat in the immediate vicinity of these houses, and to investigate the feasibility of using woodrats as biological indicators of habitat conditions.

Three species of woodrats occur in Guadalupe Mountains National Park. In 1901, Bailey (1905) collected *Neotoma albigula* in Dog Canyon. He also reported that *N. mexicana* was common at higher elevations in the Guadalupe Mountains of Texas, living in rocks and cliffs and ranging to the tops of the mountains. Davis (1940) trapped one *N. albigula* at Frijole in 1938 and one *N. mexicana* in a log cabin in The Bowl in 1939. Davis and Robertson (1944) reported *N. micropus* from Culberson County, Texas, but did not indicate their presence in the immediate vicinity of the Guadalupe Mountains. All three species of woodrats were captured within the boundaries of Guadalupe Mountains National Park during my initial mammal survey work in 1973.

## METHODS AND MATERIALS

The distribution of woodrats in Guadalupe Mountains National Park was mapped as the result of extensive trapping throughout the park in conjunction with a survey of mammals. Woodrats were captured in Sherman folding aluminum live traps, wire-mesh traps (18 x 4½ x 5 in.), and Victor rat traps. Several woodrats were shot with a 0.22 caliber pistol. Specimens were deposited in The Museum, Texas Tech University. Most specimens were prepared as museum skins and skulls, but some were skulls without skins, complete skeletons without skins, and skulls accompanied by bodies preserved in alcohol. For descriptions and locations of collecting sites and accounts of species, see Genoways et al. (1977). Use of the terms "house," "den," and "nest" follows Finley (1958). A "den" is any large outer shelter enclosing the living area of the occupant; a "house" is a den constructed by the occupant; and a "nest" is a small resting place lined with soft fibrous material.

Ten houses of *Neotoma albigula* and 10 of *N. micropus* were examined. Individuals of *N. mexicana* do not construct houses and were, therefore, excluded from this phase of the study. Only houses from which the resident woodrat had been collected were selected for analysis. House length was measured as greatest length, width at the widest point perpendicular to the length, and height was measured at the highest point. Each house was dismantled. Materials used to construct the house were separated and weighed in a canvas sling suspended from a Chatillon spring-balance (calibrated from 0 to 15 kg). All materials of insufficient combined weight to be measured and all items apparently cached in a house were listed. Length, width, and height of the houses and weight of construction materials were analyzed by a one-way analysis of variance to test for significant differences among or between means (Sokal and Rohlf 1969). When means were significantly different, the

Student–Newman–Keuls (SNK) procedure was used to determine maximal nonsignificant subsets (Sokal and Rohlf 1969).

The vegetation around each house and around 10 den sites of *Neotoma mexicana* was sampled by means of a line-intercept method, modified from the procedure described by Canfield (1941). Using the nest chamber as the midpoint, two 10-m line-intercepts were established. One intercept was oriented north and south by compass and the other was oriented east and west (Fig. 1). A list of all plant species which occurred within the plot formed by connecting the ends of line-intercepts was recorded. From these lists, floral similarity indices were computed for paired comparisons between plots. The indices were computed using the formula for Pirlot's index (Mosimann 1968).

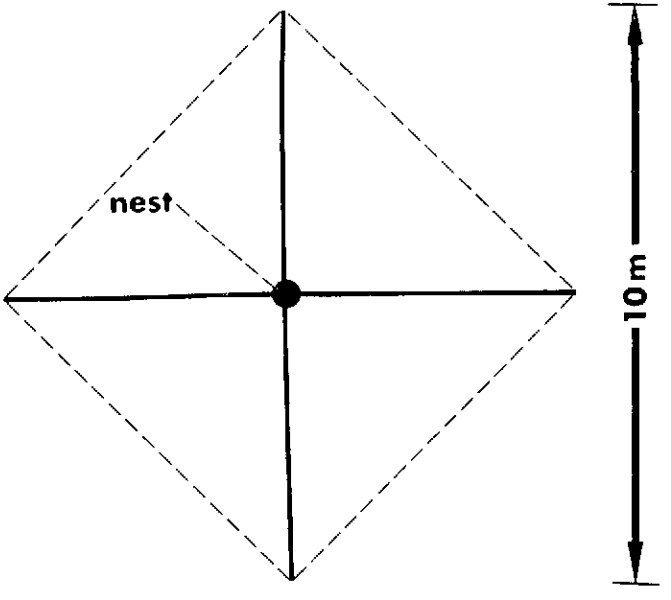



**Fig. 1.** Design for analysis of vegetation around woodrat house or den.

## RESULTS

### Woodrat Distribution

*Neotoma mexicana* probably occurs throughout the Guadalupe Mountains at elevations above 1500 m. Mexican woodrats have been collected at the southeastern base of the mountains in Bell Canyon (Davis and Robert-

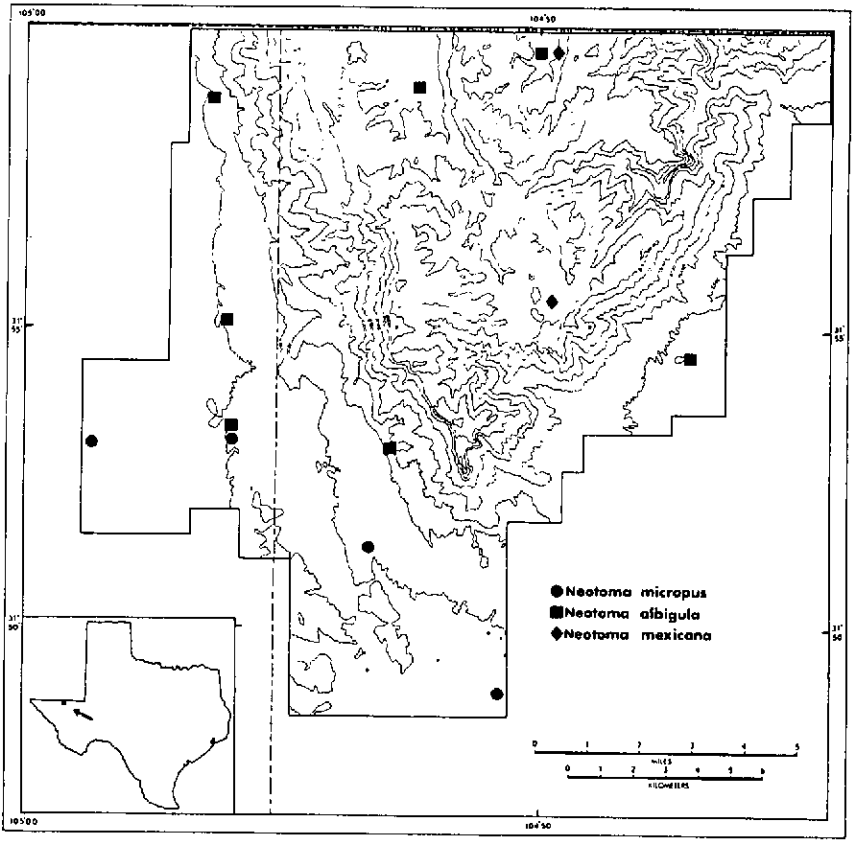



**Fig. 2.** Distribution of woodrats in Guadalupe Mountains National Park, Texas.

son 1944), on the walls and around the perimeter of Upper Dog Canyon, and in The Bowl (Fig. 2).

*Neotoma albigula* (Fig. 3) occurs around the perimeter of the mountains and on the floors of Upper Dog and West Dog Canyons which penetrate the mountain mass. On the west side of the park, the white-throated woodrat is found primarily in or along edges of dry washes extending westward from the mountains.

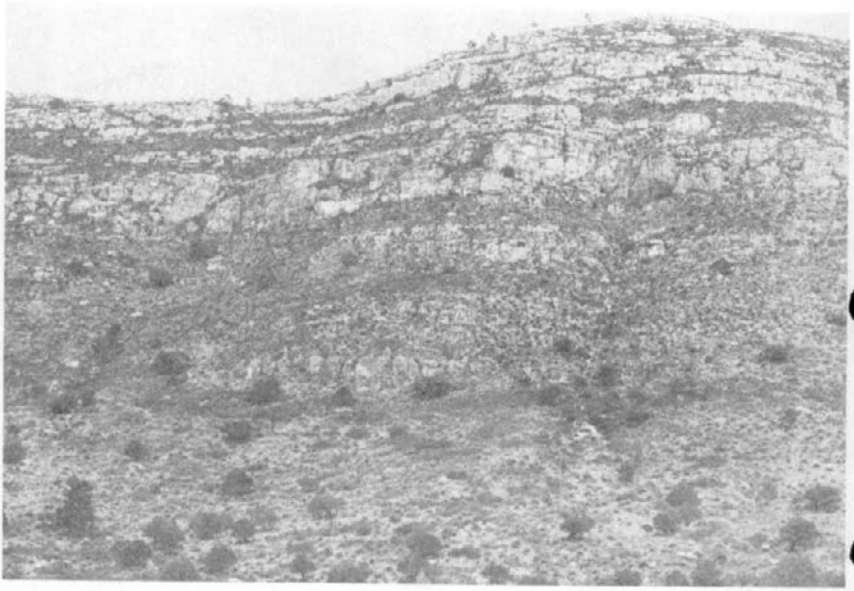
*Neotoma micropus* has been found only in the southern portion of the park. Specimens have been collected near Williams Ranch Road entrance on the southeastern boundary of the park, in a large dry wash which skirts the north edge of the central ridge of the Patterson Hills, and near Lewis Well in the extreme western area of the park.

*Neotoma mexicana* and *N. albigula* are in contact around the perimeter of Upper Dog Canyon. In 1901 Bailey (1905) collected one specimen of *N.*

Fig. 3. Adult female *Neotoma albigula*.

*albigula* in Upper Dog Canyon at 2073 m (6800 ft). He also collected four specimens of *N. mexicana*, three at 2134 m and one at 2377 m. In 1973 both species were captured in a trap line that extended from the canyon floor up the eastern wall. Specimens of *N. albigula* were captured only on the canyon floor and specimens of *N. mexicana* were found from the base of the canyon wall on up the slope (Fig. 4). *N. mexicana* seemed to be the more abundant species. In 1974 no individuals of *N. mexicana* were collected below an elevation of 2000 m, approximately 100 m above the canyon floor. Several specimens of *N. albigula* were collected 30 to 40 m above the canyon floor in 1975, indicating a possible upward shift in the zone of contact between the two species. Gehlbach (pers. comm.) and Scudday (pers. comm.) reported both *N. mexicana* and *N. albigula* in close proximity near Pratt Lodge in McKittrick Canyon in the late 1950s. No woodrats were found during extensive trapping in McKittrick Canyon in 1973 and 1974.

*Neotoma micropus* and *N. albigula* are in contact immediately north of the Patterson Hills (Fig. 5). North of this area only *N. albigula* has been captured and south of the area only *N. micropus* has been collected (Fig. 2). In a wash north of the road which extends due west of Williams Ranch House, several *N. albigula* were collected, but no *N. micropus* were found. In another wash 400 m to the south, one *N. albigula* was collected from a house that was central to several houses from which specimens of *N. micropus* were taken.



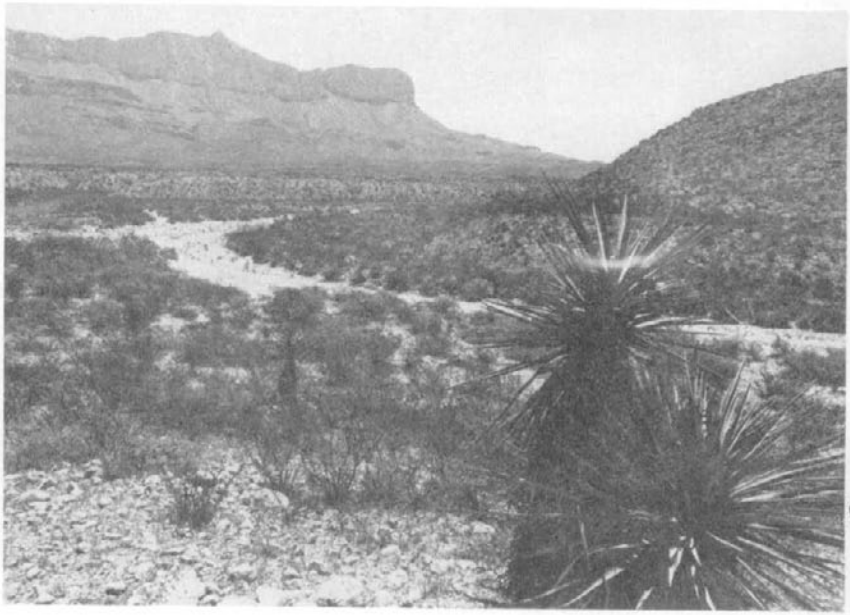


**Fig. 4.** (*Above*) Rock outcrop on the east wall of Upper Dog Canyon inhabited by *Neotoma mexicana*.

**Fig. 5.** (*Below*) Area of contact between *Neotoma albigula* and *Neotoma micropus* immediately north of the Patterson Hills.

**House Sites**

Houses inhabited by *Neotoma albigula* were found in a wide variety of sites. In Upper Dog Canyon a large number of houses had been constructed in association with fallen juniper trees or under living junipers. Houses were observed under red barberry (*Berberis haematocarpa*) and clumps of prickly pear (*Opuntia lindheimeri*) and cholla (*Opuntia imbricata*). Around the perimeter of Upper Dog Canyon and for a short distance up the slope, *N. albigula* occurs in rocks, utilizing rock crevices for shelter and filling the crevices with sticks, cactus, and debris rather than constructing a house. These rock dens resemble den sites of *N. mexicana*, but appear to have much more material, expecially cactus, stuffed into the crevices. In general, houses inhabited by *N. albigula* in Upper Dog occurred throughout the floor of the canyon wherever suitable shelter was available.

In West Dog Canyon *N. albigula* houses appeared to be concentrated in or near the dry wash on the canyon floor. Houses were observed under large shrubs, such as red barberry, along the wash. One house was on the edge of the east bank of the wash with a subterranean entrance in the side of the bank about 0.5 m below the main house. All houses observed in West Dog Canyon were located in very dense, shrubby vegetation.

In the northwest corner of the park, all *N. albigula* houses investigated were situated in large clumps of prickly pear. The cactus clumps were very dense and woodrats had piled cactus joints around the base of the clumps to form houses. This general form of house seems typical for *N. albigula* on the west side of the park. Large clumps of cactus most often occur in or along edges of dry washes on the west side, on slopes of the Patterson Hills, and isolated hills such as the Stage Coach Hills. Large clumps of *Opuntia* are not common on the creosote-bush bajada which dominates the west side of the park. *N. albigula* houses in large clumps of prickly pear were observed around the Williams Ranch House at the west base of the Guadalupe escarpment, at a locality northwest of the Ranch House and in the northwest corner of the park.

Although *Neotoma albigula* houses are predominantly found under large growths of *Opuntia* on the west side of the park, where *N. albigula* was found in close proximity to *N. micropus*, the *N. albigula* house sites were quite different. In this area only one *N. albigula* was collected from a house constructed under a large prickly pear. This house was central to several houses from which specimens of *N. micropus* had been collected. All of these houses were located in the large wash which skirts the north end of the central ridge of the Patterson Hills. In another wash approximately 400 m to the north, several *N. albigula* houses were investigated. Very few cacti are found in this wash and those that do occur are small and scattered. Every active house investigated in this wash was inhabited by an individual *N. albigula*, and all but one were situated under clumps of mesquite (*Prosopis glandulosa*). The remaining house was in a dense growth of *Brickellia laciniata*, a shrubby composite.

On the east side of the park near Nipple Hill, *N. albigula* houses are located predominantly under prickly pear or cholla.

A majority of the houses investigated that were inhabited by *Neotoma micropus* had been constructed under large clumps of prickly pear or cholla. Most sites were on the floor or along edges of dry washes. One *N. micropus* was collected from a house on a mesquite hummock near Lewis Well, and several apparently inactive houses were observed on other mesquite hummocks in this vicinity.

*Neotoma mexicana* inhabits cliffs and rocks and does not construct a house. These woodrats construct nests in rock crevices and may deposit some plant debris and other materials in crevices, but not to the extent that is characteristic of individuals of *N. albigula*. In Upper Dog Canyon *N. mexicana* are found on rocky canyon walls. These woodrats seem to prefer vertical crevices for nest sites, but will utilize deep horizontal crevices with narrow openings.

In The Bowl several Mexican woodrats have been collected in an old log cabin where a nest of shredded paper had been constructed in the far corner of an old bunk. A large number of acorns had been deposited around the nest and an old section of eaves spout was approximately one-third full of acorns. Specimens of *N. mexicana* were collected on a rock outcrop on a slope above an earthen dam in The Bowl. Woodrat signs were observed along rock outcrops near Bush Mountain and above the Blue Ridge campsite. Although no specimens were taken, these areas are probably inhabited by *N. mexicana*.

**House Analyses**

Because *Neotoma albigula* occurs in a variety of habitats within the park, houses from two distinctly different areas were selected for investigation. Five houses of *N. albigula* were examined in Upper Dog Canyon and five were examined near the Crossroads immediately north of the Patterson Hills. Four of the houses examined in Upper Dog Canyon had been constructed in association with large fallen juniper trees in an open woodland (Fig. 6), whereas the fifth house was located under a large, living alligator juniper (*Juniperus deppeana*) and was protected by large red barberry.

Of the *N. albigula* houses investigated near the Crossroads, four were located in a dry wash immediately north of the Crossroads and a fifth was in the large wash which skirts the north edge of the central ridge of the Patterson Hills. Three of these houses had been constructed under spreading, many-stemmed mesquite bushes (Fig. 7), one was in a dense growth of *Brickellia laciniata*, and one was under a large prickly pear.

Ten houses of *Neotoma micropus* were investigated in the large wash which skirts the north edge of the central ridge of the Patterson Hills. Seven of these houses had been constructed under large prickly pears (*Opuntia lindheimeri* and *O. phaecantha*) (Fig. 8), one was under a cholla, and one was under a creosote bush (*Larrea tridentata*).

**Fig. 6.** (*Above*) *Neotoma albigula* house in association with a fallen juniper in Upper Dog Canyon.

**Fig. 7.** (*Below*) *Neotoma albigula* house under mesquite in a dry wash immediately north of the Crossroads.

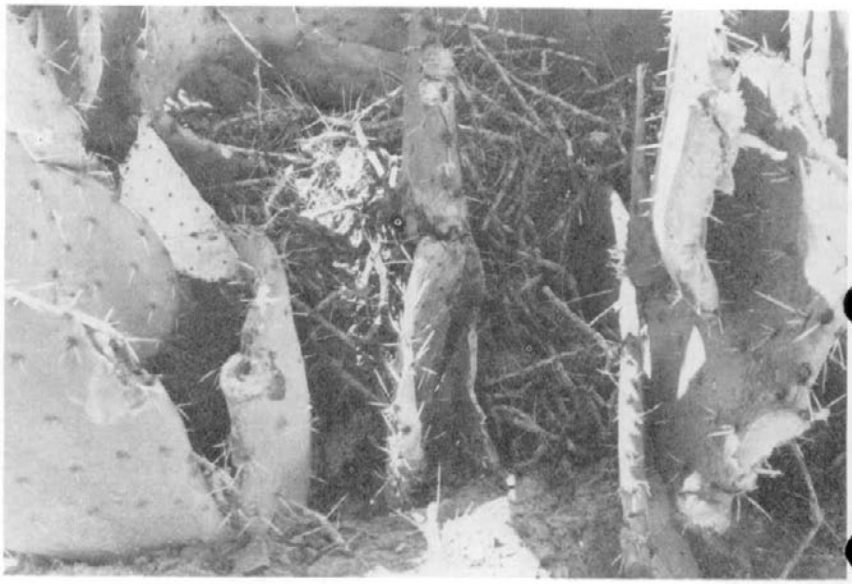


**Fig. 8.** *Neotoma micropus* house under large prickly pear in a large wash which skirts the north edge of the central ridge of the Patterson Hills.

The results of the quantification of house size and weights of materials used in constructing the house are summarized in Table 1. The means are relatively similar except for the mean weights of sticks used in den construction. Analyses of variance (ANOVA) of house length, width, and height, and weights of cholla used in construction revealed no significant differences between or among species or localities. Results of ANOVA of weights of sticks in houses are summarized in Table 2. The ANOVA yielded

TABLE 1. Mean house measurements and mean weights of construction components of woodrat houses in Guadalupe Mountains National Park.

| | *N. albigula* ($n$ = 5) Upper Dog Canyon | | *N. albigula* ($n$ = 5) Crossroads | | *N. micropus* ($n$ = 10) Crossroads | |
|---|---|---|---|---|---|---|
| **Measurements** | **Mean** | **SE** | **Mean** | **SE** | **Mean** | **SE** |
| House length | 158.4 cm | (19.8115) | 106.8 cm | (12.1507) | 133.5 cm | (13.6943) |
| House width | 75.2 cm | (12.9711) | 82.2 cm | (8.1704) | 84.2 cm | (6.4735) |
| House height | 37.7 cm | (6.5019) | 25.9 cm | (1.7493) | 29.15 cm | (3.1056) |
| Sticks | 9.66 kg | (3.1103) | 3.45 kg | (0.5508) | 2.1 kg | (0.5888) |
| Cholla | 0.99 kg | (0.3509) | 0.26 kg | (0.2358) | 1.96 kg | (0.6704) |
| Prickly pear | 0.00 kg | (0.00) | 0.02 kg | (0.0120) | 0.05 kg | (0.0354) |
| Manure | 0.45 kg | (0.1175) | 0.05 kg | (0.0316) | 0.21 kg | (0.1234) |

TABLE 2. Results of analysis of variance (ANOVA) and Student–Newman–Keuls test (SNK) on weights of sticks in houses of *Neotoma micropus* and *Neotoma albigula*. Means are in kilograms.

**ANOVA Table**

| Source | d.f. | MS | F |
|---|---|---|---|
| Among | 2 | 97.7790 | 7.1239** |
| Within | 17 | 13.7255 | |

**SNK Test**

| | | | | Rank | | |
|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 |
| | | | Mean | 2.10 | 3.46 | 9.66 |
| | | | n | 10 | 5 | 5 |
| Rank | | Mean | n | | | |
| 1 | *N. micropus* | 2.10 | 10 | —— | | |
| 2 | *N. albigula*-Crossroads | 3.46 | 5 | 1.36ns | —— | |
| 3 | *N. albigula*-Upper Dog | 9.66 | 5 | 7.56** | 6.20** | —— |

ns = Nonsignificant; ** = $P < 0.01$.

TABLE 3. Materials found in woodrat houses and number of houses in which they were found.

| Materials | *N. albigula* Upper Dog ($n$ = 5) | *N. albigula* Crossroads ($n$ = 5) | *N. micropus* Crossroads ($n$=10) |
|---|---|---|---|
| Sticks | 5 | 5 | 10 |
| Cholla | 5 | 2 | 9 |
| Tasajillo | 0 | 1 | 9 |
| Prickly pear pad | 2 | 2 | 6 |
| Prickly pear fruit | 0 | 0 | 1 |
| Manure | 5 | 4 | 8 |
| Juniper leaves | 3 | 0 | 0 |
| Juniper berries | 2 | 0 | 0 |
| Acorns | 4 | 0 | 0 |
| Barberry leaves | 2 | 0 | 0 |
| Pine needles | 1 | 0 | 0 |
| Pine cones | 1 | 0 | 0 |
| Century plant leaves | 2 | 1 | 0 |
| Mesquite leaves | 0 | 1 | 0 |
| Mesquite pods | 2 | 4 | 6 |
| Bones | 2 | 0 | 0 |
| Ocotillo | 0 | 0 | 2 |
| Yucca pod | 0 | 1 | 1 |
| Feathers | 0 | 1 | 0 |
| Old undershorts | 0 | 1 | 0 |
| Rabbit's foot | 0 | 1 | 0 |

a highly significant F value of 7.1239**. A Student–Newman–Keuls procedure (Table 2) revealed that significantly greater weights of sticks were found in *Neotoma albigula* houses in Upper Dog Canyon than in either *N. albigula* or *N. micropus* houses near the Crossroads. As shown in Table 2, the homogeneous subsets seem to be correlated with locality rather than with species.

The frequency of occurrence of materials accumulated in 20 dismantled houses is presented in Table 3. Note that sticks were found in every house and manure and cactus parts were quite common. Mesquite leaves and pods and tasajillo joints (*Opuntia leptocaulis*) were common in houses near the Crossroads, but absent from houses in Upper Dog Canyon. Juniper parts and acorns were commonly found in houses in Upper Dog Canyon, but were absent in houses from near the Crossroads.

**Vegetation Analyses**

Floral similarity indices were calculated for the paired comparison of vegetation in the immediate vicinity of each house or den to that of each

TABLE 4. Mean floral resemblance indices between and within species and localities.

| Species compared | Mean index | SE |
|---|---|---|
| *N. albigula* / *N. albigula* | 19.9244 | 3.0848 |
| *N. albigula*—Upper Dog Canyon / *N. albigula*—Crossroads | 2.7760 | 0.7900 |
| *N. albigula*—Upper Dog Canyon / *N. albigula*—Upper Dog Canyon | 40.7840 | 3.3505 |
| *N. albigula*—Crossroads / *N. albigula*—Crossroads | 41.9360 | 3.1781 |
| *N. mexicana* / *N. mexicana* | 59.8078 | 1.1697 |
| *N. micropus* / *N. micropus* | 45.9142 | 1.9564 |
| *N. albigula*—Upper Dog Canyon / *N. mexicana* | 12.6594 | 1.4474 |
| *N. albigula*—Upper Dog Canyon / *N. micropus* | 4.0648 | 0.6239 |
| *N. albigula*—Crossroads / *N. mexicana* | 0.7670 | 0.2856 |
| *N. albigula*—Crossroads / *N. micropus* | 38.4232 | 1.5246 |
| *N. mexicana* / *N. micropus* | 1.2034 | 0.2415 |

other house or den. Mean indices between and among species are summarized in Table 4. Note the very low similarity between *Neotoma albigula* plots in Upper Dog and *N. albigula* plots near the Crossroads. This resulted in a mean index among all *N. albigula* plots that was much lower than mean indices among all *N. mexicana* plots and among all *N. micropus* plots. Because of low similarity between *N. albigula* plots in Upper Dog Canyon and *N. albigula* plots near the Crossroads, plots from these two localities were considered separately. The mean similarity index between *N. micropus* plots and *N. albigula* plots near the Crossroads is much higher than the mean index between *N. albigula* plots in Upper Dog Canyon and near the Crossroads.

A modified line-intercept technique was developed to estimate coverages of plant species in the vicinity of a woodrat house, because the floral similarity index does not reflect frequency or coverage of a particular species within a plot, but merely its presence. To standardize the technique, the nest chamber was used as the midpoint of each transect. Traditional vegetation analysis methods are constructed to obtain a random sample; however, the

TABLE 5. Dominant plants on woodrat house or den plots, estimated percent coverages of plant species on the plots, and percent of sampled plots on which the dominants were found.

| Species | % coverage | Frequency (%) |
|---|---|---|
| *Neotoma mexicana* ($n$ = 10) | | |
| *Nolina micrantha* | 11.08 | 80 |
| *Muhlenbergia pauciflora* | 9.595 | 100 |
| *Dasylirion leiophyllum* | 7.985 | 80 |
| *Cercocarpus montanus* | 7.19 | 90 |
| *Quercus undulata* | 3.575 | 80 |
| *Neotoma albigula*—Upper Dog Canyon ($n$ = 5) | | |
| *Stipa tennuissima* | 23.17 | 80 |
| *Bouteloua gracilis* | 3.11 | 80 |
| *Xanthocephalum sarothrae* | 2.86 | 100 |
| *Lycurus phleiodes* | 2.5 | 80 |
| *Muhlenbergia repens* | 1.64 | 60 |
| *Neotoma albigula*—Crossroads ($n$ = 5) | | |
| *Prosopis glandulosa* | 17.32 | 60 |
| *Larrea tridentata* | 8.38 | 80 |
| *Brickellia laciniata* | 6.63 | 60 |
| *Muhlenbergia porteri* | 6.48 | 80 |
| *Setaria leucopila* | 0.79 | 80 |
| *Neotoma micropus* ($n$ = 10) | | |
| *Larrea tridentata* | 17.39 | 100 |
| *Opuntia lindheimeri* | 9.71 | 50 |
| *Prosopis glandulosa* | 9.54 | 50 |
| *Muhlenbergia porteri* | 5.94 | 60 |

method developed for this study was standardized so that each plot would be sampled in the same manner. It should be noted here that the house is not necessarily the center of the resident woodrat's home range. Mean percent coverages of dominant plant species on plots are listed in Table 5. The percent of plots on which the species were found is also listed in Table 5. A plant was considered to be dominant only if it was present in 50% or more of the plots. Note that plots around *N. micropus* houses and those of *N. albigula* near the Crossroads have similar dominants with somewhat different coverages. The presence of *Opuntia lindheimeri* as a dominant on *N. micropus* plots in contrast to the absence of that plant on *N. albigula* plots is significant.

In addition to ground coverage, understory cover and canopy cover were also measured. It is theoretically possible, therefore, to record coverages greater than 100%. These results must be interpreted as estimates of plant coverages in relationship to house or den sites and not as random samples of the vegetation of the area. Plots around houses of *N. albigula* in Upper Dog Canyon and near the Crossroads were considered separately because of their low floral similarity indices.

## DISCUSSION

### Woodrat Distribution

The ranges of *Neotoma mexicana*, *N. albigula*, and *N. micropus* overlap in Texas from the Guadalupe Mountains and Davis Mountains westward (Hall and Kelson 1959). However, geographic range descriptions of *Neotoma* can be misleading, because where two or more species of woodrats occur in the same area, they often establish distinct zones of contact with little or no overlap. The distribution of woodrats in Guadalupe Mountains National Park conforms to this pattern (Fig. 2). Throughout the park the woodrat distribution is best described as microallopatry, with narrow zones and areas of microsympatry. Similar situations have been described in other areas where ranges of two or more species of woodrats overlap (Bailey 1905, 1931; Finley 1958; Cameron 1971; Wright 1973). Reasons for this habitat partitioning are complex and vary depending upon species involved and the nature of the habitat.

Finley (1958) reported that ecological distribution of woodrats is primarily determined by climbing ability, house construction ability, and diet. In addition, water economy probably influences distribution (Lee 1963; Boice and Boice 1968; Boice 1969; Birney and Twomey 1970).

According to Finley (1958), *Neotoma mexicana* is the most agile climber of the woodrats species in Guadalupe Mountains National Park, followed in ability by *N. albigula* and *N. micropus*. Distributional patterns observed in the park correlate with these reported differences in climbing ability, with *N. mexicana* inhabiting steep cliffs and rocky slopes, *N. albigula* occurring from gentler rocky slopes out onto the flats, and *N. micropus* found only on the flats.

House-building activities are apparently correlated with the collecting instinct of woodrats. Finley (1958) reported that *N. albigula* and *N. micropus* exhibit strong collecting instincts and are capable of constructing large houses. The collecting instinct of *N. mexicana* is much weaker relative to that of the other two species, and individuals of this species do not build houses. Where individuals of *N. albigula* lived in rock crevices in Upper Dog Canyon, large amounts of sticks, cactus joints, and other materials have been carried to the den site and were stuffed into crevices. Rock dens of *N. mexicana* in the same area have very little accumulated material.

Food-habit studies (Vorhies and Taylor 1940; Spencer and Spencer 1941; Finley 1958; Wood 1969) suggest that *N. albigula* and *N. micropus* utilize cacti and other succulents to a large extent for food. Finley (1958) reported that *N. mexicana* apparently dislikes cactus.

Interrelationships between desert-dwelling species of woodrats and species of cactus (*Opuntia* spp.) have been well documented (Vorhies and Taylor 1940; Spencer and Spencer 1941; Vorhies 1945; Finley 1958; Lee 1963; Raun 1966; Brown et al. 1972). *Opuntia* spp. are utilized for shelter, food, and water. Woodrats must depend on vegetation as a source of water because they cannot subsist on metabolic water (Schmidt-Nielsen et al. 1948; Schmidt-Nielsen and Schmidt-Nielsen 1952). *Opuntia* is an excellent water source because it has a high water content throughout the year (Lee 1963) and its cell sap has a low osmotic pressure (Korstian 1924).

**House Analyses**

Analyses of representative houses of *Neotoma albigula* and *N. micropus* support preliminary observations that house size and weights of materials used to construct a house are more dependent on availability of materials than on differences in degree of collecting instinct between the two species. Finley (1958) reported that houses of *N. albigula* and *N. micropus* found in similar habitats were indistinguishable. The results of this study substantiate Finley's observation. The significant difference in weights of sticks in *N. albigula* houses in two diverse habitats reflects the opportunistic nature of this species. Differences can probably be attributed to availability of juniper sticks in Upper Dog Canyon where most houses are located in an open juniper woodland.

Although no significant differences were revealed between houses of *Neotoma albigula* and *N. micropus* where the two species are microsympatric, there was a striking difference in house sites. Only one *N. albigula* house was located under a cactus in the zone of contact, whereas 80% of the *N. micropus* houses had been constructed under cactus (*Opuntia* spp.). Olsen (1973) postulated that shelter-site selection is based on the criterion of cover near the ground, and he found no significant response to stem types.

It is notable that, although cholla was present on only two of the five *N. albigula* plots in Upper Dog Canyon, all houses contained cholla joints (Table 3). Although woodrats can drag cholla joints without much trouble,

they have difficulty handling large prickly pear pads. Prickly pear pads are found in greatest numbers in houses which have been constructed at the base of a living prickly pear. Pads found in other houses were always small in size. In areas where tasajillo was present, joints and fruits from this cactus were present in 90% of the houses.

**Vegetation Analyses**

The floral similarity indices computed for this study proved to be useful for preliminary analyses. A low index may indicate that two areas are so dissimilar that no additional analysis is required, but if the index is high, additional statistical techniques may be employed to further analyze the data. An examination of the similarity indices suggested that it would be best to consider the *N. albigula* plots in two different localities separately (Table 4). Vegetation on house plots of *N. albigula* at the Crossroads closely resembled vegetation on house plots of *N. micropus* in the same area, but exhibited little resemblance to plots of *N. albigula* in Upper Dog Canyon. These results are consistent with results of house analyses. With the exception noted above, all indices between species were much lower than indices within species. Although floral similarity does not reflect the frequency or coverage of plant species, it must be noted that the mere presence or absence of a plant species may be more important than its relative abundance.

The modified line–intercept method designed for this study facilitates the description of vegetation in the immediate vicinity of a woodrat house or den. Standardization of the method allows comparison of vegetation surrounding different houses. Use of perpendicular line–intercepts tends to emphasize plants in the center of the plot and, therefore, emphasizes the plant selected for a house site. This bias was designed into the method because the plant chosen for a house site often provides shelter, food, and water and, therefore, may be the most important plant in the life of the resident woodrat. A quadrat method of vegetation analysis was tested during this study, but was not considered to be nearly as satisfactory as the line–intercept method.

**Woodrat Ecology**

Finley (1958) suggested that *Neotoma mexicana* and *N. albigula* are sufficiently divergent ecologically to limit interspecific competition. Vegetation data from this study indicate that these two species are found in quite different habitats in Guadalupe Mountains National Park in spite of the fact that they are in close contact around the perimeter of Upper Dog Canyon. The area of microsympatry generally coincides with an ecotone between the chaparral-like vegetation of the canyon wall and the open canyon woodland of the canyon floor. In the absence of *N. mexicana*, *N. albigula* could probably inhabit much of the area now occupied by *N. mexicana*, with the possible exception of vertical cliffs. *N. mexicana* would not invade the canyon floor to a great extent because of the limited number of rocky den

sites. Finley (1958) reported that an individual *N. mexicana* will occasionally invade an unoccupied *N. albigula* house near a rocky slope, but there is no evidence that Mexican woodrats ever construct a house. The partitioning of habitat in Upper Dog Canyon apparently is influenced strongly by differences in climbing ability, house-building ability, and vegetation requirement or preferences.

There are contrasting reports on the preferred habitat of *Neotoma albigula*. Bailey (1905) never found *N. albigula* away from rocky situations in west Texas and described the species as a cliff dweller. Vorhies and Taylor (1940), on the other hand, found *N. albigula* in almost every habitat type in the Lower Sonoran zone in Arizona. They were common in the Upper Sonoran zone and present in the Transition zone up to 7000 ft with one specimen taken at 8200 ft in the Santa Rita Mountains. Bailey reported that *N. albigula* in west Texas apparently belonged to the Upper Sonoran zone, but extended into the Lower Sonoran along cliffs and rocky gulches. A preliminary examination of *N. albigula* distribution in Guadalupe Mountains National Park would lead to the same conclusion. The key to this paradox is probably the presence of *N. micropus* in west Texas, whereas the distribution of this species does not extend into Arizona.

Finley (1958) could not distinguish between ecological requirements of *Neotoma albigula* and *N. micropus* and concluded that they competed for house sites wherever they came in contact. He thought that the two species could coexist at low population levels with little competition, but that with higher populations, competition could become intense. Wright (1973) concluded that competitive exclusion of *N. micropus* by *N. albigula* may be occurring where the two species coexist in the Mesilla Valley of New Mexico.

*Neotoma albigula* occurs in a variety of habitats in Guadalupe Mountains National Park and appears to have less specific habitat requirements than *N. mexicana* or *N. micropus*. Where *N. albigula* and *N. micropus* are in contact on the west side of the park, *N. albigula* has apparently shifted to a secondary habitat and diet. Diet studies (Vorhies and Taylor 1940; Spencer and Spencer 1941; Finley 1958; Wood 1969) suggest that both *N. albigula* and *N. micropus* utilize cacti to a large extent for food. Field observations durting this study support those suggestions with one significant exception. Cacti were apparently being used for food at every *N. micropus* house investigated as evidenced by an abundance of partially eaten cactus joints and fruits. This same statement can be made for every *N. albigula* house observed except those at the zone of contact with *N. micropus*. Although the mean floral similarity index is relatively high between house plots of the two species in this area, the relative percent coverages are different. There is one important difference—*Opuntia* was present at only one of five *N. albigula* sites examined at the zone of contact. The one plot with *Opuntia* present was located in the midst of several *N. micropus* houses. There was no indication whether the house was constructed by the resident *N. albigula* or whether it had moved into a vacant *N. micropus* house. In contrast to this area of

microsympatry, all other specimens of *N. albigula* collected on the west side of the park were captured near houses constructed under growths of *Opuntia*. Where *N. albigula* and *N. micropus* are in close proximity, *N. albigula* houses were located predominantly under mesquite. This apparent shift in habitat selection must be accompanied by a shift in diet. It appears that *N. albigula* utilizes cactus for food throughout the park except at the zone of contact with *N. micropus* where cactus are almost totally absent from *N. albigula* house sites.

The observations discussed above support the principle of competitive exclusion postulated by Gause (1934). *Neotoma albigula* may be avoiding direct competition with the larger, and possibly more aggressive *N. micropus* by shifting to a secondary habitat and diet. A similar situation has been described with *N. lepida* and *N. fuscipes* in California (Cameron 1971). It is quite possible that behavioral differences exist between *N. albigula* and *N. mexicana* that may be preventing *N. albigula* from invading areas where *N. mexicana* is present.

In summary, the distribution of *Neotoma albigula* in Guadalupe Mountains National Park may be limited more by the presence of the other two species of woodrats than by habitat limitations. The distribution of *N. mexicana* is limited by availability of favorable habitat, and the distribution of *N. micropus* is limited by the presence of *N. albigula* and availability of favorable habitat.

Ecological observations and data from this study are consistent with current systematic interpretations concerning these three species. *Neotoma albigula* and *N. micropus* are considered to be closely allied (Anderson 1969; Finley 1958; Birney 1973). *N. mexicana* is placed in the same subgenus (*Neotoma*) as *N. albigula* and *N. micropus* (Goldman 1910), but is not as closely related to the other two species as they are to each other. *N. micropus* is considered intermediate between *N. floridana* and *N. albigula* (Anderson 1969; Finley 1958; Birney 1973) and hybrids are known between *N. floridana* and *N. micropus* and between *N. micropus* and *N. albigula*. Several woodrats live-trapped in zones of contact during this study were karyotyped, but no evidence of hybridization was found. All three species found in Guadalupe Mountains National Park can be distinguished karyotypically (Baker and Mascarello 1969).

Woodrats comprise an important component of the ecosystem in Guadalupe Mountains National Park. They are among the most abundant mammalian species in the park and their role is complex. The following vertebrates that occur in the park have been reported to prey upon woodrats: snakes, hawks, owls, roadrunner, skunks, badger, gray fox, ringtail, coyote, and bobcat (Bailey 1931; Vorhies and Taylor 1940; Linsdale and Tevis 1951; Raun 1966). Vorhies and Taylor (1940) and Spencer and Spencer (1941) concluded that woodrats consume only small amounts of grass material. Woodrats often have been blamed for the spread of cactus, but there is no evidence to support this accusation. To the contrary, a cactus plant selected

as a site for a woodrat house is apparently harmed by debris collected by the rat (Vorhies and Taylor 1940). Spencer and Spencer (1941) reported woodrats tend to restrict the spread of cholla. My field observations do not suggest that cactus populations are being harmed to any great extent by woodrat activity. Woodrats are an important food source for carnivores in Guadalupe Mountains National Park. They apparently have a minimal effect on the flora of the park and do not pose a serious threat to the food resources of other animals.

**Woodrats as Biological Indicators**

One of the primary objectives of this study was to determine the feasibility of using woodrats as biological indicators. Populations of woodrats reflect changes in the vegetation with which they are associated. Numbers of *Neotoma albigula* tend to increase as the result of overgrazing (Vorhies and Taylor 1940). Heavy grazing may promote growth of *Opuntia* and mesquite by reducing competition from grasses and by reducing frequency of fires by limiting the amount of fuel. Increases in *Opuntia* and mesquite would provide more woodrat shelter sites. Because *N. micropus* prefers similar shelter sites, a similar response to overgrazing would be expected. The decrease in grazing pressure that accompanied the creation of Guadalupe Mountains National Park may result in a decrease in numbers of *N. albigula* and *N. micropus*.

Raun (1966) reported that a large-scale die-off of prickly pear was accompanied by disappearance of a *Neotoma micropus* population which used cactus for shelter. Loss of vigor and rotting of cactus apparently were caused by 4 years of abnormally high rainfall. Wright (1973) postulates that range extension by *N. albigula* at the expense of *N. micropus* in the Mesilla Valley of New Mexico is in response to successional changes in vegetational composition as a result of human activity. Vorhies and Taylor (1940) refer to *N. albigula* as an "animal weed."

It would be feasible to utilize woodrats as a biological indicator in Guadalupe Mountains National Park. Shifts in the zones of contact between species could be detected easily and would indicate a change in habitat conditions favoring one species over the other. A continued warming trend over a number of years could result in the reduction of *Neotoma mexicana* habitat on the walls of Upper Dog Canyon. This would facilitate the invasion of *N. albigula*. The increase in the quality and quantity of grassland in the park should result in reduced abundance of cacti and, therefore, reduced numbers of *N. micropus* and *N. albigula*. The grassy meadows in Upper Dog Canyon are fragile. Increased human use in this area will probably damage the grassland and result in increased numbers of cacti and, consequently, increased numbers of *N. albigula*. Range extensions and increased numbers of *N. albigula* may indicate general habitat degradation in the park. This may be caused by human impact, climatic changes, or may be a result of wildlife activity. Species of cactus are severely harmed by fire (Dwyer and

Pieper 1967; Wright 1972; Heirman and Wright 1973), thus an increase in frequency of fire, whether natural or by prescription burning, would reduce the populations of *N. micropus* and *N. albigula*.

Although it is evident that woodrats could be useful biological indicators, a combination of monitoring systems would be desirable to detect habitat changes and assess human impact. The monitoring of changes in the vegetation should be of highest priority. Our knowledge of effects of vegetational changes on mammalian populations is limited and this information is necessary in order to make meaningful resource management decisions. Once we know how changes in vegetation are reflected in mammal populations, the distribution and abundance of mammalian species can be predicted from vegetational analyses. The small mammal populations should be periodically monitored, and vegetational changes should be correlated with changes in small mammal demography. To implement such a program, a system of environmental impact monitoring could be designed to include a series of permanent grids for monitoring small mammal populations combined with a plan for monitoring the vegetation on each grid. Data resulting from periodic utilization of this system would be invaluable in assessing human impact, ramifications of changing climatic conditions, and responses to prescribed burning.

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# *Status of the Guadalupe Mountain Vole,* Microtus mexicanus guadalupensis

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Ecologists in recent years have been involved increasingly in programs attempting to define and assemble management programs for areas of human impact on environments that contain esthetically pleasing associations of plants, animals, and physiography. Preservation of ecosystems in their natural state generally becomes more difficult with increasing human activity. These efforts have been concerned largely with the biotic components that are most visible to the human visitor—the plants and the larger diurnal animals. For the most part, the smaller and nocturnal animals have been ignored in these environmental management plans. This trend is being reversed and ecologists and resource management specialists should be encouraged to include all biotic components in their management decisions. All biotic components should be recognized as a resource in their own right.

One group of organisms that frequently are overlooked in this regard are the rodents. These small, secretive, and relatively unknown mammals seldom enter into consideration when resource management plans are drafted. This viewpoint is perhaps justified in some cases, when the affected populations are large or widespread locally and, therefore, are not subject to total elimination from the environment by increasing human activity. However, when populations of any organism are few in number or limited geographically, special consideration needs to be given to preservation of their habitat to prevent loss of what may be unique genetic, physiological, or environmental associations.

The Guadalupe Mountain vole, *Microtus mexicanus guadalupensis*, may constitute one such rodent. It occurs typically in small, frequently isolated populations and, in some portions of its range (specifically that which includes the Guadalupe Mountains National Park) may be threatened by increasing human activity.

The Guadalupe Mountain vole is an inhabitant of the Transition Zone of the scattered mountains of central New Mexico. Here it is found in the dry bunchgrass meadows between stands of yellow pine and fir, generally above

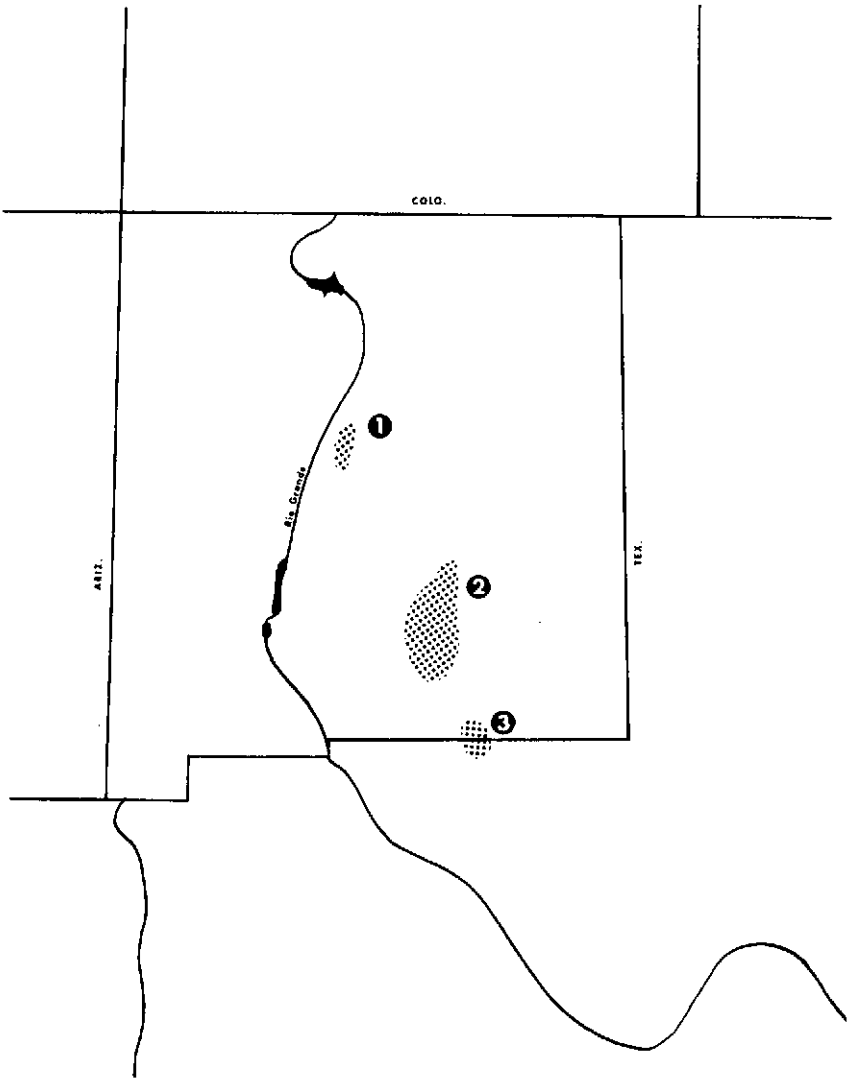


**Fig. 1.** Geographic range of the Guadalupe Mountain vole, *Microtus mexicanus guadalupensis*. The vole inhabits portions of the (1) Manzano; (2) Capitan–Sacramento; and (3) the Guadalupe Mountain ranges of New Mexico.

2000 m but occasionally somewhat lower on northern exposures and in protected canyons. It is more tolerant of xeric conditions than other species of microtines inhabitating this area (Findley and Jones 1962), and may be found at considerable distances from any permanent water source.

The majority of the mammal distribution patterns in the southwestern United States may be explained as a result of an oscillating series of boreal expansions and contractions in the late Pleistocene (Findley 1969). These historical events have left populations of boreal mammals, including the Guadalupe Mountain vole, isolated on the scattered mountain ranges of the area, where they inhabit the remnants of the boreal forest at the higher elevations. Because many of the mountain masses involved are rather small in total area, the boreal habitats are correspondingly small. Thus, because of this restricted habitat, the relict populations of boreal mammals also are frequently rather small, both in distributional area and in total numbers. The scattered nature of these southwestern mountain ranges makes it quite unlikely that recolonization of areas from which these boreal relicts might be extirpated would ever occur (Brown 1971). The effects of man's activities on these small, isolated populations and their habitat are therefore of concern if we are to preserve these associations for future generations.

The geographic range of the Guadalupe Mountain vole encompasses the Manzano, Capitan, Sacramento, and Guadalupe mountain ranges (Fig. 1), and is separated from the other subspecies of Mexican voles by the Rio Grande Valley. These mountain ranges are rather restricted in area, and except for the Capitans and Sacramentos, are separated by areas of arid habitat unsuitable for microtines.

Habitat suitable for the voles is not, of course, uniform within these mountain ranges, but is located primarily along natural drainage areas. This results in a pattern of more or less isolated populations of the vole within each mountain range, many of which are small in size, and in the Guadalupe Mountain vole being listed in the "status undetermined" category of the "Threatened Wildlife of the United States" published by the U.S. Department of the Interior. The occurrence of the Guadalupe Mountain vole at scattered localities within the Guadalupe Mountains National Park is therefore of interest not only because the vole constitutes a part of the present fauna but because its continued existence within the park may be questionable.

Within the park itself, the vole is apparently limited by the presence of bunchgrass meadows of creeping muhly (*Muhlenbergia repens*), needlegrass (*Stipa tenuissima*), and blue grama (*Bouteloua gracilis*). Suitable areas of these grasses are scattered over the park, primarily in some of the steeper canyons and on north-facing slopes. Populations of the Guadalupe Mountain vole have been found in Upper Dog Canyon, Lost Peak, The Bowl, Guadalupe Peak, and near Bush Mountain (Fig. 2). Interpretation of high altitude photographs of the park and field work of others have suggested that suitable habitats may also be found in other areas indicated in Fig. 2. These areas, which total approximately 650 acres, comprise less than 1% of the total park area. Although these areas of extensive grass cover constitute the primary habitat for the voles, individuals have been trapped in

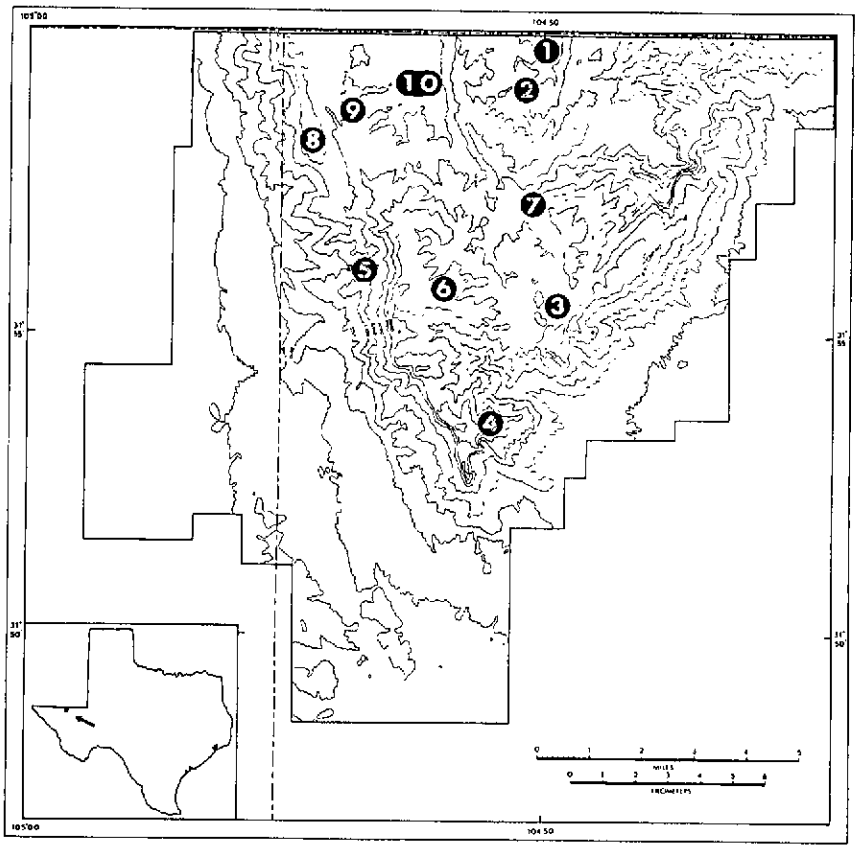


**Fig. 2.** Verified and possible populations of the Mexican vole, *Microtus mexicanus guadalupensis*, in Guadalupe Mountains National Park. Verified populations are located at: (1) Upper Dog Canyon; (2) Lost Peak; (3) The Bowl; (4) Guadalupe Peak Campground; and (5) Bush Mountain. Possible habitat for the vole exists at (6), a stand of scattered aspen midway between The Bowl and Bush Mountain; (7) Upper McKittrick Canyon; (8) PX Flat; (9) The Cox Tank area; and (10) West Dog Canyon.

Upper Dog Canyon on steep hillsides where there was a minimum of grass cover and on rocky hillsides dominated by agave (*Agave lecheguilla*), beargrass (*Nolina micrantha*), and sotol (*Dasylirion leiophyllum*) with scattered bunchgrasses. In both cases however, extensive areas of grass were no more than 100 m away and these individuals were probably forced to these less desirable habitats by relatively high population densities in the more favorable habitat.

Previous studies have indicated that the Guadalupe Mountain vole may be found on the dry ridgetops, beneath shinnery oak where little grass cover

was present (Bailey 1905, 1931). However, a somewhat more recent survey found voles only in grassy areas of the park (Davis 1940). An extensive survey of small mammals within Guadalupe Mountains National Park carried out during 1973–74 indicates that while the Guadalupe Mountain vole may be found in these dry, seemingly atypical microtine habitats, the meadow areas of the park support the bulk of the vole populations. These grassy areas apparently provide the primary refuges and in times of excessive population density, voles are capable of surviving for some time in the more xeric and unprotected habitats on hillsides and ridgetops.

Because meadows or grassy areas are necessary for these voles, and because the same types of areas are ideal for campsites, picnics, and other human activity, a source of conflict is possible. In view of the rather fragile nature of the grasslands in the park, location of campsites or other high to moderate use areas within, or in proximity to, meadows could easily result in habitat degradation and consequent loss of valuable vole habitat. Over the northern portion of its range, the Guadalupe Mountain vole is found in more extensive habitat and is perhaps better able to withstand moderate amounts of temporary habitat loss. In the Guadalupe Mountains, however, any moderate loss of habitat, temporary or permanent, could put the vole in serious danger of being lost forever as a member of the park's fauna.

The verified populations of the vole are not large. Although I have no population data to substantiate this statement, 2 years of field experience with the vole gives the impression that the density is maintained normally at a low level compared to other microtines. Trap-night data comparing the Guadalupe Mountain populations with populations to the north indicate that the densities in the park are only about one-half of those to the north. In addition, replacement of individuals lost to the population is slow. Because the extinction rate varies inversely with the population size (Brown 1971), this characteristic low density in habitats of restricted area makes these voles very susceptible to extinction of local populations.

Recruitment of individuals to replace those lost to a population is largely a function of the reproductive strategy of the species. The small litter size of the Mexican vole has been pointed out by other investigators (Brown 1968; Choate and Jones 1970). Typical litters range from one to five young, with a mean of about 2.3. These small litters, however, are borne continuously throughout the year. This strategy is typical of a species operating near the carrying capacity of the environment. The low litter size requires only a minimal expenditure of energy for reproduction, with the reproductive stress distributed uniformly over the year. Because bearing and rearing of young constitutes a risk for the parent involved, this reproductive strategy probably represents a physiological adaptation to communities with intense intraspecies competition. Although this reproductive strategy may be well suited for the replacement of individuals lost to the population from the normal causes of mortality in a stable environment (such as the tropics), it is

less than adequate to rebuild rapidly populations that have suffered catastrophic losses. We evidently are dealing with a small mammal that has the reproductive strategy of a tropical montane rodent, but is living in a temperate montane habitat. Any large-scale population decrease caused by habitat loss may constitute a deficit from which the vole may never recover. For this reason, special consideration needs to be given to preservation of the few natural meadow areas of the park which provide the primary habitat for this small mammal.

In this regard, the effects of fire on these natural areas of grassland is cause for concern. Any large-scale shift of faunal components of these meadows due to fire could place the Guadalupe Mountain vole in jeopardy. On the other hand, fire could conceivably enhance these habitats for the vole by shifting the faunal composition. Until our knowledge of the fire ecology of the meadow areas of the park allows prediction of the effects of fire on the floral components, particularly those plant species which most directly affect the Guadalupe Mountain vole, burning of these grasslands should be viewed with pessimism.

Another factor to be considered in this regard is the effect of the amount of litter on the soil surface. There are some indications that colonization of burned habitat by voles is dependent upon the accumulation of a certain minimal quantity of litter (Cook 1959). This may mean that burned vole habitat could not successfully be recolonized for at least a year, or until at least one season's growth of vegetation had been converted into litter. Absence of this concealing litter would subject any voles that survived the fire to rather high predation losses, and in view of the low density and low reproductive value of the vole, would constitute a high probability of extinction of that particular population. The effects of fire on the habitats favorable to the vole would seem to be of considerable importance to the proper management of the species within the Guadalupe Mountains National Park, and certainly merits further study.

## SUMMARY

Assessment of the status of the Guadalupe Mountain vole within the park must take into consideration three factors—(1) the pattern of distribution (i.e., small isolated populations); (2) the low density that seems to be characteristic of the subspecies; and (3) the low litter size. Any factors impinging upon the voles or their habitat must be evaluated with these three factors in mind.

The two problems that seem to be most important to the future of the Guadalupe Mountain vole are: (1) human impact on the grasslands inhabited by the vole (e.g., campsite locations, visitor traffic, hiking trails); and (2) the effects of fire on the preferred meadow habitats.

Although the future of the Guadalupe Mountain vole within the park cannot be taken for granted, proper management procedures can maximize

the chances that it will remain as a part of the unique fauna of the Guadalupe Mountains National Park.

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# *Food Habits of Mule Deer on Foothills of Carlsbad Caverns National Park*

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The mule deer (*Odocoileus hemionus*) has been the major forage consumer on Carlsbad Caverns National Park since livestock use ended in the 1940s. Warnings of range overuse by deer in the early 1960s raised numerous questions about deer–range relationships. Many of these questions could be answered only after the diet of the park deer was established.

No studies of deer food habits had been conducted in the park. Data on areas comparable to the higher mountainous portion of the park were available from Anderson et al. (1965). However, similar information useful in establishing the diet of deer on the lower foothills was meager. Therefore, this study of deer diet on the park foothills was initiated in 1967 as a major research project.

Data collection ended in 1971. Circumstances precluded final analysis and report preparation before this senior author retired from his position of Research Biologist and Evans terminated as Biological Technician, in early 1973.

## STUDY AREA

The area covered by this study is the east end of Carlsbad Caverns National Park and adjacent area shown in Fig. 1. It included about 6900 ha (17,000 acres) over two-thirds of which is in the park.

Most of the park area is part of the limestone reef which forms the Guadalupe Mountains. The reef slopes gradually upward to the southwest and is dissected by the relatively shallow Walnut Canyon and deep Rattlesnake Canyon which drain to the east. Canyon sides are often very steep.

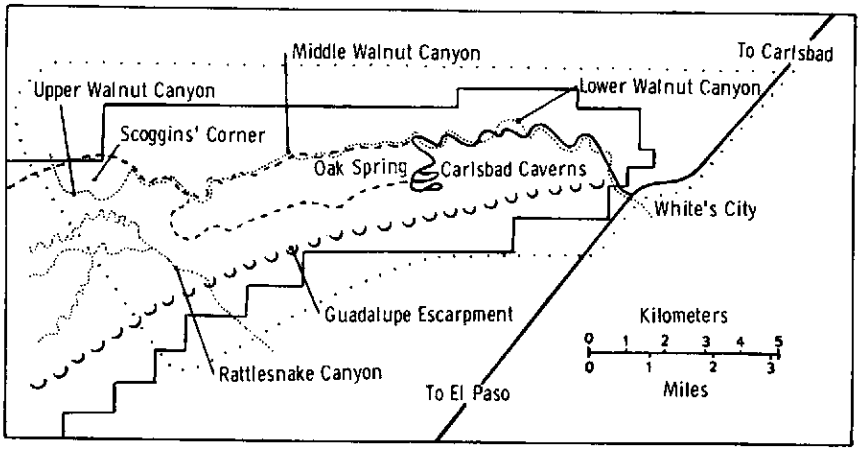


**Fig. 1.** Study area for deer food habits research, Carlsbad Caverns National Park. Heavy solid represents surfaced roads, dashed line represents unsurfaced roads, and the widely spaced dotted line represents the boundary of the study area.

Elevations of the area range from 1070 m (3500 ft) on the plain below the escarpment to 1520 m (5000 ft) on the upper ridges. The fine textured soils derived from limestone are generally shallow, seldom more than 15 cm deep on south facing slopes and ridges. Greatest soil depths are on canyon bottoms and on the low plains.

Climate is semi-arid continental with 78% of the annual rainfall (36 cm or 14 in.) at the Caverns Station falling from May through October. Droughts are common. Recorded annual extremes have been 11 cm in 1951 and 110 cm in 1941.

Forage growth is mostly in early response to precipitation; shallow soils mixed with rocks and gravel result in low moisture retention. Precipitation records suggest that the 1966 growing season was generally good, perhaps a significant factor in the supply of cholla fruit (*Opuntia imbricata*) during the 1967–68 period. Forage growth was limited severely in 1967 by a drought which began in October 1966 and extended through October 1967, with precipitation normal or above only in June. Precipitation the following winter and summer was generally above normal except for June 1968. The 1968 growth of forage, including cholla fruit, was good with forbs abundant in late summer. Precipitation in 1969 was almost consistently below normal until October. Growth of shrubs and production of cholla fruit were poor although there was a good crop of catclaw mimosa (*Mimosa biuncifera*) and redberry juniper fruits (*Juniperus pinchotii*) late in the season.

Above-normal precipitation in the 1969–70 winter promoted spring growth, but 1970 spring and early summer moisture was down, and production of cholla fruit and other browse was only fair. Late summer pre-

cipitation promoted a good supply of forbs. Heavy hail in early October 1970 nearly eliminated succulent forage on the western side of the study area. Consistently below normal precipitation from November until late July 1971 caused severe drought in which shrubs suffered dieback (perhaps associated with subzero temperatures in January). A definite shortage of succulent forage prevailed in spring and early summer 1971, and forbs and half-shrubs produced only limited forage in late summer.

A shrub–succulent community occupies the ridgetops. Dominant plants are sotol (*Dasylirion leiophyllum*), lechuguilla (*Agave lecheguilla*), oak (*Quercus* spp.), and redberry juniper. These are joined by shaggy mountain mahogany (*Cercocarpus breviflorus*), catclaw mimosa, and skeleton goldeneye (*Viguiera stenoloba*) on the west, and ocotillo (*Fouquieria splendens*), prickly pear (*Opuntia* spp.), and Wright aloysia (*Aloysia wrightii*) on the east (Glass and Reisch 1972). Common grasses are three-awns (*Aristida* spp.), curlyleaf muhly (*Muhlenbergia setifolia*), gramas (*Bouteloua* spp.), and slim tridens (*Tridens muticus*).

The canyon walls are characterized by desert myrtlecroton (*Bernardia obovata*), oak, mountain mahogany, and various daleas (*Dalea* spp.). The canyon bottoms support a shortgrass–shrub community. Sotol, redberry juniper, lechuguilla, and cholla are common. Prickly pear, aloysia, and mariola parthenium (*Parthenium incanum*) enter the composition in the lower regions. Mescat acacia (*Acacia constricta*) dominates the gravelly sites. Creosote bush (*Larrea divaricata*) controls on the low, gravelly plains. Grasses at the low evaluations are black grama (*Bouteloua eriopoda*), hairy tridens (*Tridens pilosus*), fluffgrass (*Tridens pulchellus*) and three-awns.

Deer were the only ungulates on the park range during the study. Cattle, sheep, and deer used the adjacent area. The deer population on the park foothills reached a relatively high level in 1966–67, dropped sharply by the next year, then gradually built to a moderately high level in 1970–71 before dropping again.

## METHODS

The greatest amount of data came from direct observation of feeding deer, mostly in the morning but occasionally in the evening, between June 1967 and December 1970. Most of these observations were along the main road between White's City and the Caverns Visitor Center, service roads in the vicinity of the park headquarters, and along the ridge road and canyon road that extend west to the head of Walnut Canyon. The usual procedure was to drive a car and watch for a feeding deer. After stopping the car, one observer would watch the deer's mouth with field glasses to try to establish the exact feeding site. The other observer would use a stop watch to record time, and he would watch for landmarks by which to direct his partner to the feeding site. It was important that the man without field glasses keep his position in the automobile so he could maintain a sighting and direct his partner to the

site after the deer had ceased feeding, or the men had reached observational limits. An observation was recorded only when browsing evidence was found on close examination. (This precluded erroneous observations possible when plants were close together, but it also caused us to discard some observations of forbs eaten in entirety.) Plant parts eaten and feeding time to the nearest tenth of a minute were recorded for each taxon. If field identification was not possible, a plant sample was taken for later identification.

A separate entry was made for each continuous feeding (without a break of a tenth of a minute). Each feeding was termed an "observation" which in most cases was on one plant, if a shrub or large forb. But, if feeding was on small forbs, grass, or shrub clones, observation referred only to a continuous feeding on the taxon involved. A maximum feeding time of 7 minutes was established for record of individual observations.

The original plan was to collect 50 paunches from deer killed in the park between November 1967 and April 1968. However, due to litigation, collection was terminated in December 1967 after 15 paunches were collected. Those deer were taken on representative portions of the entire study area, six in November and nine in December.

Paunches also were salvaged from deer killed by automobiles in and near the park between June 1967 and December 1971. Of the 24 paunches collected by this method, 21 were from deer killed in the park on the main road between White's City and the Caverns Visitor Center, and 3 were from deer killed along U.S. Highway 62–180 extending along the base of the hills near White's City.

In addition, paunches were collected from deer killed by hunters on lands adjacent to the park. Nineteen usable paunches were obtained between 1967 and 1970. Of these, 18 were near the "Scoggins' Corner" area at the upper limit of the study area, and 1 from the base of the escarpment near the mouth of Rattlesnake Springs Canyon at the lower limit of the study area. All 19 of these deer were taken in November (New Mexico deer hunting season) during the 4-year period. The New Mexico Game and Fish Department approved taking of paunches from all deer killed by automobiles and those killed by hunters outside the park.

The routine procedure for taking the paunch sample was to knead the paunch, then slit open the rumen and hand pick the sample to be representative of the rumen contents. Early in the study two quarts of the material were saved, but later the material was squeezed by hand to eliminate liquid and only one quart was saved. In a few cases the rumen contained insufficient material so it was supplemented from the reticulum. As soon as possible, the sample was taken to the laboratory and washed over a fine screen before preservation in formalin.

All paunches were analyzed by the point-analysis method (Chamrad and Box 1964). However, we followed two changes in procedure from the ori-

ginal method. The paunch material was washed on 6- and 3-mm screens. Material too coarse to pass the 6-mm screen was chopped by hand so that finally it all passed that screen (A. D. Chamrad, pers. comm. 1968). The sample used for analysis was taken from the material retained by the 3-mm screen. It was washed into a pan and thoroughly mixed before water was drawn off, leaving the plant parts barely suspended (Chamrad 1966). One hundred points, termed "hits," were read for each paunch sample.

Only limited effort was given to tracking deer in snow for feeding record. Tracks were followed and "read" for feeding stops. For most tracking, records were made for each plant fed on—an "instance"—and for estimated volume of forage utilized on that plant. An estimated volume unit (EVU) was arbitrarily established as equivalent of one fruit of cholla or three twigs of skeleton goldeneye. The rare occurrence of snowcover, the extreme difficulty for human foot travel over the hidden rocks and between the armed plants, and reduced activity of deer all presented problems in this method. Samples obtained between March 1969 and Janury 1971 were of variable size—from 25 to 100 EVU's and from 25 to 100 instances—due to experimentation and to limits of data on some tracking sites. All were near roads between White's City and the head of Walnut Canyon.

Data were analyzed by sectors within the study area when possible, and by season of the year. Two seasons were recognized: growing season (GS) and nongrowing season (NGS). The GS was arbitrarily established as May through October. Since almost 80% of the average annual precipitation falls during these 6 months and most of the forage growth occurs then, this was a logical unit for consideration of forage availability. The NGS, from November through April, is generally too cold and often too dry for any appreciable forage growth.

Data were additionally analyzed with regard to available forage, as judged from field observations during the several seasons and from rainfall records at the park. The bulk of forage consumed during the NGS is from the previous GS. (Cholla fruits though may persist from a year before.) The 1968 and 1970 GS's were rated good; thus the 1968–69 and 1970–71 NGS's were good. The 1967, 1969, and 1971 GS's were rated poor; thus the 1967–68, 1969–70, and 1971–72 NGS's were poor.

One paunch, from 19 September 1971, was assigned to good GS because forbs were rather abundant then in the area of the auto kill, and the deer paunch analysis yielded 74 hits on forbs and only 22 on shrubs. (This deviation from using a 1971 paunch in the poor GS category did not conflict with treatment of observed feeding data because there were no observations after June 1971.) Another paunch, from an auto kill at White's City, was deleted from treatment because 61 of the 100 hits were on Chinese elm (*Ulmus pumila*), belvedere (*Kochia scoparia*), and poplar (*Populus* sp.), presumed to be from the town area.

For two snow-tracking sites where only feeding instances were recorded,

EVU's were calculated by use of EVU:instance ratios on other sites.

The senior author directed the study and participated in all phases. Cooke jointly participated in collecting deer paunches and in feeding observations until August 1968, and he also analyzed most of the 1967 and 1968 paunches. Evans resolved many of the plant identification problems with assistance from Dr. Barton Warnock of Sul Ross State University, and Evans and Richard Young, recently at the University of New Mexico in Albuquerque, participated in tabulation and initial analysis of data.

Plant nomenclature follows Correll and Johnston (1970).

All of the foregoing research was done while the authors were employees of the National Park Service. Final analysis of data and preparation of this report were a contributed effort by Kittams and Evans; National Park Service support for some costs encountered is acknowledged.

## RESULTS AND DISCUSSION

Data for establishing the diet of deer on the foothills came from 1083.3 min. during 664 observations of deer feeding, from paunches of 57 deer, and from evidence of deer feeding during snow cover with volume of forage estimated and instances counted. A total of 102 taxa were recognized as being eaten by deer.

### Growing Seasons

All data for the growing seasons are presented in Table 1. Most (95%) of the observed feeding time during good GS's was in 1968, which was consistently good and thus should enhance representation of good forage seasons. Likewise, 86% of the observed feeding in poor GS's was during 1967, late in an extended severe drought, and should give a reliable measure of poor GS's. Taxa eaten by deer during growing seasons were 36 shrubs, 31 forbs, and 3 grasses.

Observed feeding shows a greater relative use of shrubs during poor GS's and more use of forbs during good GS's. The numbers of shrub taxa represented in the two types of season were nearly the same, although there were considerably more data for poor GS's. Several taxa were represented in only one category. In good GS's, Roemer acacia (*Acacia roemeriana*) leaves with some stems and fruits, and sotol stalks which are produced with good moisture, led in observed feeding time and number of observations. Silver dalea (*Dalea argyraea*) leaves with some stems, catclaw mimosa leaves with some fruit and stems, and mountain mahogany contributed. In poor GS's, Roemer acacia leaves with some stems dominated among taxa taken in feeding time and in observations. Catclaw mimosa was important, and lechuguilla stalks and redberry juniper fruits with leaves and stems contributed. It seems curious that lechuguilla stalks, regarded as a choice food, were more important in poor GS's. The lower relative showing of redberry

TABLE 1. Records of deer feeding on foothills, Carlsbad Caverns area during growing seasons 1967–71. All table entries are on a percentage basis.

| | Observations of deer feeding in good and poor growing seasons | | | | Analyses of deer paunches in good and poor growing seasons | | | |
|---|---|---|---|---|---|---|---|---|
| | Good | | Poor | | 3 paunches from good | | 12 paunches from poor | |
| Food Item | 222.5 Minutes | 158 Observations | 399.2 Minutes | 225 Observations | 300 hits | Frequency in 3 deer | 1200 hits | Frequency in 12 deer |
| | | | Shrubs | | | | | |
| *Acacia angustissima* | | | | | | | 1 | 17 |
| *Acacia constricta* | T | 1 | 1 | 3 | 6 | 33 | 2 | 50 |
| *Acacia roemeriana* | 23 | 20 | 39 | 34 | 36 | 100 | 30 | 83 |
| *Agave lecheguilla* | 2 | 2 | 7 | 3 | 1 | 67 | 6 | 33 |
| *Aloysia wrightii* | | | T | T | | | | |
| *Atriplex canescens* | 1 | 1 | 1 | T | | | | |
| *Bernardia obovata* | 3 | 4 | 1 | 2 | | | | |
| *Brickellia californica* | T | 1 | T | T | | | | |
| *Celtis reticulata* | | | | | | | 3 | 33 |
| *Cercocarpus breviflorus* | 7 | 6 | | | | | | |
| *Chilopsis linearis* | 1 | 1 | | | | | | |
| *Cissus incisa* | | | | | | | T | 17 |
| *Clematis drummondii* | | | | | 2 | 33 | | |
| *Dalea argyraea* | 8 | 9 | 3 | 7 | | | 4 | 50 |
| *Dalea formosa* | 2 | 3 | 2 | 4 | 2 | 67 | 1 | 25 |
| *Dasylirion leiophyllum* | 20 | 9 | T | T | | | | |
| *Echinocereus stramineus* | | | | | 3 | 33 | | |
| *Fallugia paradoxa* | 2 | 3 | 1 | 1 | | | 8 | 67 |
| *Fendlera rupicola* | | | | | | | T | 8 |
| *Fouquieria splendens* | T | 1 | T | T | | | | |
| *Gymnosperma glutinosum* | | | | | | | 1 | 17 |
| *Juglans microcarpa* | 1 | 1 | 4 | 3 | | | 5 | 58 |
| *Juniperus pinchotii* | T | 1 | 7 | 7 | | | 3 | 67 |
| *Mimosa biuncifera* | 8 | 9 | 18 | 12 | | | 3 | 50 |
| *Mimosa borealis* | T | 1 | | | | | | |
| *Opuntia* spp. | T | 1 | 3 | 1 | 16 | 33 | 2 | 16 |
| *Opuntia imbricata* | | | 2 | 2 | | | 2 | 17 |
| *Parthenium incanum* | 3 | 1 | T | T | 1 | 33 | T | 8 |
| *Prosopis glandulosa* | | | 1 | 1 | | | T | 8 |
| *Ptelea trifoliata* | | | T | 1 | | | | |
| *Quercus* spp. | | | | | 1 | 33 | 2 | 33 |

TABLE 1. (continued)

| Food Item | Observations of deer feeding in good and poor growing seasons | | | | Analyses of deer paunches in good and poor growing seasons | | | |
|---|---|---|---|---|---|---|---|---|
| | Good | | Poor | | 3 paunches from good | | 12 paunches from poor | |
| | 222.5 Minutes | 158 Observations | 399.2 Minutes | 225 Observations | 300 hits | Frequency in 3 deer | 1200 hits | Frequency in 12 deer |
| *Rhus microphylla* | | | 1 | 2 | 1 | 33 | 8 | 42 |
| *Rhus trilobata* | 3 | 4 | 1 | 3 | | | T | 8 |
| *Ungnadia speciosa* | | | | | 1 | 33 | T | 8 |
| *Xanthocephalum* spp. | T | 1 | | | | | | |
| *Yucca torreyi* | | | | | | | T | 8 |
| Unidentified shrubs | | | | | 1 | 33 | 1 | 33 |
| All shrubs | 85 | 77 | 92 | 88 | 71 | | 82 | |
| Forbs | | | | | | | | |
| *Acalypha lindheimeri* | T | 1 | | | T | 33 | 1 | 8 |
| *Artemisia ludoviciana* | T | 1 | | | 1 | 33 | 4 | 8 |
| *Bahia pedata* | 3 | 3 | | | 1 | 33 | | |
| *Chenopodium* spp. | 5 | 4 | | | | | | |
| *Commelina erecta* | | | T | T | | | | |
| *Croton pottsii* | | | T | T | | | T | 8 |
| *Dyschoriste decumbens* | | | | | | | T | 8 |
| *Dyssodia* spp. | | | | | | | T | 17 |
| *Eriogonum* spp. | T | 2 | 1 | 3 | T | 33 | | |
| *Euphorbia* spp. | | | | | 1 | 33 | 3 | 33 |
| *Galium* sp. | | | | | | | T | 8 |
| *Gaura* spp. | | | | | | | 1 | 8 |
| *Gilia rigidula* | | | | | | | T | 8 |
| *Hoffmanseggia densiflora* | | | | | | | 1 | 8 |
| *Ibervillea tenuisecta* | 1 | 1 | 1 | T | | | | |
| *Ipomoea lindheimeri* | 1 | 1 | T | 1 | | | | |
| *Machaeranthera scabrella* | | | | | | | T | 8 |
| *Melampodium leucanthum* | T | 1 | | | | | | |
| *Monolepis nuttaliana* | T | 1 | | | | | | |
| *Paronychia jamesii* | | | | | | | T | 8 |
| *Plantago* spp. | | | | | | | T | 8 |
| *Portulaca* sp. | T | 1 | T | T | | | | |
| *Rhynchosia texana* | 1 | 1 | 3 | 3 | T | 33 | 1 | 25 |

TABLE 1. (continued)

| Food Item | Observations of deer feeding in good and poor growing seasons: Good 222.5 Minutes | Good 158 Observations | Poor 399.2 Minutes | Poor 225 Observations | Analyses of deer paunches in good and poor growing seasons: 3 paunches from good 300 hits | 3 paunches from good Frequency in 3 deer | 12 paunches from poor 1200 hits | 12 paunches from poor Frequency in 12 deer |
|---|---|---|---|---|---|---|---|---|
| *Salsola kali* | | | | | | | T | 8 |
| *Sida procumbens* | | | | | 4 | 33 | | |
| *Siphonoglossa pilosella* | T | 1 | | | 15 | 33 | T | 17 |
| *Sphaeralcea angustifolia* | | | | | 1 | 67 | | |
| *Stenandrium barbatum* | 1 | 1 | | | 2 | 33 | 2 | 33 |
| *Thamnosma texana* | | | | | 1 | 33 | T | 8 |
| *Viguiera dentata* | T | 1 | T | T | | | | |
| *Viguiera longifolia* | 1 | 2 | | | | | | |
| Unidentified forbs | 1 | 4 | 1 | 1 | 3 | 100 | 1 | 42 |
| All forbs | 15 | 23 | 6 | 10 | 29 | | 16 | |
| Grasses | | | | | | | | |
| *Bouteloua curtipendula* (grn) | T | 1 | | | | | | |
| *Sorghum halepense* (grn) | | | 1 | T | | | | |
| *Stipa* sp. (grn) | | | T | T | | | | |
| Unidentified grasses (grn & dry) | | | T | 1 | | | 2 | 58 |
| All grasses | T | 1 | 2 | 2 | | | 2 | |
| Unidentified plant material | | | | | | | T | 33 |

juniper in good GS's than in poor GS's probably reflects a low preference, since the leaves and stems are always abundantly available.

The number of recognized forb taxa observed eaten in good GS's was twice that in poor GS's, for which we had more feeding records. Ranking taxa were goosefoot (*Chenopodium* spp.) and bluntscale bahia (*Bahia pedata*) in good GS's, and Texas snoutbean (*Rhynchosia texana*) in poor GS's.

Direct observations of feeding indicate that deer spent over twice as long feeding on individual lechuguilla plants in the GS as in the NGS. Fruit stalks

were mostly eaten in the GS. Probably the deer's preference for the relatively scarce tender stalks and greater volume of the one stalk on each plant account for the longer feeding time than on leaves during the NGS. (Deer were eating small plants in entirety during the NGS.) The only other shrubs with appreciable use in both GS and NGS were redberry juniper and silver dalea, and each had the same feeding time per plant for the two seasons. This is rather surprising in view of the presumed difference between foraging conditions in the two seasons.

Most of the auto-killed deer paunches from GS's were from poor ones. The paunches from both good and poor GS's were well distributed by months and years but the sample is very small for good GS's.

Relative amounts of forage classes found in paunches agree with the observed feeding, indicating more use of shrubs in poor GS's and more of forbs in good GS's. However, in paunches, shrubs are consistently less and forbs more than in the observed feeding. This may be due to bias with feeding observations caused by feeding time on forbs being so short, or plants so fully consumed that we could not obtain data. However, quicker digestion of forbs than of shrubs, and the chance of not hitting low-occurring items in 100 hits per paunch would similarly seem to bias paunch analyses.

Good GS paunches had only half the recognized shrub taxa found in poor GS paunches. Forb taxa were much less in good GS paunches, probably due in part to the small sample during good GS's. Roemer acacia leaves were the major good GS item in hits and frequency, followed by prickly pear fruits and some mescat acacia leaves and stems. (Most of the prickly pear was *Opuntia engelmannii* but it was not separated from other species.) Among forbs, only hairy tubetongue (*Siphonoglossa pilosella*) and spreading sida (*Sida procumbens*), both recorded in only the September 1971 deer, had an appreciable number of hits. Poor GS paunches had a major showing of Roemer acacia, and several other items of note: Apache plume (*Fallugia paradoxa*), littleleaf sumac (*Rhus microphylla*), lechuguilla leaves, and little walnut (*Juglans microcarpa*) leaves with some fruit. The low percentage of poor GS hits on redberry juniper, even though present in two-thirds of the paunches, is surprising. Forbs of note were Louisiana sagewort (*Artemisia ludoviciana*) and euphorbia (*Euphorbia* spp.). Grasses were very minor, showing only in the poor GS's.

Differences between the data from observed feeding and from paunches may be due to the different locations represented.

**Nongrowing Seasons**

Data for the NGS's are treated in two categories, good and poor (Tables 2 and 3). Seventy-five percent of observed feeding during good NGS's was in 1968–69; and 90% of the observed feeding time during poor NGS's was in 1967–68; thus, the two types of NGS's are well represented.

Recognized taxa eaten by deer in NGS's were 39 shrubs, 32 forbs, and 2 of the grass and sedge category. Twenty-five shrubs and 15 forbs were common

TABLE 2. Records of deer feeding on foothills in Carlsbad Caverns area in nongrowing seasons 1967-68 to 1971-72, after good and after poor growing seasons. All table entries are on a percentage basis.

| | Observations of deer feeding 1967-1968 to 1970-1971 | | | | Analyses of deer paunches: Auto kills along surfaced roads | | | | Analyses of deer paunches: Hunter kills by "Scoggins' Corner" November only 1967-1970 | | | | Analyses of deer paunches: Study and hunter kills over foothills Nov.-Dec., 1967 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | After good | | After poor | | 4 paunches after good | | 4 paunches after poor | | 6 paunches after good | | 12 paunches after poor | | 16 paunches All after poor | |
| Food item | 155.7 Min. | 95 Obs. | 305.9 Min. | 186 Obs. | 400 hits | Frequency in 4 deer | 400 hits | Frequency in 4 deer | 600 hits | Frequency in 6 deer | 1200 hits | Frequency in 12 deer | 1600 hits | Frequency in 16 deer |
| Shrubs | | | | | | | | | | | | | | |
| *Acacia constricta* | | | | | | | | | | | | | 1 | 6 |
| *Acacia greggii* | | | | | | | | | | | | | T | 6 |
| *Acacia roemeriana* | 3 | 3 | | | 2 | 25 | 13 | 50 | | | 2 | 33 | 7 | 44 |
| *Agave lecheguilla* | 3 | 4 | 24 | 31 | 1 | 50 | 23 | 75 | 2 | 50 | T | 17 | 23 | 69 |
| *Bernardia obovata* | | | 2 | 2 | | | | | 1 | 50 | | | | |
| *Celtis reticulata* | | | | | 3 | 25 | | | | | 3 | 50 | 2 | 12 |
| *Cercocarpus breviflorus* | | | | | | | | | 9 | 33 | T | 17 | T | 6 |
| *Clematis drummondii* | | | | | | | | | | | T | 8 | | |
| *Condalia ericoides* | 1 | 1 | | | | | | | | | | | | |
| *Croton fruticulosus* | | | | | | | T | 25 | | | | | | |
| *Dalea argyraea* | 8 | 12 | T | 1 | 2 | 50 | | | | | 1 | 25 | T | 12 |
| *Dalea formosa* | 4 | 6 | T | 1 | 3 | 50 | T | 25 | | | 1 | 17 | 2 | 44 |
| *Dasylirion leiophyllum* | | | | | T | 25 | | | T | 17 | | | | |
| *Ericameria laricifolia* | | | | | | | | | 2 | 17 | 1 | 25 | | |

TABLE 2. (continued)

| Food Item | Analyses of deer paunches | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Observations of deer feeding 1967-1968 to 1970-1971 | | | | Auto kills along surfaced roads | | | | Hunter kills by "Scoggins' Corner" November only 1967-1970 | | | | Study and hunter kills over foothills Nov.-Dec., 1967 | |
| | After good | | After poor | | 4 paunches after good | | 4 paunches after poor | | 6 paunches after good | | 12 paunches after poor | | 16 paunches All after poor | |
| | 155.7 Min. | 95 Obs. | 305.9 Min. | 186 Obs. | 400 hits | Frequency in 4 deer | 400 hits | Frequency in 4 deer | 600 hits | Frequency in 6 deer | 1200 hits | Frequency in 12 deer | 1600 hits | Frequency in 16 deer |
| *Fallugia paradoxa* | | | | | 7 | 75 | T | 25 | 19 | 50 | 18 | 83 | 8 | 50 |
| *Fendlera rupicola* | | | T | 1 | | | | | | | | | | |
| *Gymnosperma glutinosum* | 2 | 1 | T | 1 | 1 | 50 | | | 4 | 83 | T | 8 | | |
| *Juglans microcarpa* | | | | | 14 | 50 | | | 9 | 17 | 9 | 58 | T | 6 |
| *Juniperus pinchotii* | 10 | 7 | 28 | 27 | 3 | 25 | 23 | 100 | 1 | 67 | 6 | 75 | 20 | 88 |
| *Menodora longiflora* | | | | | 3 | 25 | | | T | 17 | T | 8 | | |
| *Menodora scabra* | | | | | | | | | 1 | 17 | | | | |
| *Mimosa biuncifera* | 13 | 7 | | | | | 4 | 25 | | | T | 17 | 2 | 25 |
| *Nolina texana* | | | T | 1 | | | | | | | | | | |
| *Opuntia* spp. | 6 | 4 | 5 | 5 | 14 | 50 | 20 | 75 | | | | | 4 | 38 |
| *Opuntia imbricata* | 22 | 20 | 29 | 17 | 10 | 25 | | | 4 | 67 | 20 | 75 | 10 | 50 |
| *Opuntia leptocaulis* | | | 1 | 2 | | | | | | | | | | |
| *Parthenium incanum* | 7 | 5 | 1 | 1 | 1 | 50 | 6 | 25 | | | T | 8 | 1 | 25 |
| *Quercus* spp. | 1 | 1 | | | | | | | 36 | 100 | 35 | 83 | 11 | 31 |
| *Rhus microphylla* | | | | | | | | | | | | | 1 | 19 |
| *Rhus virens* | | | | | | | | | | | | | 1 | 6 |
| *Ungnadia speciosa* | | | | | 6 | 25 | | | | | | | | |

TABLE 2. (continued)

| Food Item | Observations of deer feeding 1967-1968 to 1970-1971 | | | | Analyses of deer paunches | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Auto kills along surfaced roads | | | | Hunter kills by "Scoggins' Corner" November only 1967-1970 | | | | Study and hunter kills over foothills Nov.-Dec., 1967 | |
| | After good | | After poor | | 4 paunches after good | | 4 paunches after poor | | 6 paunches after good | | 12 paunches after poor | | 16 paunches All after poor | |
| | 155.7 Min. | 95 Obs. | 305.9 Min. | 186 Obs. | 400 hits | Frequency in 4 deer | 400 hits | Frequency in 4 deer | 600 hits | Frequency in 6 deer | 1200 hits | Frequency in 12 deer | 1600 hits | Frequency in 16 deer |
| *Viguiera stenoloba* | | | 5 | 5 | T | 25 | 2 | 25 | T | 33 | | | | |
| *Xanthocephalum* spp. | 4 | 5 | T | 1 | 6 | 75 | 3 | 25 | 1 | 33 | T | 25 | T | 6 |
| *Yucca baccata* | | | 1 | 1 | | | | | | | | | | |
| *Yeca torreyi* | | | | | T | 50 | | | 1 | 17 | | | | |
| Unidentified shrubs | | | | | 2 | 25 | | | T | 33 | T | 25 | T | 6 |
| All shrubs | 85 | 78 | 97 | 94 | 76 | | 95 | | 92 | | 98 | | 95 | |
| Forbs | | | | | | | | | | | | | | |
| *Ambrosia confertiflora* | T | 1 | | | | | | | | | | | | |
| *Artemisia ludoviciana* | T | 1 | | | 2 | 25 | | | | | | | | |
| *Chenopodium* spp. | 1 | 2 | | | | | | | | | | | | |
| Cruciferae | | | T | 1 | | | | | | | | | | |
| *Dyschoriste decumbens* | | | | | T | 25 | | | | | | | | |
| *Erigeron modestus* | 1 | 1 | | | | | | | | | | | | |
| *Erigeron* spp. | | | | | 3 | 25 | T | 25 | | | | | | |
| *Erigonum* spp. | 2 | 3 | | | 2 | 25 | | | | | | | T | 6 |

TABLE 2. (continued)

| | Observations of deer feeding 1967-1968 to 1970-1971 | | | | Analyses of deer paunches | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Auto kills along surfaced roads | | | | Hunter kills by "Scoggins' Corner" November only 1967-1970 | | | | Study and hunter kills over foothills Nov.-Dec., 1967 | |
| | After good | | After poor | | 4 paunches after good | | 4 paunches after poor | | 6 paunches after good | | 12 paunches after poor | | 16 paunches All after poor | |
| Food Item | 155.7 Min. | 95 Obs. | 305.9 Min. | 186 Obs. | 400 hits | Frequency in 4 deer | 400 hits | Frequency in 4 deer | 600 hits | Frequency in 6 deer | 1200 hits | Frequency in 12 deer | 1600 hits | Frequency in 16 deer |
| *Euphorbia* spp. | | | | | T | 25 | | | | | T | 8 | | |
| *Hedyotis nigricans* | | | | | | | | | T | 17 | | | | |
| *Hymenoxys acaulis* | | | | | 1 | 25 | | | | | T | 8 | | |
| *Ibervillea tenuisecta* | | | | | T | 25 | | | | | | | | |
| *Lepidium virginicum* | | | | | 7 | 50 | | | | | | | | |
| *Machaeranthera scabrella* | | | | | T | 25 | | | T | 17 | | | | |
| *Melampodium leucanthum* | 1 | 2 | | | | | | | | | | | | |
| *Notholaena sinuata* | | | | | 1 | 25 | 1 | 50 | | | | | T | 6 |
| *Paronychia jamesii* | 1 | 1 | | | | | | | 1 | 17 | | | | |
| *Phyllanthus polygonoides* | | | | | T | 25 | | | | | | | | |
| *Pinaropappus roseus* | 1 | 1 | | | | | | | | | | | | |
| *Polygala* spp. | | | | | T | 25 | | | 2 | 17 | | | | |
| Polypodiaceae | | | | | | | | | T | 17 | | | | |
| *Rhynchosia texana* | | | | | 1 | 25 | | | | | T | 8 | | |
| *Siphonoglossa pilosella* | 3 | 2 | | | T | 25 | | | | | | | | |
| *Sisymbrium linearifolium* | 2 | 2 | | | | | | | | | | | | |
| *Sphaeralcea angustifolia* | | | | | | | | | | | | | T | 6 |

TABLE 2. (continued)

| Food Item | Observations of deer feeding 1967-1968 to 1970-1971 | | | | Analyses of deer paunches | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Auto kills along surfaced roads | | | | Hunter kills by "Scoggins' Corner" November only 1967-1970 | | | | Study and hunter kills over foothills Nov.-Dec., 1967 | |
| | After good | | After poor | | 4 paunches after good | | 4 paunches after poor | | 6 paunches after good | | 12 paunches after poor | | 16 paunches All after poor | |
| | 155.7 Min. | 95 Obs. | 305.9 Min. | 186 Obs. | 400 hits | Frequency in 4 deer | 400 hits | Frequency in 4 deer | 600 hits | Frequency in 6 deer | 1200 hits | Frequency in 12 deer | 1600 hits | Frequency in 16 deer |
| *Sphaeralcea* spp. | | | | | 1 | 75 | | | | | T | 17 | | |
| *Stenandrium barbatum* | | | | | T | 25 | | | | | T | 17 | 1 | 19 |
| *Thamnosma texana* | 2 | 1 | | | | | | | T | 33 | | | T | 6 |
| *Viguiera* spp. | | | | | | | | | | | | | T | 6 |
| Unidentified forbs | 3 | 4 | | | 2 | 75 | 2 | 50 | T | 17 | T | 8 | 1 | 19 |
| All forbs | 15 | 22 | T | 1 | 21 | | 3 | | 4 | | 1 | | 3 | |
| Grasses and Sedges | | | | | | | | | | | | | | |
| *Carex* | | | | | | | | | | | | | T | 6 |
| Gramineae | | | 2 | 5 | 2 | 75 | 2 | 75 | 2 | 83 | 1 | 42 | 1 | 25 |
| All grasses and sedges | | | 2 | 5 | 2 | | 2 | | 2 | | 1 | | 1 | |
| Unidentified Items | | | | | | | | | | | | | | |
| Dicot | | | | | | | T | 25 | 2 | 83 | T | 17 | T | 6 |
| Monocot | | | | | T | 25 | | | | | | | | |
| Plant material | | | | | | | T | 25 | T | 33 | | | 1 | 38 |
| All unidentified items | | | | | T | | T | | | | | | 1 | |

to both growing and nongrowing seasons. Three more shrubs and one more forb were noted by all methods in NGS's than in GS's. But direct feeding records were greater by one-third in GS's, while nearly 3 times as many paunches were examined in NGS's. Thus, the following comparisons to GS findings would be due in part to those differences: less shrub (19 vs. 26) and forb (12 vs. 17) taxa recorded in direct feeding observations; more shrub (16 vs. 10) and forb (17 vs. 14) taxa found in paunch examinations. It is interesting to note further that snow tracking, done only in NGS's, revealed four shrubs and three forbs not represented in direct feeding observations nor in paunches from NGS's.

The above results from uneven sampling preclude a conclusion as to relative variety of shrubs and forbs in the diets of the two types of seasons. However, it does seem significant that all taxa represented in only one season—11 shrubs and 16 forbs in GS, and 14 shrubs and 17 forbs in NGS—appear to be minor items of the diet, with the exception of skeleton goldeneye in the NGS.

Observed feeding time and number of observations show greater relative use of shrubs in poor NGS's and of forbs in good NGS's. Numbers of recognized shrub taxa were relatively few and nearly the same (13 and 15) in good NGS's and in poor NGS's, even though nearly twice as much data was collected in poor NGS's. Ten taxa were in only one category. Cholla fruits with a few stems was the leader in good NGS feeding time and observation, but several other species were important: catclaw mimosa leaves and fruit, redberry juniper leaves and stems, silver dalea leaves and stems with some fruits, and mariola parthenium leaves and stems with some fruits. In poor NGS's, observed feeding was mostly on redberry juniper leaves and stems, cholla fruits and stems, and lechuguilla leaves. (Of these, only cholla fruits are thought to be quality food for deer.) Additionally, only prickly pear stems with a few fruits and skeleton goldeneye leaves, dry flower heads and stems were of consequence. Feather dalea (*Dalea formosa*) and broomweed (*Xanthocephalum* spp.) were of importance only in good NGS's, and skeleton goldeneye in only the poor NGS's.

A considerable variety of forbs was taken in good NGS's, in contrast to the one taxon in poor NGS's with twice the feeding time and observations. Limited grass use was observed in poor NGS's only.

Three of the paunches from auto kills were from the 1967–68 period and two from the 1968–69 period. The group of eight paunches from deer killed on roads showed heavy use of shrubs in poor NGS's, and appreciable use of forbs in good NGS's. A greater variety of shrubs was eaten in good NGS's. Most shrubs taken in poor NGS's were also taken in good NGS's. Walnut (mostly leaves), prickly pear fruits and cholla fruits led in good NGS's, but they made up only one-third of the hits. Other plants well represented in hits and frequency were Apache plume and broomweed. In poor NGS's, most of the hits accompanying high frequency were on redberry juniper leaves and

stems, lechuguilla leaves, and prickly pear pads, with an appreciable showing of Roemer acacia leaves and a few stems, and some mariola parthenium. (Roemia acacia browse is available in the nongrowing season only during April when new leaves and succulent stems appear and in late fall when a few leaves remain green.)

Hunter kills from the "Scoggins' Corner" area were mostly from upper elevations where oak is common and mountain mahogany is present on some sites. Since all samples were from the same month, they should indicate diet differences due to forage availability. The greater number of shrub taxa from poor NGS's (two more) than from good NGS's may be due to the fact that the sample size is twice as large. Likewise, the fact that few forbs were found in the good NGS paunches with only one more taxon than from poor NGS paunches may be due to the relatively small sample. The pattern of relatively more hits on shrubs in poor NGS's and of more hits on forbs in good NGS's is less prominent than with the autokills taken over the full nongrowing season. Likewise, there is considerable similarity in number of hits and frequency between types of nongrowing seasons on the major items—oak leaves with a few stems, Apache plume leaves and stems, and walnut leaves with a few stems—which made up about two-thirds of the hits in good and poor NGS paunches. Greater use of mountain mahogany in good NGS's could well be a reflection of availability, and greater use of redberry juniper in poor NGS's may be due to lack of better food.

One hunter-killed deer was grouped with the study kills to give representation of the deer diet over the entire foothills in late fall 1967. The high proportion of shrub material taken in late fall 1967 agrees with other data for poor NGS's. Lechuguilla leaves and redberry juniper leaves and stems were leaders, both with rather high frequencies, but other taxa contributed appreciably: oak leaves, and cholla fruits with a few stems, and lesser amounts of Apache plume and Roemer acacia.

Many of the shrubs represented in the foothills-wide deer were also represented in the "Scoggins' Corner" area poor NGS deer, but amounts of taxa varied greatly There was much more lechuguilla and redberry juniper taken foothills-wide, and much more oak, cholla, Apache plume, and walnut taken at "Scoggins' Corner," which suggests that drought conditions were more severe on the lower foothills with regard to late fall forage.

Data from snow tracking were divided by type of season: 225 EVU's in good NGS's and 264 in poor NGS's. Tracking records appear to be well distributed over the area between White's City and the head of Walnut Canyon. Forage classes utilized were 94% shrubs and 6% forbs in good NGS's vs. 88% shrubs and 12% forbs in poor NGS's. Leading items in good NGS's were cholla stems with some fruits 22%, and broomweed 18%; followed by Apache plume 14%, redberry juniper 13%, and skeleton goldeneye 8%. In poor NGS's, oak led with 30%. Other items of 8 to 12% were redberry juniper, cholla stems, skeleton goldeneye, broomweed, and the forb pepper-

TABLE 3. Deer utilization of plants during snow cover on selected sites, 1969-71, Carlsbad Caverns foothills, after good and after poor growing seasons. All table entries are on a percentage basis.

| | Lower Walnut Canyon | | Headquarters Area | | | Upper Walnut Canyon | |
|---|---|---|---|---|---|---|---|
| | After good | After poor | After good | | After poor | After good | After poor |
| Food item | 3 sites 25 EVU* ea Jan. 8, 1971 | 2 sites 50 & 25 EVU Mar. 21, 1970 | 4 sites 25 EVU ea Jan. 6-8, 1971 | 287 Calculated EVU–2 sites Mar. 17-18, 1969 | 1 site 100 EVU Dec. 30, 1969 | 2 sites 25 EVU ea Jan. 5, 1971 | 1 site 57 EVU Dec. 31, 1969 |
| | | | Shrubs | | | | |
| *Acacia roemeriana* | | | 1 | | | | |
| *Agave lecheguilla* | | | 4 | 17 | | | |
| *Aloysia wrightii* | 4 | | | | | | |
| *Baccharis pteronioides* | | | | | | 4 | |
| *Bernardia obovata* | | | | 3 | | | |
| *Berberis trifoliolata* | | 5 | | | | | |
| *Cercocarpus breviflorus* | | | | | | | 7 |
| *Dalea argyraea* | | | 7 | 9 | 2 | | |
| *Dalea formosa* | | 3 | 3 | 46 | 3 | | 2 |
| *Dasylirion leiophyllum* | | | | T | | | |
| *Ericameria laricifolia* | | | | | 3 | | |
| *Fallugia paradoxa* | 23 | | | | | 30 | |
| *Gymnosperma glutinosum* | 5 | 3 | | 4 | 2 | | 12 |
| *Juniperus pinchotii* | 3 | 12 | 13 | 6 | 4 | 30 | 23 |
| *Menodora longiflora* | | | 4 | 1 | | | |
| *Mimosa biuncifera* | | | | | | 2 | |
| *Opuntia* spp. | | 3 | | | | | |
| *Opuntia imbricata* | 20 | 37 | 17 | 5 | | 34 | |
| *Parthenium incanum* | 5 | 3 | 4 | T | | | |
| *Quercus* spp. | | | | | 49 | | 53 |

TABLE 3. (continued)

| Food item | Lower Walnut Canyon | | Headquarters Area | | | Upper Walnut Canyon | |
|---|---|---|---|---|---|---|---|
| | After good | After poor | After good | | After poor | After good | After poor |
| | 3 sites 25 EVU* ea Jan. 8, 1971 | 2 sites 50 & 25 EVU Mar. 21, 1970 | 4 sites 25 EVU ea Jan. 6-8, 1971 | 287 Calculated EVU–2 sites Mar. 17-18, 1969 | 1 site 100 EVU Dec. 30, 1969 | 2 sites 25 EVU ea Jan. 5, 1971 | 1 site 57 EVU Dec. 31, 1969 |
| *Rhus microphylla* | 3 | | | | | | |
| *Senecio longilobus* | | | 2 | | | | |
| *Viguiera stenoloba* | 21 | 12 | 3 | 5 | 19 | | |
| *Xanthocephalum* spp. | | 5 | 40 | 1 | 18 | | 4 |
| All shrubs | 84 | 83 | 98 | 97 | 100 | 100 | 100 |
| | | | Forbs | | | | |
| *Artemisia ludoviciana* | | | | T | | | |
| *Bahia pedata* | | | 1 | | | | |
| Cruciferae | | 1 | | | | | |
| *Descurainia pinnata* | | 4 | | | | | |
| *Draba* sp. | | 12 | | | | | |
| *Eriogonum* spp. | | | | 1 | | | |
| *Melampodium leucanthum* | | | | 1 | | | |
| *Sisymbrium linearifolium* | | | 1 | | | | |
| *Sphaeralcea* spp. | 4 | | | | | | |
| *Stenandrium barbatum* | | | | 1 | | | |
| Unidentified forbs | 12 | | | T | | | |
| All forbs | 16 | 17 | 2 | 3 | | | |

*EVU = Estimated Volume Units.

weed (*Lepidium virginicum*). Oak was used only in poor NGS's, redberry juniper was the same in good and poor NGS's, and shrubs ranked lower and forbs higher in poor NGS's, suggesting that factors other than type of season were involved. Accordingly, data were treated by individual sites (Table 3). Observations from Middle Walnut Canyon were omitted because of the small sample (32 EVU's).

Snow tracking samples from Lower Walnut Canyon showed nearly equal amounts of shrubs and forbs eaten in good and poor NGS's, but composition differed. Apache plume leaves and stems, skeleton goldeneye leaves and stems, and cholla stems and fruits made up two-thirds of estimated volume in good NGS's; whereas, in poor NGS's, cholla stems were over one-third of the volume, and skeleton goldeneye, redberry juniper leaves and stems and the forb draba (*Draba* spp.) together made up one-third. Draba and other succulent mustards (*Cruciferae*) probably were available in March because of the above normal winter precipitation.

At headquarters, a ridge site, nearly all volume was browse. Recorded EVU's in good NGS's showed broomweed leaves, stems, and fruits as a high leader, followed by cholla stems and fruits and juniper leaves and stems. Calculated EVU's from feeding instances near headquarters differed, having feather dalea leaves and stems a strong leader followed by lechuguilla leaves and some silver dalea leaves and stems. The differences between observed and calculated EVU composites suggest samples were too small for the different times or areas sampled. The poor NGS sample at headquarters had a different leader: oak leaves and stems, with appreciable amounts of skeleton goldeneye and broomweed leaves and stems.

At Upper Walnut, all deer tracked had fed entirely on shrubs. Prickly pear stems and fruits and redberry juniper and Apache plume leaves and stems shared most of the good NGS volume. In poor NGS's, oak leaves and stems were more than half of the total, followed by redberry juniper leaves and stems, and less of tatalencho (*Gymnosperma glutinosum*) leaves and stems.

Considering all three sites in both types of seasons, the most volume consistently eaten was of redberry juniper, followed by cholla, skeleton goldeneye, and broomweed. Additional study is needed to perfect the technique of estimating volume and to establish the effect, if any, of snow cover on the deer's feeding habits. Although snow cover usually lasts only a few days each winter on the foothills, tracking deer in it gives much more data for the hour of effort than does direct feeding observation.

**Generalized Diet**

A generalized diet of deer on the park foothills was developed from data presented here with consideration of sample size, time of year and location, and distribution and growth habits of plants. Shrubs comprise the bulk of the year-round diet. During the average growing season, Roemer acacia leaves with some stems is by far the leading item. Other shrubs of some

importance are catclaw mimosa leaves with some fruits and stems; lechuguilla fruit, stalks, and leaves; silver dalea leaves and stems; prickly pear fruits and pads; redberry juniper leaves, stems, and fruits; walnut leaves, fruits, and stems; Apache plume leaves, stems, and fruits; mescat acacia leaves and stems; feather dalea leaves and stems; and sotol fruit stalks when available. Top ranking forbs are tubetongue, shaggy stenandrium (*Stenandrium barbatum*), and sagewort. Roemer acacia is a less prominent leader during good growing seasons and sotol, prickly pear fruits, silver dalea, mescat acacia, catclaw mimosa, and mountain mahogany are also of some importance. During poor growing seasons, browse use is especially high. Roemer acacia is supplemented by catclaw mimosa, lechuguilla stalks, redberry juniper, walnut, Apache plume, silver dalea, and prickly pear pads.

Shrubs comprise even more of the diet during the nongrowing season. The average diet then includes cholla fruit with stems and redberry juniper as co-leaders, followed by lechuguilla leaves, prickly pear pads and some fruits; catclaw mimosa leaves and some fruits; walnut; and silver dalea. At upper elevations oak leaves and Apache plume are important. Occasional use of forbs—mostly mustards with some tubetongue, wild buckwheat (*Eriogonum* spp.), and fleabane (*Erigeron* spp.)—occurs when moisture and temperature are especially favorable.

In good nongrowing seasons, cholla fruit is the leader, followed by catclaw mimosa, prickly pear fruits, silver dalea, redberry juniper, walnut, and Apache plume, with some forbs if winter weather is favorable. In poor nongrowing seasons, redberry juniper probably ranks first, closely followed by cholla fruits and stems, and lechuguilla with some oak and prickly pear pads.

Variety of forbs in the diet, and of shrubs to a lesser extent, is greater during good growing and good nongrowing seasons.

In an average year, Roemer acacia is taken from May to November, mostly May–July when leaves and twigs are succulent. For other important taxa, relative availability appears to be a determining factor in time of utilization:

| | | | |
|---|---|---|---|
| Mescat acacia | August | through November; | most October–November |
| Redberry juniper | October | through April; | most November–February |
| Cholla | November | through April; | most December–March |
| Lechuguilla | December | through April; | most March–April |
| Prickly pear | January | through March. | |

This pattern of plant use suggests that the critical foraging period for deer on the park foothills usually extends from January through March.

**Comparative Studies**

The Texas Game and Fish Commission (Uzzell 1958) collected deer to study food habits in the Trans-Pecos region in 1956 and 1957, covering a

period of sustained drought. One of the study areas, the Sierra Diablo Range, about 120 km southwest of Carlsbad Caverns, has limestone formation similar to that of the Guadalupes, and the elevation overlaps that of the upper part of our study area. Vegetation was juniper–oak–pinyon woodland, but the paunch analyses indicate it was similar to that in our study area. In a collection of seven deer between September and November, the top food item in volume and frequency was lechuguilla; littleleaf sumac and oaks (*Quercus undulata* and *Q. pungens*) contributed, with some Ashe juniper (*J. ashei*). A collection of 17 deer in December to February had oak leaves first in volume and frequency, followed by Englemann prickly pear pads, Ashe juniper, lechuguilla, and cholla fruit. Allowing for the variation in species of juniper, and considering that most of our prickly pear used by deer was Engelmann and that the September–November collections extended into our nongrowing season, we find comparability with the deer diet on the caverns foothills. The position of lechuguilla is reassuring, because some questions have been raised locally about our rating of this plant with its viciously pointed leaves.

The New Mexico study of deer food habits between 1956 and 1960 (Anderson et al. 1965) was conducted in the Guadalupe Mountains, mostly on the Lincoln National Forest, which extended within 10 km of the Caverns study area. It was done mostly on juniper-pinyon woodland at elevations above the park foothills. The 93 deer paunches analyzed for that study showed wavyleaf oak (*Q. undulata*), juniper (*J. monosperma* and *J. deppeana*), mountain mahogany and yuccas (*Yucca* spp.) as leaders. Forbs exceeded even the browse throughout a year of heavy precipitation. The importance of oak where present is borne out in our collections on the higher foothills, and there is no doubt that mountain mahogany on the park's mountain range is a major food for deer. Yuccas taken on the forest are very sparse in our study area. Certainly we had no evidence of such heavy use of forbs as was recorded there. In total, the results of that study appear to be more applicable to the mountains in the park than the foothills.

In late spring 1969, a drought period, deer were found to be eating bark from madrone trees (*Arbutus xalapensis*) in McKittrick Canyon, Guadalupe Mountains National Park, to such an extent as to change the aspect of the canyon. The Texas Parks and Wildlife Department, in cooperation with the National Park Service, collected four deer in the canyon to verify the use of madrone bark. Results are given in Table 4. The canyon bottom is an evergreen woodland containing madrone and a variety of shrubs. It is of special interest here because of its differences from the caverns study area, even though only 40 km away. The canyon is narrow and deep, and the floor at 1585 m (5200 ft) elevation has permanent water. The high use of oak suggests that the deer were hard pressed for forage and could have been stripping the madrone bark because of the shortage of quality foods. Certainly a number of the species found as low-occurring items are regarded as choice foods on

TABLE 4. Plants found in paunches of four deer from McKittrick Canyon, Guadalupe Mountains National Park, 16 June 1969.

| Food item | Plant parts eaten | Percent of 400 hits | Percent Frequency |
|---|---|---|---|
| | Shrubs | | |
| *Acacia roemeriana* | Stems | T | 25 |
| *Agave lecheguilla* | Leaves | T | 25 |
| *Arbutus xalapensis* | Bark mostly, few leaves | 7 | 100 |
| *Ceanothus greggii* | Leaves | T | 25 |
| *Celtis reticulata* | Leaves | T | 25 |
| *Cercocarpus breviflorus* | Leaves and stems | 1 | 25 |
| *Dalea argyraea* | Stems | T | 25 |
| *Fallugia paradoxa* | Leaves and stems | 1 | 50 |
| *Menodora longiflora* | Leaves | T | 25 |
| *Mimosa biuncifera* | Leaves and stems | 9 | 100 |
| *Parthenium incanum* | Leaves | T | 25 |
| *Prunus virens* | Leaves | T | 25 |
| *Quercus* spp. | Leaves and stems | 70 | 100 |
| *Rhus trilobata* | Leaves and stems | 3 | 25 |
| *Rhus virens* | Leaves and few stems | 2 | 50 |
| Unidentified shrubs | | T | 25 |
| All shrubs | | 96 | |
| | Forbs | | |
| *Acalypha lindheimeri* | | 1 | 50 |
| *Dalea nana* | | T | 25 |
| *Erigeron* spp. | | T | 25 |
| *Euphorbia* spp. | | T | 50 |
| *Machaeranthera blephariphylla* | | T | 25 |
| Unidentified forbs | | 1 | 50 |
| All forbs | | 3 | |
| | Grasses | | |
| Gramineae | | 1 | 75 |

the caverns range, but no information is at hand on the quantity that may have been available. Several of the taxa found are among those taken by the caverns foothills deer. Proportions, of course, may well be a reflection of the different vegetation.

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# *Biomes of the Guadalupe Escarpment: Vegetation, Lizards, and Human Impact*

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When an area becomes a national park, its biotic features must be interpreted to the public. The interpretive scheme must be simple—its elements easily recognized in the field, its synthetic features readily understood—and the scheme should be of such general applicability that a park visitor will become familiar with living landscapes throughout his travels. The biome concept fulfills these particulars; because biomes can be named for their vegetative structure, the functional significance of this is comprehensible (e.g. evergreen versus deciduous species), and biomes are repeatable units of landscape on a continental scale. Moreover, park visitors can identify the vegetative appearance of biomes without necessarily having to identify the plant species and speak of biomes in familiar language.

I have defined plant formations in the Guadalupe Escarpment region and now wish to test the scheme against faunal patterns since biomes are groups of plants and animals whose ecologic niches overlap to a greater extent than expected by chance. What animals make the best indicators of biomes? Surely they must have spatial niches congruent with particular vegetation-types and be conspicuous to park visitors. I have not studied mammals, but certain rabbits and squirrels have potential, whereas nocturnal rodents do not, except perhaps through signs of their activities. Birds must be considered, for they are primarily visual and diurnal like man. Among terrestrial reptiles, snakes are avoided through fear, but lizards have qualifications similar to birds and are even more meaningful to man because they too are earthbound. Are lizards useful and objective biome indicators? I shall investigate this possibility.

Regardless of whether plant and lizard niches are coincident, human impact may disrupt the structure and distribution of biomes. The features of secondary succession caused by man are as important as those of natural biomes, expecially on the Guadalupe Escarpment only recently released from livestock grazing. Therefore, I shall present data on plants and lizards

in an area of Guadalupe Mountains National Park protected from grazing, alongside an area grazed simultaneously, and provide temporal information on plant and lizard succession along a pipeline construction scar in Carlsbad Caverns National Park. First, however, I offer a brief review of the vegetative basis of biome pattern in the Guadalupe ecosystem and corroborative evidence for part of this pattern in the spatial-behavioral niches of certain lizards.

## VEGETATION

Five plant formations (hypothetical biomes) are delineated on the Guadalupe Escarpment between U.S. Highway 62–180 and the crest and between Walnut and Pine Springs canyons (Fig. 1). Each is substantiated by quantitative, physiognomic distinctions (Gehlbach 1967). The borders between formations in Fig. 1 are approximate centers of major change in the living landscape, where plant life forms that determine a particular formation are least coincident. The most xeric sites, denoted by the Desert Formation (Biome)-class, are lowland flats and south or west-facing slopes, whereas the most mesic sites, indicated by the Woodland and Forest Formation (Biome)-classes, are east or north-facing slopes inside canyons, the drainageways, and the Escarpment-top exposures.

Vegetation is taller and plant biomass increases in the xeric to mesic environmental gradient. Dominant shrubs are microphyllous, grow singly, and are widely spaced on flats and gravelly hills at the base of the Escarpment. These give way to clonal groups and multiple species clumps dominated by succulent and semisucculent species—an entirely different physiognomy—on rock outcrops in the lowlands and canyon slopes. I believe the Shrub Desert Formation is indicated by the microphyllous species, *Larrea tridentata, Flourensia cernua*, and *Acacia constricta*, for example. By contrast, the prevalence of clones and other clumps with succulent and semisucculent shrubs is indicative of the Succulent Desert Formation. *Agave lecheguilla* and *Dasylirion leiophyllum* are chief indicators, but *Viguiera stenoloba* and *Juniperus pinchotii* are also important. The growth form index (deciduous/evergreen + succulent species) of the Succulent Desert Formation is 0.35, whereas that of the Shrub Desert Formation is 1.12.

Similar physiognomic differences obtain between the Deciduous and Evergreen Woodland formations. The first is denoted by broadleaf deciduous species, the second by evergreens, both broad- and needleleaved species. Growth form indices are 3.07 and 0.37, respectively. A tree stratum, averaging less than 5 m in height with an open canopy, distinguishes the two woodlands from the shrub-dominated deserts and the Coniferous Forest Formation with its taller trees and closed canopy. Broadleaved deciduous trees grow primarily at springs and in streambeds at low elevations but become the dominant growth form on stream terraces and in canyonheads

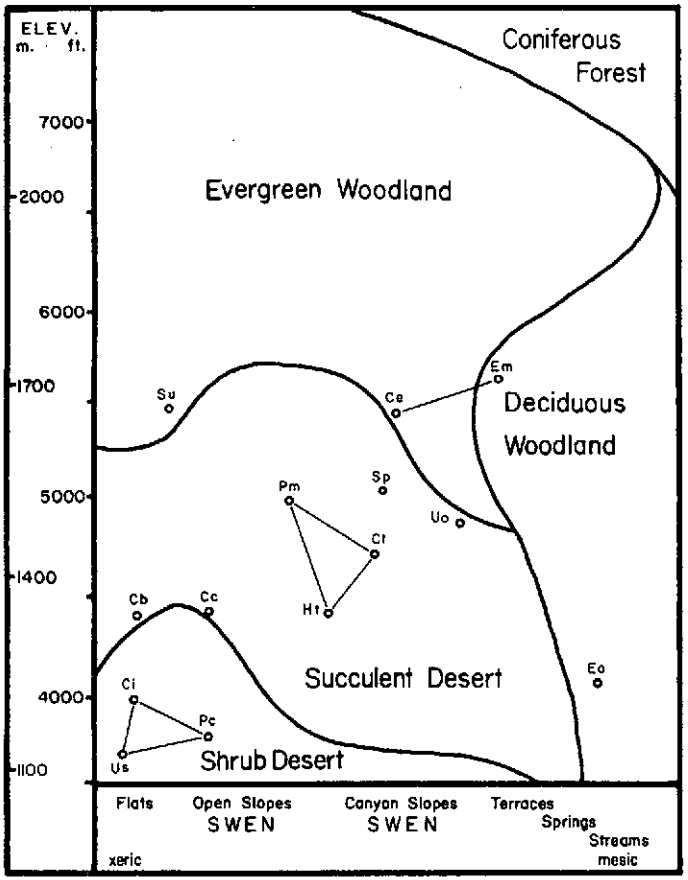


**Fig. 1.** Plant formations of the Guadalupe Escarpment, New Mexico–Texas. Positions of lizards in the environmental gradient, determined by polar ordination of maximum IV's are indicated: Us, *Uta stansburiana*; Pc, *Phrynosoma cornutum*; Ci, *Cnemidophorus inornatus*; Cc, *Crotaphytus collaris*; Cb, *Coleonyx brevis*; Ht, *Holbrookia texana*; Ct, *Cnemidophorus tessellatus*; Pm, *Phyrnosoma modestum*; Sp, *Sceloporus poinsetti*; Uo, *Urosaurus ornatus*; Su, *Sceloporus undulatus*; Eo, *Eumeces obsoletus*; Ce, *Cnemidophorus exsanguis*; Em, *Eumeces multivirgatus*. Species joined by lines are significantly associated with each other ($\chi^2 > 4.5$, $P < 0.01$).

above ca. 1500 m. Broadleaf evergreens dominate north-facing slopes at this elevation and are joined by conifers on more xeric sites.

Deciduous woodland dominants form a typical gradient series. *Populus wislizenii* occurs largely outside canyons, *Juglans microcarpa*, inside canyons, but as the stream gradient increases, *Ostrya knowltonii* and

*Fraxinus velutina* replace these species and are themselves replaced by *Acer grandidentatum* and *Quercus muhlenbergii*, especially on upper terraces, around springs, and in canyonheads. Evergreen woodland dominants are *Quercus grisea* (complex), *Juniperus deppeana*, *Arbutus texana*, and eventually *Pinus edulis* in the xeric to mesic gradient. This last species is replaced by *Pinus ponderosa*, *P. flexilis*, and *Pseudotsuga menziesii*, all indicators of Coniferous Forest at cool-wet sites such as The Bowl.

TABLE 1. The relationships of interpretive terminologies applied to living landscapes of the Guadalupe Escarpment. Terms within each row are roughly equivalent to one another.

| Plant formation | Life zone | Life belt | Association |
|---|---|---|---|
| Shrub Desert | Lower Sonoran | Plains | Desert Grassland<br>Desert Scrub |
| Succulent Desert | Lower Sonoran | Roughlands | Desert Scrub |
| Evergreen Woodland | Upper Sonoran | Roughlands | Pinyon–Juniper |
| Deciduous Woodland | Lower Sonoran to Canadian | Plains to Montane | Mountain<br>Riparian |
| Coniferous Forest | Transition to Canadian | Montane | Petran Montane<br>Pine–Fir–Oak |

Each of the five plant formations corresponds with one or more synecological units applied to the Guadalupe landscape by other investigators (Table 1). Unfortunately, these interpretive schemes are misleading because they fail to recognize particular living landscapes or employ confusing terminology. For example, the Life Zone system subsumes Shrub and Succulent deserts under the term Lower Sonoran, which derives from a region and vegetation potentially outside park visitor experience. Life Belts also fail to make important distinctions, and the Association scheme's array of nondescript and unfamiliar terms defies practical usage (e.g., what is a scrub or petran?).

## LIZARDS

The methodology for landscape assay, applied in 1959–69, has been described (Gehlbach 1967), but some techniques peculiar to lizards require special comment. Twenty-two 1 to 5 ha plots were devoted to censusing lizards and vegetation concurrently. Six each were in Shrub Desert, Succulent Desert, and Evergreen Woodland, formations with the most lizard species (Fig. 1); three were in Deciduous Woodland, and one was in the relatively inaccessible Coniferous Forest. Adult lizards were counted independently by two persons walking a plot in transects 15 m apart, beginning

simultaneously on opposite sides. Ground surface cover was checked and returned to its original position along each transect. Plots were censused for 2 to 11 successive days between 10 and 12 a.m. MST in June–September, until no increases in number and density of species were recorded, and resampled in 2 to 4 summers.

Data were reduced to mean density and frequency (number of days seen) per species per plot from the independent surveys. Fourteen species with importance values (IV = % density + % frequency) of at least 20 qualified for polar ordination analysis (Bray and Curtis 1957) since I wished to focus on species that were sufficiently abundant and/or frequent to have indicator value. The 14 were ordinated in the arrangement of plant formations by plotting the 22 samples according to elevation-topography and Ecosystem Index axes (Gehlbach 1967) and retaining only the maximum IV position of each species for graphic interpretation (Fig. 1; see Beals 1960). Then, Chi-square analysis of species associations was performed on the frequency data.

*Uta stansburiana, Phrynosoma cornutum*, and *Cnemidophorus inornatus* comprise a group of significantly associated, closely located species. All are xerically adapted and by gradient position clearly indicative of the Shrub Desert Biome (Fig. 1). Moreover, these three are diurnal species that can serve the park visitor in recognizing the Shrub Desert Biome. By contrast, the spatial niches of *Coleonyx brevis*, a nocturnal species, and *Crotaphytus collaris*, another conspicuous lizard, are centered in the Shrub Desert-Succulent Desert transition on hot-dry flats or rocky slopes at ca. 1300 m. These two are potential indicators of the vegetational continuum.

*Holbrookia (Cophosaurus) texana, Phrynosoma modestum*, and *Cnemidophorus tessellatus* are significantly associated and as characteristic of the Succulent Desert Biome as the *stansburiana–cornutum–inornatus* group is of the Shrub Desert. Furthermore, *H. texana* and *C. tessellatus* are abundant, diurnal ground dwellers, easily seen by the visitor on nature trails as in the Walnut Canyon area of Carlsbad Caverns National Park. Like its Shrub Desert congener, *P. modestum* is less active and more cryptic than its associates and, therefore, apparently less useful for interpretation. The niches of *Sceloporus poinsetti* and *Urosaurus ornatus* are also focused in Succulent Desert but closer to the desert-woodland transition. Their gradient positions reveal rock-dwelling, climbing habits in canyons with three plant formations juxtaposed according to elevation, slope, and exposure.

Because the woodland and forest formations offer more shade than the two deserts, diurnal lizards are comparatively scarce in them. Except for *Cnemidophorus exsanguis* and *Sceloporus undulatus*, no heliothermic species typically occur in these tree-dominated units. Only *C. exsanguis* suggests Evergreen Woodland, but its niche is marginal here, and it is significantly associated with *Eumeces multivirgatus* in the transition between Evergreen and Deciduous woodlands. The spatial niches of *E. multivirgatus* and another non-heliotherm, *E. obsoletus*, are focused near the xeric edge of

Deciduous Woodland. These two skinks and *C. exsanguis* are indicators of the Woodland Biome-class, certainly, if not of specific biomes.

*Sceloporus undulatus* is the most widespread species on the Guadalupe Escarpment. Although focused on hot-dry sites of the Succulent Desert-Evergreen Woodland transition, this lizard occurs in all plant formations. If I add its Chi-square values, *S. undulatus* has the lowest positive and negative sums and thus the least degree of association or disassociation with the other lizards. Interestingly, *C. collaris* is next in the association heirarchy, followed by *C. brevis* and the other continuum species. But *S. undulatus* and *C. collaris* are large and diurnal by contrast with *C. brevis*. By comparison, just how useful are they in landscape interpretation?

A lizard's large size and conspicuous behavior clearly increase its usefulness for interpretation. Moreover, relative conspicuousness plus niche congruence with a particular plant formation enhance a lizard's interpretive value as does its strong association and/or disassociation with other species. Thus, I have devised a Utility Index ($UI = C \times F/K$) to lizard species using the following parameters: C, conspicuousness = mean snout-vent length of adults multiplied by 1.0 if nocturnal or sub-fossorial, 1.5 if diurnal but cryptic or with a short daily or seasonal activity period, or 2.0 if diurnal and readily observed; F, fidelity = sum of species' $\chi^2$ values regardless of sign; K, congruity = 1 if spatially centered in a certain plant formation by polar ordination of maximum IV, or 2 if centered in transition zone between formations (1000 Ecosystem Index units on each side of EI overlap, see Gehlbach 1967:Table 7).

With the exception of *P. modestum*, lizards previously suggested as indicative of the validity of Shrub and Succulent Desert biomes have high UI's (Table 2). Species that are ubiquitous (*S. undulatus*), small and hard to observe (*C. brevis*), or centered in the transition zones between formations (*C. collaris*) have low UI's by comparison. Thus, species with UI < 500 are impossible to use for synthetic (biome) interpretation, and those with UI's between 500 and 1000 are not convincing demonstration of biomes but may become indicators when considered collectively (e.g., the significant association of *P. modestum* with *H. texana* and *C. tessellatus* or *C. exsanguis* with *E. multivirgatus*).

The ecologic divergence of species within *Phrynosoma* and *Cnemidophorus* and the implied reduction of competition allows additional interpretation. *P. cornatum* inhibits Shrub Desert, *P. modestum*, Succulent Desert, and a third species (*P. douglassi*) lives only in grassland remnants in the Evergreen Woodland and Coniferous Forest (Gehlbach and Holman 1974). *C. inornatus* occurs in Shrub Desert generally, *C. tigris*, in arenaceous areas of this biome, and *C. gularis*, in grassland remnants here, whereas *C. tessellatus* denotes Succulent Desert and *C. exsanguis*, the desert-woodland transition (*C. tigris, C. gularis, P. douglassi*, and *Crotaphytus wislizeni* are the comparatively scarce and/or infrequent, non-

TABLE 2. Guadalupe Escarpment lizards ranked according to Utility Index (UI = C × F/K).

| Utility Index | Species | Components of Utility Index | | | |
|---|---|---|---|---|---|
| | | Conspicuousness (C) | | Fidelity (F) | Congruity (K) |
| | | Mean S-V (mm) | × No. | $\Sigma \chi^2$ | No. |
| 2754 | *Cnemidophorus inornatus* | 54 | 1.5 | 34 | 1 |
| 2538 | *Uta stansburiana* | 47 | 2.0 | 27 | 1 |
| 2442 | *Phrynosoma cornutum* | 74 | 1.5 | 22 | 1 |
| 1746 | *Sceloporus poinsetti* | 97 | 2.0 | 18 | 2 |
| 1436 | *Cnemidophorus tessellatus* | 87 | 1.5 | 11 | 1 |
| 1360 | *Holbrookia texana* | 68 | 2.0 | 10 | 1 |
| 784 | *Eumeces obsoletus* | 98 | 1.0 | 16 | 2 |
| 736 | *Urosaurus ornatus* | 46 | 2.0 | 16 | 2 |
| 712 | *Eumeces multivirgatus* | 57 | 1.0 | 25 | 2 |
| 599 | *Phrynosoma modestum* | 57 | 1.5 | 7 | 1 |
| 560 | *Cnemidophorus exsanguis* | 83 | 1.5 | 9 | 2 |
| 180 | *Crotaphytus collaris* | 90 | 2.0 | 2 | 2 |
| 114 | *Sceloporus undulatus* | 57 | 2.0 | 2 | 2 |
| 75 | *Coleonyx brevis* | 50 | 1.0 | 3 | 2 |

ordinated lizards). The two species of *Sceloporus* and two of *Eumeces* are also potential examples of competitive exclusion (Fig. 1).

There are still other questions of interpretive value. For instance, if Succulent Desert vegetation developed from the Evergreen Woodland (Axelrod 1958; Wells 1966), has a distinctive lizard fauna developed with it? On the Guadalupe Escarpment certain Succulent Desert lizards are distinctive, indeed, and support the recognition of separate Succulent and Shrub Desert Biomes (*see* Shreve 1942; Gehlbach 1967). Moreover, these Succulent Desert indicators (*H. texana, C. tesselatus, P. modestum*) denote the Chihuahuan Desert Region with fidelity equal to that of dominant plants (e.g., *Agave lecheguilla* and *Viguiera stenoloba*), because they extend barely, if at all, into the Sonoran Desert Region. Are the lizard indicators useful in defining the Succulent Desert Biome elsewhere in the Chihuahuan Desert Region?

On the north side of the Chisos Mountains, Texas, the Shrub Desert Formation gives way to the Succulent Desert Formation at 1060 to 1460 m (Gehlbach 1967). Coincidently, *C. tigris* of the Shrub Desert is replaced by *C. scalaris* (Degenhardt 1966), the Chisos counterpart of *C. tessellatus* in Succulent Desert. However, *H. texana* is abundant down to 850 m. *H. texana* occupies a more xeric position in this Chisos Mountains environmental gradient than on the Guadalupe Escarpment, exactly as described for such Succulent Desert plants as *A. lecheguilla* and *V. stenoloba* by Gehlbach (1967). I believe its downward shift corresponds to that of the vegetation, and *H. texana* remains a valid Succulent Desert indicator in company with *C. scalaris*.

As indicated by York and Dick-Peddie (1969), some of the Shrub Desert Biome—perhaps the Succulent Desert also—was Desert Grassland until the 1870–90 era of overgrazing. Now, with protection from livestock and the recognition of fire as a natural factor, grass coverage is increasing on the Guadalupe Escarpment (Kittams 1972). If grasses become dominant and the Grassland Formation (Biome)-class requires interpretation, I suggest that *Cnemidophorus gularis* be considered as a potential indicator of Desert Grassland and *Phrynosoma douglassi* of Montane Grassland.

## HUMAN IMPACT

To study temporal change in the Succulent Desert Biome caused by pipeline construction, I placed four 0.2-ha study plots astride the construction scar at 1311 m on a north-facing slope in Bat Cave Draw, Carlsbad Caverns National Park. The scar, completely denuded of vegetation, was created in 1963. Lizards were counted as described above and vegetation sampled in 2-m radius, circular plots within each larger plot. To assay secondary succession in Evergreen Woodland affected by livestock grazing, I placed a 1-ha plot inside a fence and another immediately outside it at 1585 m in Bear Canyon, Guadalupe Mountains National Park. Lizards were counted as usual,

and vegetation sampled along two 60-m point-quarter transects in each plot (*see* Gehlbach 1967).

Plant succession on the pipeline scar follows the customary ecologic pattern of increasing species richness and equitability (Table 3). The summer dry (June) and wet (September) floral differences are expected. Unexpectedly, however, woody species are not important in the revegetation sequence of Succulent Desert, by contrast with Shrub Desert, nor are leading dominants as important as in the secondary succession of Shrub Desert (Muller 1940; Vasek et al. 1975). Instead, *Salsola kali* rapidly gives way to a variety of grasses. The successional importance of grasses in the

TABLE 3. Secondary succession on a pipeline scar in the Succulent Desert, Guadalupe Escarpment. Mean relative density from 2 to 4, 0.2 ha study plots is given for selected species (those with at least 50% frequency on a specific date). Species dominant in nearby, undisturbed plots are marked with an asterisk.

| Species | September 1964 | June 1965 | September 1966 | June 1967 |
|---|---|---|---|---|
| | PLANTS | | | |
| *Salsola kali* | 54 | 1 | 1 | |
| *Tridens pilosus** | 26 | 19 | 35 | 4 |
| *Croton corymbulosus* | 2 | 7 | 3 | |
| *Euphorbia fendleri* | 1 | 6 | 1 | |
| *Verbena wrightii* | | 9 | 5 | |
| *Aristida glauca* | | | 8 | |
| *Enneapogon desvauxii* | | | 7 | |
| *Bouteloua gracilis* | | | 4 | |
| *Leptoloma cognatum* | | | 3 | 4 |
| *Tridens muticus** | | | 2 | 4 |
| *Viguiera stenoloba** | | | | 3 |
| *Leptochloa dubia* | | | | 3 |
| *Panicum hallii* | | | | 6 |
| *Mimosa biuncifera* | | | | 6 |
| *Andropogon barbinodis* | | | | 17 |
| *Muhlenbergia setifolia** | | | | 21 |
| Species Richness (S) | 6 | 7 | 12 | 11 |
| Equitability (Shannon–Weiner $H'\log_2$) | 1.8 | 2.4 | 2.7 | 3.0 |
| | ADULT LIZARDS | | | |
| *Holbrookia (Cophosaurus) texana** | 43 | 38 | 41 | 29 |
| *Cnemidophorus tessellatus** | 14 | 31 | 12 | 11 |
| *Crotaphytus collaris* | 29 | | 6 | 11 |
| *Phrynosoma modestum** | | 8 | 6 | 7 |
| *Cnemidophorus exsanguis* | | 8 | 6 | |
| *Sceloporus poinsetti** | | 8 | 6 | |
| *Sceloporus undulatus* | | | 23 | 21 |
| Species Richness (S) | 4 | 6 | 7 | 8 |
| Equitability (Shannon–Weiner $H'\log_2$) | 1.8 | 2.0 | 2.4 | 2.5 |

Succulent Desert is substantiated by a similar study of a pipeline scar in the Chisos Mountains, Texas (Whitson 1974).

Lizards exhibit a successional pattern similar to that of plants on the pipeline scar. Lizard species richness and equitability increase concomitantly with the S and $H'$ of plants ($r = 0.86, 0.95$, respectively, $P < 0.05$; Table 3). Regardless of dry and wet seasonal differences in relative abundance—many adults of *Cnemidophorus* are torpid in September—there may be a trend toward lower density per species due to increased coverage of vegetation and preference of the listed heliotherms for open ground. It is significant that *H. texana* and *C. tessellatus*, two indicators of undisturbed Succulent Desert, are present throughout the temporal sequence. I have observed such fidelity after fire in this biome when increased grass cover produces habitat similar to that of seral vegetation on this pipeline scar (*see* Kittams 1972).

If climax dominant plants are eliminated and slow to reinvade during secondary succession, but dominant lizards remain or reappear more quickly than the plants (Table 3), lizards may be better indicators of biomes on impacted sites. However, this hypothesis must be tested against grazing impact because pipeline construction and grazing may have very different effects on plants and lizards. In any biome grazing is constant disturbance that displaces lizards mechanically while attracting heliothermic species through the production of habitat. Conversely, construction is a one-time factor. Lizards will tend to reinvade following cessation of the mechanical disturbance, but increasing vegetation cover may counteract the invasion.

In the Evergreen Woodland, an increase in disturbance indicator plants accompanies grazing (e.g., *Aster hirtifolius, Croton corymbulosus*, and *Gutierrezia sarothrae*, Table 4). *Fallugia paradoxa* and *Brickellia lacinata*, woody species of naturally disturbed sites such as streambeds (Gehlbach 1967), are important only in the grazed plot. Especially palatable species such as *Quercus grisea* and *Dalea formosa* are affected adversely there. Of the lizards, only *C. exsanguis* remains unaffected in the woodland indicator group; both species of *Eumeces* decline. Two Succulent Desert species (*H. texana* and *P. modestum*) become more abundant, and one (*C. tessellatus*) declines.

The appearance of grazed Evergreen Woodland begins to approximate that of Succulent Desert because diversity falls (*see* Table 4, Fig. 1). There is a net loss of one plant and one lizard, and equitability declines by 0.3 in plants and in lizards. Although the lizard component seems more stable, since its relative change in equitability is slightly less (9% versus 10% in plant $H'$), there are revealing changes in species composition among the eight lizards that should be equally abundant in both plots on the basis of their proximity. Are *C. collaris, H. texana*, and *P. modestum* responding positively and *C. tessellatus, E. multivirgatus*, and *E. obsoletus* negatively to changes in vegetation-type as shown by increases and decreases in IV's,

TABLE 4. Secondary succession in adjacent protected (1946-62) and grazed plots of Evergreen Woodland, Guadalupe Escarpment. Importance value of each plant and lizard in August 1962 is given.

| Species | Protected | Grazed |
|---|---|---|
| PLANTS | | |
| *Quercus grisea* (complex) | 133 | 83 |
| *Rhus trilobata* | 132 | 103 |
| *Mimosa biuncifera* | 100 | 132 |
| *Juniperus pinchotii* | 74 | 58 |
| *Tridens muticus* | 58 | 23 |
| *Tridens pilosus* | 43 | 159 |
| *Lesquerella fendleri* | 30 | 7 |
| *Nolina microcarpa* | 29 | 23 |
| *Viguiera stenoloba* | 29 | 59 |
| *Opuntia phaeacantha* | 20 | 28 |
| *Cassia roemeriana* | 13 | 6 |
| *Opuntia imbricata* | 6 | 12 |
| *Euphorbia vermiculata* | 6 | 7 |
| *Mimosa borealis* | 75 | |
| *Thelesperma longipes* | 51 | |
| *Viguiera cordifolia* | 39 | |
| *Dalea formosa* | 37 | |
| *Aristida glauca* | 32 | |
| *Muhlenbergia emersleyi* | 22 | |
| *Dasylirion leiophyllum* | 13 | |
| *Eriogonum harvardii* | 8 | |
| *Verbena perennis* | 8 | |
| *Fallugia paradoxa* | | 31 |
| *Croton corymbulosus* | | 23 |
| *Brickellia laciniata* | | 9 |
| *Aster hirtifolius* | | 9 |
| *Polygala obscura* | | 8 |
| *Condalia ericoides* | | 7 |
| *Abutilon incanum* | | 6 |
| *Gutierrezia sarothrae* | | 5 |
| Species Richness (S) | 22 | 21 |
| Equitability (Shannon-Weiner $H'\log_2$) | 3.9 | 3.6 |
| ADULT LIZARDS | | |
| *Cnemidophorus exsanguis* | 39 | 38 |
| *Sceloporus undulatus* | 26 | 22 |
| *Cnemidophorus tessellatus* | 13 | 5 |
| *Holbrookia texana* | 4 | 11 |
| *Phrynosoma modestum* | 4 | 17 |
| *Eumeces multivirgatus* | 4 | |
| *Eumeces obsoletus* | 9 | |
| *Crotaphytus collaris* | | 5 |
| Species Richness (S) | 7 | 6 |
| Equitability (Shannon-Weiner $H'\log_2$) | 2.5 | 2.2 |

respectively? If so, what magnitude of faunal change is apparent to the park visitor?

I think the Utility Index can answer this question. If the change in IV or density of a lizard, i.e., its difference in experimental versus control plots or the first versus last stages of a time series, is divided into its UI ($UI/\Delta IV = P_i$), and the dividend is added to the similarly calculated dividends of all lizards in the plots and divided by the sum of unadulterated UI's of the same species, the resulting percentage reflects the amount of succession ($\Sigma P_i / \Sigma(UI)_i \times 100$). For the Evergreen Woodland example (Table 4), this procedure reveals that 23% of the indicator value of the lizard fauna is gone. Calculated separately for the increasers and decreasers named above, I find 13% and 15% changes, respectively. In the Succulent Desert example (Table 3), I note a 32% change in the September lizard fauna and a 19% change in the June fauna—a mean of 26%.

## SUMMARY

Shrub Desert, Succulent Desert, Evergreen Woodland, Deciduous Woodland, and Coniferous Forest are plant formations on the Guadalupe Escarpment. Because of distinctive physiognomy, each is easily identified by visitors to Carlsbad Caverns and Guadalupe Mountains National Parks. The Shrub and Succulent deserts are further indicated by characteristic groups of lizards. Neither woodland formation has such a group, but the woodland formation-class can be distinguished from each desert by means of lizard faunas. Thus, each desert qualifies as a biome.

Secondary succession in the Succulent Desert, incident to pipeline construction, is similar to that following fire and is quite dissimilar to secondary succession in the Shrub Desert. Weedy invaders give way to grasses, and climax dominants are relatively unimportant. Lizards typical of Succulent Desert are less affected. In the Evergreen Woodland, livestock grazing affects lizards and plants in similar fashion, producing a desert-like aspect with some species increasing and others decreasing in importance. Lizards are potentially equal to plants in the interpretation of human impact as well as natural landscapes.

Because of differences in size, behavior, and ecologic distribution, lizards are more or less useful to the general public as biome indicators. A Utility Index accentuates those species attributes that facilitate observation in particular biomes and ranks the 14 most abundant and frequently seen lizards. Species at the top of the list can be used most effectively to interpret living landscapes to the park visitor. In addition, the Utility Index can be used to indicate the magnitude of secondary succession on impacted sites. Such interpretation is necessary because of the pervasive influence of man on the Guadalupe Escarpment.

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# *Research in National Parks*

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This was our first involvement with research in the National Parks and we would like to make some observations concerning interactions among basic researchers, park personnel, and the philosophy on which our park systems are based. Our conclusions are not based only on our own experiences, but also on conversations with other basic researchers (especially those who contributed to this symposium) and with park personnel who have aided and worked with other researchers who were not employed by the National Park Service.

The National Parks are excellent places to conduct some types of basic research. A prerequisite for any research in a National Park is that it must not be detrimental to the park or to the basic goals of the park. If a plan for basic research harmonizes with the park's ecosystem and goals, the worker has several things to his advantage: (1) There generally are good records concerning the history of the park relative to human impact, weather, and past management plans. Such records are extremely valuable to many types of biological investigations. (2) Human interference generally can be controlled by proper site selection and with the aid of park personnel. (3) Park personnel are an extremely valuable adjunct to research. We were assisted in many ways, but their understanding of the biology of the park, logistical support, and observations during our study were the most notable. We never found park personnel less than cooperative. (4) Ecosystems within the park boundary often are less altered than comparable sites on private and other types of public lands. (5) Long range studies can be set up with reasonable assurance that they can be carried to completion.

The above are some of the advantages that research within the park offers to the basic researcher. Some comments are needed relative to what value such research is to the park and to the responsibility of the basic researcher to the park. Basic research adds to knowledge of our natural resources and our national heritage within the park. Such data always are valuable when preparing an inventory or establishing goals for a specific park. However, we found most of the basic researchers unaware of the need to communicate knowledge from basic research to park personnel so that it can be used in

park planning. Researchers conducting basic biological research within park boundaries are the best qualified personnel to evaluate the nature and value of the park's biological systems. This is not to say that researchers should set park policy, but it is essential that their findings are available to park personnel who are responsible and trained to set park policies and goals.

The subject of this symposium is a park rich in unique biological systems and situations that are of considerable esthetic and educational value to park visitors. A delicate balance must be achieved between meeting the needs and wishes of the general public and protecting the fragile nature of the ecosystem. At the present time, most of the park is accessible only by walking and it seems best that a considerable portion remains that way.The establishment of a biological preserve that will protect and harbor many of the unique species of the park also should be considered. During and following the symposium it became apparent that most participants would welcome an educational plan to aid visitors in enjoying the park, although there was no general agreement as to what that plan should be. However, this was a "first meeting" of the group and many ideas were undergoing the refinement of discussion and counter-discussion. If a group (probably consisting of 5 to 10 park personnel with an equal number of outside scientists) worked on such an educational plan over several meetings, a feasible plan with alternatives probably would result.

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