THE MAMMALS OF
THE EDWARDS PLATEAU,
TEXAS

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INTRODUCTION

The Edwards Plateau is the southern-most extension of the Great Plains of North America. The name of the region is taken from the Edwards limestone formation, which underlies most of the region treated in this study. An exception to this is a portion of the Llano Uplift occurring in the northeastern portion of the study area in Concho, Llano, Mason, McCulloch, Menard, and San Saba counties. The region covers approximately 40,000 square miles in central Texas, and all or part of 42 counties.

Naturalists have been active in this region since the early nineteenth century. Jean Louis Berlandier, the Swiss naturalist, studied the plants and animals around New Braunfels and the Comal County area in the years 1828-1834 (Pool, 1975). Other early naturalists on the Edwards Plateau included Ferdinand Roemer, a German who arrived in Texas in 1845, and subsequently, published works dealing with the topography, geology, mineral products, botany, and zoology around the New Braunfels area (Sellards et al., 1932). Dr. Thomas Hopkins Webb, a zoologist, passed through part of the Edwards Plateau around 1857, while associated with John Russel Bartlett and the Mexican Boundary Survey Commission (Sellards et al., 1932; Pool, 1975). At the end of the nineteenth century, the naturalist Mr. H. P. Attwater collected information and specimens of mammals from Bexar and Kerr counties and the surrounding area; sending many of the specimens and his field notes to Dr. J. A. Allen at the American Museum of Natural History. Allen (1896) subsequently published this information, thus contributing to information concerning mammals in the Edwards Plateau region.

Vernon Bailey surveyed the flora and fauna of Texas at the beginning of the twentieth century (1905) and discussed the natural history and distributions of many mammals from the Edwards Plateau. He also designated several new species in his Biological Survey of Texas. Bailey utilized specimens and field notes taken by biological survey workers, specimens examined from the United States National Museum of Natural History and the American Museum of Natural History, and observations from local residents such as the Kerr County naturalist, Howard Lacey. William B. Davis and workers from Texas A&M University, College Station, Texas, collected mammals from the Edwards Plateau, and Davis discussed the mammalian fauna of the region in his three books on the mammals of Texas (Davis, 1960, 1974; Davis and Schmidly, 1994). W. Frank Blair and associates at the University of Texas at Austin collected mammal specimens from the region, primarily in the 1950’s, and Blair published work on bats of the region (Blair, 1952). Walter W. Dalquest and colleagues from Midwestern State University, Wichita Falls, Texas, collected specimens of mammals primarily from the central and western Edwards Plateau in the 1960’s. Dalquest and Kilpatrick (1973) published a study on pocket gophers found on the Edwards Plateau. Many researchers from various institutions have done systematic studies of selected mammalian taxa which occur on the Edwards Plateau; for example Carter (1962) on Tadarida brasiiliensis, Schmidly (1972) on Peromyscus pectoralis, Yates and Schmidly (1977) on Scapopus aquaticus, Kennedy and Lindsay (1984) on Procyon lotor, Schmidly and Reid (1986) on Felis rufus, Baker et al. (1988) on lasiurine bats, Manning et al. (1988) on Antrozous pallidus, and Stangl et al. (1991) on Erethizon dorsatum to list but a few studies.

Robert L. Packard and associates from Texas Tech University began collecting mammals from the Edwards Plateau and vicinity, and their work often centered around the Texas Tech University Center at Junction, Kimble County, Texas. The mammalian faunas of the surrounding physiographic regions have been reported upon previously (Blair, 1952; Schmidly, 1977, 1983; Dalquest and Horner, 1984; Choate, 1991). This work is an attempt to consolidate much of the information on mammalian biogeography and natural history on the Edwards Plateau into a single source. The Edwards Plateau is the last distinct region in Texas to be reported on in this fashion.
METHODS

This project was instigated in the fall of 1989, and information on mammals occurring in the Edwards Plateau region was intensively gathered through the summer of 1994. A total of 5749 museum specimens has been examined from the Edwards Plateau and immediately adjacent areas. Scientific literature has been surveyed to obtain additional information concerning the distribution and systematics of mammals in the study area. I attempted to trap, salvage, and visually survey mammals within each of the 42 counties of the Edwards Plateau. Taxonomy and order of presentation of mammalian species into species accounts follows Jones and Jones (1992) unless otherwise indicated in text.

General distributional information was taken primarily from Hall (1981), Schmidly (1983), and other appropriate sources. Precise distributions of mammals on the Edwards Plateau were developed from specimens examined and other records of mammals residing in the region.

Species accounts begin with distributional information on each species occurring on the Edwards Plateau. Descriptive information for each species follows, and natural history information is subsequently given. External and selected cranial measurements are given in text for most species. All measurements presented in the species accounts are in millimeters. Species accounts end with lists of specimens examined and additional records of occurrence for each species. Lists of specimens examined are arranged alphabetically by county. Specific localities within each county begin with those farthest north and west and end with the extreme southeastern locality. The total number of specimens examined of each taxon is given in parentheses at the beginning of the specimens examined section, and the total number of individuals from each specific locality is given at the end of each locality. Lists of additional records include literature records of mammals from the Edwards Plateau and, in some cases, sight records recorded by me while surveying within the study area. Also included in additional records are many museum specimens from Texas A&M University not personally examined by me. The Texas Cooperative Wildlife Collection was flooded in 1993 and, due to reclamation and relocation efforts, examination of all specimens listed on spreadsheet printouts provided by G. B. Baumgardner was not possible.

Dichotomous identification keys for all of the mammals that presently reside on the Edwards Plateau are provided within the accounts of species. Introduced, probable, extralimital, and extirpated mammals are not included within the identification keys. The identification keys are constructed so that either live specimens or standard museum skins and skulls may be identified to species. An exception to this rule occurs whenever a family of mammals is represented by only a single species on the Edwards Plateau, such as the opossum, porcupine, and beaver. Those particular mammals may be adequately identified by utilizing the ordinal and familial identification keys. Existing keys such as those found in Barbour and Davis (1969), Davis (1974), Hall (1981), Jones et al. (1983), Schmidly (1991), Jones and Manning (1992), and other sources are utilized and are supplemented with mensural and other characters that apply more strictly to the mammals found on the Edwards Plateau. Character states presented within the keys apply only to adult mammals.

Specimens found in the specimens examined lists were examined by me or, in a few cases, by trusted associates and other established researchers. Mitutoyo digital calipers were used to take cranial measurements, and external measurements were obtained from specimen labels and in some instances from literature sources. External measurements taken from specimen tags were used only if the preparator was known to be a careful and meticulous researcher, except in cases where only a few records of a species were available for the Edwards Plateau. In those cases, the external measurements recorded on specimen labels were used if they fell within all accepted size ranges for the particular species. External measurements have been rounded to the nearest millimeter, excepting cases where fractional units may be helpful in species discrimination. Cranial measurements are recorded to the nearest one-hundredth millimeter. Sources describing the cranial measurements are given in text.
The majority of localities of specimens taken from specimen labels were recorded in statute miles from a population center within a county. Most trained researchers record mileage of collecting localities from mileposts within a township (such as a post office, or the county courthouse if the community is the county seat) or from the center of the community, and I have done the same in my own collecting efforts on the Edwards Plateau. Upon examination of museum specimens, however, it is obvious that not all preparators record localities in the same fashion. In some instances, localities were given from the city limits of a community; which, in many cases, have either expanded or been consolidated within a metropolitan area. In other instances, preparators have given localities from mileposts which are familiar to them, but are difficult to specifically pinpoint on a map. Examples of this would be the locality (Bexar County; I-35 at rest stop between markers 129-130) or (Comal County; Wagoner Ranch). I have attempted to approximate any problematic localities, but, in the event that this proved to be impossible, specimens of uncertain localities were mapped in the center of the specified county. Specimens of problematic localities were only mapped if records of occurrence were considered to be uncommon enough to justify inclusion on distribution maps.

Localities were pinpointed on topographic maps utilizing mileage coordinates given on specimen labels. The localities were then converted to universal transverse mercator (UTM) coordinates using a UTM coordinate grid obtained from Forestry Suppliers, Inc., Jackson, Mississippi. Coordinates were rounded to the nearest 100 meters. Topographic map scale was 1:250,000. If a particular collecting locality could not be pinpointed utilizing topographic maps, it was recorded within the specimen lists as it appears on the museum specimen tag.

All or parts of 42 Texas counties are included within the Edwards Plateau. The counties of concern are: Bandera, Bexar, Blanco, Burnet, Callahan, Coke, Coleman, Comal, Concho, Crane, Crockett, Ector, Edwards, Gillespie, Glasscock, Hays, Howard, Irion, Kendall, Kerr, Kimble, Kinney, Llano, Mason, McCulloch, Medina, Menard, Midland, Nolan, Reagan, Real, Runnels, San Saba, Schleicher, Sterling, Sutton, Taylor, Tom Green, Travis, Upton, Uvalde, and Val Verde. Locations of the counties and the location of the Edwards Plateau within Texas are illustrated in Figure 1.

Symbols plotted upon distribution maps represent areas with a radius of approximately five miles. This is done to reduce clutter when depicting the distributions of taxa that have been collected intensely in limited areas, or taxa with especially well-defined distributions. Localities not represented on the distribution maps are underlined in the specimens examined and additional records sections. Dots are utilized to indicate records of specimens examined. Circles represent sight records and, in limited instances, personal communication records. Triangles are used to map literature records, and squares are used to designate additional records and inexact localities. Sight records are taken from my observations while in the study area and are recorded in my field notes. My field notes and related records are deposited in the Museum of Texas Tech University.

Specimens collected during the course of this study are deposited in the Museum of Texas Tech University. Those specimens and previously collected specimens from the Edwards Plateau deposited at Texas Tech University are not represented by a collection acronym in the specimens examined lists. Other institutions and collections surveyed for mammals from the Edwards Plateau include the Texas Cooperative Wildlife Collection, Texas A&M University (TCWC), Midwestern State University Collection of Recent Mammals (MWSU), Strecker Museum, Baylor University (SM), West Texas A&M, Canyon (WTAM), Vertebrate Collections, Southwest Texas State University (SWTU), Texas Natural History Collection (TNHC), and Angelo State University Natural History Collection (ASNHC).

I have omitted synonymies of species names within species accounts because that information is readily available in other literature sources such as Hall (1981), Schmidly (1983), or the Mammalian Species series published by the American Society of Mammalogists.

The base map of the Edwards Plateau was drafted by me utilizing several sources of information. Appropriate sheets from the Geologic Atlas of Texas series (1:250,000 scale), Bureau of Economic Geology, University of Texas at Austin were utilized, as was the General Soils Map of Texas (1973). Vegetation and plant community studies, such as those of Diamond et al. (1987), and Gould (1975), were consulted for addi-
tional information on appropriate delineation of the region. The Balcones Fault zone was considered as a boundary in the south and east. The Colorado River was utilized to some extent in the north and west. Far northwestern boundaries in Crane, Ector, and Midland counties were difficult to discern by visual means alone. Subsurface geology, soils, and my own judgment were utilized to establish the boundary of the Edwards Plateau in this area of the study. The map, as a whole, is in good agreement with other maps that attempt to delineate the Edwards Plateau. The Stockton Plateau, immediately west of the Pecos River, is often considered to be part of the Edwards Plateau. This area was not included in the study because it is sometimes placed with the more arid Trans-Pecos region (Tharp, 1939) and Schmidly (1977) treated mammals of the area in his *Mammals of Trans-Pecos Texas*.

Numbers of a particular species occurring on the Edwards Plateau that are deposited in museum collections do not necessarily infer information on that species' abundance in the region. Stangl and Jones (1987) discovered both a geographic and seasonal bias of mammals deposited in the mammal collections of both Midwestern State University and Texas Tech University. This bias is due, in part, to research efforts of individuals at the institutions, timing of courses wherein mammals are collected by students and others for study, and other factors such as the regional nature of some mammal collections. I have attempted to collect specimens from all counties of the Edwards Plateau, but I have also relied upon regional representation of mammals in collections of such institutions as Angelo State University and Southwest Texas State University. Areas surrounding institutions with mammal collections were...
lightly surveyed by me because of a tendency for a regional bias in mammal collections and greater numbers of mammals from areas close to these institutions being deposited in their mammal collections. Particular taxa may be present in greater numbers in mammal collections because of past research upon those taxa, and, thus, do not readily provide abundance data for the Edwards Plateau. In addition, some mammals, such as pocket mice, bats, pocket gophers, and ground squirrels, are more active during particular seasons of a year, whereas, other mammals may be obtained throughout the year. Some mammals are more readily collected than others, and some mammals, such as skunks and weasels, are either avoided by most collectors or are difficult to obtain. All of these factors help to create bias in numerical representation of a particular species from the Edwards Plateau. Any inference of population numbers taken from these types of data should be considered along with other factors, such as a species’ overall distribution, ecology, and life history.
ENVIRONMENT OF THE EDWARDS PLATEAU

GEOLOGY

The geologic history of the Edwards Plateau region and associated Llano Uplift region dealt with in the study is a complex one. The study area contains a portion of the Llano Uplift in Blanco, Gillespie, Kimble, Llano, Mason, McCulloch, and San Saba counties (Fig. 2). The Llano Uplift is of Precambrian and Cambrian age (600 million years and older) and was once overlain by Cretaceous limestone formations that have since been eroded away. The Edwards Plateau stratigraphy was deposited during the Cretaceous period approximately 63 to 135 million years ago. A small portion of the Edwards Plateau occurs as an outlier in Callahan, Coke, Nolan, and Taylor counties, and is designated as the Callahan Divide (Sellards et al., 1932). The Callahan Divide is composed of limestone formations similar to those found throughout the Edwards Plateau, proper, and was formed during the same period of time.

The Llano Uplift is formed of marine sediments basally. These strata are devoid of fossils, and, thus infer the great age of this geologic formation. The sediments became indurated and later intrusive magma elements pushed through the sediments giving rise to the black granite and marble elements that may now be observed in exposed sections throughout the region.

Figure 2. Geologic regions of the Edwards Plateau.
Limestone-forming sediments were deposited over the Precambrian and Cambrian rocks, but subsequent faulting and foldings elevated the region and created a doming effect. The Llano Uplift is approximately 1000 feet above sea level, and the nearest Precambrian formations are 4000 or more feet below sea level (Sellards et al., 1932).

The Edwards Plateau, with its numerous geologic formations, is the result of persistent marine inundation, sedimentation, reef formation, and faulting events (Rose, 1972). Conditions during the formation of the Edwards limestone and associated limestone formations varied locally, and resulted in the deposition, and genesis of differing limestone elements across the region. Depositional environments ranged from tidal flat marine environments to restricted marine environments (Rose, 1972). Evidence for the differing environments is supported by both paleontologic and lithologic studies of the various strata throughout the region (Matthews, 1951; Moore, 1964; Rose, 1972).

The Edwards Plateau was submerged during the Cretaceous by an epicontinental body of water called the Fredericksburg Sea. This marine environment instigated the development of a rudistid reef province over the central Texas craton (Frost, 1967). The Stuart City reef trend also formed a barrier reef along the margins of the ancestral Gulf of Mexico basin, thus, isolating the Edwards Plateau region from the southern, pelagic, marine environments (Rose, 1972). Water levels appear to have been lower in the northern parts of the Edwards Plateau, and the waters were warm, clear, and of normal salinity over much of the region (Matthews, 1951). The limestone elements formed over mostly Cambrian-age strata and the Edwards limestone formation is much thicker and more extensive in the southern Edwards Plateau than in the northern regions (Frost, 1967).

The genesis of rudistid reefs in the area and faulting and tectonic activities along the Luling and Balcones Fault zones changed the nature of the sedimentation environments by isolating some areas of the Edwards Plateau. Marly elements and fine-grained sediments were deposited over the Edwards limestone in many of these areas. Discolored limestone elements and muddy limestones indicate turbid conditions (Moore, 1964). In addition, isolated areas sometimes became hypersaline or may have originated over surfaces with high magnesium concentrations. The Edwards limestone underwent diagenesis into dolomite elements in these hypersaline environments (Moore, 1964). Dolomitization of the limestone forming sediments may also have occurred during the original deposition of the sediments or when the Edwards formation was buried beneath other sediment types (Rose, 1972).

After the deposition of the limestone strata in the Edwards Plateau region, the area was subsequently uplifted as a result of tectonic activity along the Balcones Fault. The entire region was raised about 2000 feet with very little folding, which resulted in an extensive, flat plateau. The limestone throughout the region has undergone extensive erosion, resulting in the exposure of older limestone formations in some areas of the Edwards Plateau, while, in other areas, the Edwards limestone is still subsurface (Riskind and Diamond, 1988). Two generalized geologic sections are illustrated in Figure 3.

Subsurface erosion of the Edwards limestone formation as a result of water percolating through fissures along the Balcones Fault has created an important underground aquifer. The Edwards Aquifer recharge zone extends along the Balcones Fault from northcentral Kinney County northeast to Hays County, covering an area approximately 30 miles in width and 175 miles in length. The Edwards Aquifer and its drainage and watershed area includes all or parts of 13 counties in the extreme southern and southeastern Edwards Plateau. Major surface streams which collect surface runoff water include the West Nueces River, Nueces River, Dry Frio River, Frio River, Sabinal River, Seco Creek, and Hondo Creek (Thornhill, 1987). The water is confined in the Edwards limestone primarily by compression between the older, more resistant Glen Rose limestone below and the Del Rio Clay formation above (Fig. 3).

Recharge of the aquifer has averaged approximately 600,000 acre-feet per year, but varies depending upon rainfall and drought conditions each year (Hardin, 1987). Water moves easily through the aquifer, with rates of up to one mile per year being recorded. Water moves initially to the south and then toward the east and northeast (Hardin, 1987). The major traditional outlets of the Edwards Aquifer are the Guadalupe River, Comal Springs in Comal County, and San Marcos Springs in Hays County (Hardin, 1987). The Edwards Aquifer contributes major percentages of water to the
Figure 3. Generalized geological sections of the Edwards Plateau. Note difference in depth and thickness of Edwards limestone formation and location of Edwards aquifer.
Blanco, Guadalupe, and San Marcos Rivers, especially during times of drought. Comal Springs has contributed up to 65.3 percent of the Guadalupe River's flow, and San Marcos Springs has contributed up to 86.9 percent of flow to the San Marcos and Blanco rivers at their confluence during abnormally dry years (Thornhill, 1987). Average discharge through various spring outlets, prior to withdraw by wells, may have been as great as 600,000 acre-feet per year. Recorded discharge highs at Comal and San Marcos Springs totaled 390,000 acre-feet per year prior to 1927 (Thornhill, 1987). The Edwards Aquifer appears to have only a small storage capacity and any withdrawn water is equated as a one-to-one exchange between recharge and discharge levels. Well withdrawals have increased in recent years around metropolitan areas, such as San Antonio and San Marcos, with the result of reduced spring flow levels in Comal and San Marcos Springs (Thornhill, 1987).

**PHYSIOGRAPHY**

The Edwards Plateau is highest in elevation in the northwestern portion and lowest around the Balcones Fault zone in the south and east. Elevation at Big Lake, Reagan County, in the northwest is 734 meters above sea level and decreases to 167 meters at Austin, Travis County (Riskind and Diamond, 1988). Throughout most of the eastern and central portions of the region, the terrain is composed of small hills (hence the name Hill Country) and valley systems.

The most highly dissected and variable terrain on the Edwards Plateau is found along the Balcones Fault zone on the eastern and southeastern areas. Riskind and Diamond (1988) term this area the Balcones Canyonlands. Numerous deep stream and river channels are found in this area and relief of some of these areas is high. For instance, hills rise above the Frio River, west of San Antonio to a height of 524 m and the valley areas are 372 m in elevation (Riskind and Diamond, 1988). The Llano Uplift in the northeastern portion of the region is also elevated, with Enchanted Rock (north of Fredericksburg) elevated 130 m above the surrounding landscape.

The central Edwards Plateau is less broken and dissected than the Balcones canyonlands, but limestone formations and rocky slopes are still evident in many areas. Much of this area is savannah-like in aspect, with grasslands predominating and small mottes of trees in many cases. Breaks in the Plateau occur in the riverine systems within the central Edwards Plateau.

Most of the northern Edwards Plateau presents the aspect of a mesa region. The Cretaceous limestone formations forming the base of the Edwards Plateau are elevated above the Rolling Plains region in this area and form hills with steep slopes and almost level summits. An exception to this occurs in the area around Midland and Odessa on the far northwestern Edwards Plateau. Where the Edwards Plateau and Llano Estacado interdigitate in this area, the terrain has been eroded to a flat, relatively unbroken plain. No major watercourses are found in this portion of the Edwards Plateau, excepting the Pecos River to the south and west.

The extreme southwestern Edwards Plateau is relatively flat and unbroken in Crockett County, but the area increases in relief farther south around the Devils River and in Val Verde County. The area is essentially treeless. Thin soils cover the area and on many slopes the vegetation appears to be persisting in discrete levels because of the highly eroded nature of the region.

Numerous rivers and streams either have their headwaters on or flow through the Edwards Plateau. Some of the major rivers include the Colorado, Concho, Devils, Llano, Medina, Pecos, Perdenalis, San Antonio, San Saba, and Frio (Fig. 4). The Devils River and its immediate tributaries on the far western Edwards Plateau are frequently dry, but are subject to periodic flash floods. The more eastern rivers may also flood upon occasion and water runoff into rivers and streams throughout the region is high. The predominately shallow soils and elevated terrain contribute to water runoff rates.

Reservoirs have been created on the Edwards Plateau and adjacent areas in order to supply urban areas with water. Most have been constructed by damming across rivers in the region. Some of the major reservoirs are the Amistad Reservoir in Val Verde County (on the Rio Grande), Lake Buchanan in Burnet and Llano counties (on the Colorado River), Medina Lake between Medina and Bandera counties (on the Medina River), Twin Buttes Reservoir in Tom Green County (on the Concho River), E. V. Spence Reservoir in Coke County (on the Colorado River), and Stacy Reservoir between Coleman, Concho, and Runnels counties (on the Colorado River). The greatest number of impoundments
are located along the course of the Colorado River on the Edwards Plateau, however, excluding the Rio Grande, the other rivers have their headwaters on the Edwards Plateau and, thus, are not as extensive within the Edwards Plateau.

CLIMATE

The climate of the Edwards Plateau falls within two broad climate classifications within the state of Texas. The two climatic regimes are: 1) a subtropical steppe climate on the far western Edwards Plateau that extends eastward roughly through Howard and Sterling counties in the north, Schleicher County in the central Edwards Plateau, and Uvalde County in the south, and 2) a subtropical subhumid climate is prevalent in the central Edwards Plateau and has its eastern limits along the Balcones Fault zone in Travis, Hays, and Comal counties (Larkin and Bomar, 1983). The subtropical steppe climate of the western Edwards Plateau is characterized by prevailing semi-arid to arid conditions throughout the year. The subtropical subhumid climate of the remainder of the Edwards Plateau is characterized by hot summers and dry winters (Larkin and Bomar, 1983).

Average annual precipitation (taken from 1951 to 1980 averages) varies greatly from lows in the western section to highest annual precipitation at the Balcones Fault on the eastern margin of the Edwards Plateau (Table 1). Average annual precipitation ranges from 12 inches per year in Crane County on the west to a high of 32 inches per year in Travis and Bexar counties (Fig. 5) to the east (Larkin and Bomar, 1983). Most precipitation on the Edwards Plateau falls in the form of rain. An exception to this west to east rainfall gradient is along the Balcones Fault zone. Rainfall levels in Kendall County in the southwest are almost the same as those in the far western counties.
Table 1. Annual climatic profiles of selected counties of the Edwards Plateau. Counties were selected to represent a transect from the western to the eastern margins of the Edwards Plateau. Temperature is in degrees Fahrenheit and precipitation is in inches. Data from Griffiths and Bryan, 1987

<table>
<thead>
<tr>
<th>County</th>
<th>Temperature</th>
<th>Precipitation</th>
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<tbody>
<tr>
<td>Upton Co.</td>
<td>80</td>
<td>52</td>
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<td>Reagan Co.</td>
<td>77</td>
<td>48</td>
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<tr>
<td>Irion Co.</td>
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<td>50</td>
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<td>Schleicher Co.</td>
<td>76</td>
<td>49</td>
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<td>Menard Co.</td>
<td>79</td>
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<td>Mason Co.</td>
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<td>51</td>
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<tr>
<td>Llano Co.</td>
<td>79</td>
<td>53</td>
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<tr>
<td>Burnet Co.</td>
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<tr>
<td>Travis Co.</td>
<td>79</td>
<td>58</td>
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Figure 5. Map depicting rainfall isoclines on the Edwards Plateau. Precipitation is measured in inches. Isoclines are based upon 30 year averages.
as those for Travis County to the east (Bomar, 1983). The Balcones Escarpment causes an abrupt rise in air currents, and this rise tends to channel more warm, moist air originating in the Gulf of Mexico into adjacent western areas; thus causing an increase in precipitation in the area (Bomar, 1983). Precipitation rates tend to be highest in the spring and autumn months, with an east to west decrease in precipitation levels in the summer months (Bomar, 1983; Riskind and Diamond, 1988). Evapotranspiration rates throughout the region are also highest in the summer months due to a decrease in precipitation and an increase in daily temperatures.

Flooding occurs in the region as a result of the slope-and-valley nature of the terrain and sparse groundcover in many areas. Tropical storms tracking through the Edwards Plateau have been responsible for some flooding events in the past (Bomar, 1983). Localized flooding may occur when thunderstorms build up in discrete areas in the spring and autumn months. Hail may occasionally be formed in these convectional thunderstorm events and cause damage to some areas, and tornadoses have damaged the communities of Rocksprings, Burnet, and New Braunfels in the past (Bomar, 1983).

Average annual high and low temperatures (taken from 1951 to 1980 averages) tend to vary along a southwest to northeast gradient. Average annual temperatures are highest on the southwestern Edwards Plateau; the coldest annual temperatures tend to occur in the north and northeast. The extreme northwest Edwards Plateau, where it borders the Llano Estacado, usually has the coldest winter temperatures (Larkin and Bomar, 1983). Temperatures may become low enough over most of the Edwards Plateau for snow to fall. The region usually receives a few snowfalls each year, but the accumulation of snow is ordinarily only a few inches at best (Bomar, 1983). Periods of snowfall normally last only a few days, and snow is most likely to occur in January and February (Bomar, 1983).

Prevailing wind directions (taken from 1961 to 1980 averages) are often variable across the Edwards Plateau, as are wind speeds. Winds tend to be the strongest in the western and northern regions (Larkin and Bomar, 1983), but speeds are seasonally variable and much fluctuation may occur as the result of strong fronts entering the Edwards Plateau from the North in winter and the encroachment of tropical storms from the South-east in spring and summer months. Wind direction in the months of March through August is predominately from the South to Southeast. Wind direction in the months of September through November is generally from a southerly or southeasterly direction; however, a higher percentage of days occurs with winds out of a northerly direction. At Midland, Texas, for instance, the winds are west northwest in direction greater than 26 percent of the time during this interval. Winter months, December through February, see an increase in the percentage of days with winds from the North at locations like San Antonio and Austin. Winds at Del Rio on the southwestern and Midland on the northwestern Edwards Plateau remain, respectively, in southeasterly and southern directions (Larkin and Bomar, 1983).

SOILS

Soils are formed by the disintegration and decomposition of underlying parent material. Most parent material of soils on the Edwards Plateau is of a sedimentary nature, with the exception of a portion of the parent material in the Llano Uplift region, which is igneous and metamorphic in origin. Environmental factors such as temperature, moisture, topography, and vegetation contribute to the kinds of soils formed in any particular area (Brady, 1974). Conversely, soils play a major deterministic role in the types of vegetation found in any particular location. Soils formed from limestone parent material are usually high in basic mineral content and tend to support species of trees that can tolerate high levels of metallic cations (Brady, 1974). Most soils occurring throughout the Edwards Plateau have been described as shallow, stony, and thermic in nature (Anonymous, 1981; Riskind and Diamond, 1988).

Five major orders of soils are found on the Edwards Plateau (Godfrey et al., 1973). Soil orders are primarily based upon soil morphology and soil genesis (Brady, 1974). The soil orders within the study area include Mollisols, Alfisols, Aridisols, Vertisols, and Inceptisols. Mollisols on the Edwards Plateau are formed from lower Cretaceous sedimentary rocks of limestone, chalk, and limy earths. These soils are mostly shallow to moderately deep and remain soft in structure when dry. Alfisols are mineral soils with a distinct silicate clay horizon (Brady, 1974) and, on the Edwards Plateau, are formed from weathered granite and sandstone material. Pre-Cambrian granites, gneisses, and schists are also found within the soil regolith (Godfrey
et al., 1973). Aridisols on the Edwards Plateau were formed in dry regions from Cambrian shales, limestones, sandstones, and outwash materials (Godfrey et al., 1973). Aridisols are thermic and sometimes sandy on the Edwards Plateau. Vertisols are limited on the Edwards Plateau and were developed from chalks, shales, marls, and calcareous clays of upper Cretaceous age. Vertisols, because of higher clay content, are prone to cracking and some subsequent mixing of horizons when dry (Godfrey et al., 1973; Brady, 1974). Inceptisols are relatively new in origin and usually have not been as intensively weathered as other soils on the Edwards Plateau. Soil profiles are not as developed in this order as are profiles in the preceding orders. Inceptisols within the region were formed from lower Cretaceous sedimentary rocks and are shallow to moderately deep (Godfrey et al., 1973).

Mollisols and a minor percentage of Vertisols are found on the Callahan Divide and throughout the central Edwards Plateau (Fig. 6; A). The soils in this region are mostly from Tarrant, Kavett, and Tobosa soil series units. These soils are calcareous and clayey and are formed overlimestone, interbedded limestone, and marls. They are level to hilly in relief and support mixed grasses and live oak and juniper vegetation. Soil depths in this region range from approximately 25 to 101 cm (Godfrey et al., 1973).

Aridisols, with a minor percentage of Mollisols, are found in the northwestern Edwards Plateau (Fig. 6; B). Major soils in this area include Reagan, Conger, and Ector soils, with the Reagan soil series dominating. The regolith is formed of calcareous, loamy materials developed over indurated limestone or weakly cemented to indurated caliche. Ector soils are usually found on steep slopes within this area and bedrock is commonly within 50 cm of the soil surface (Godfrey et al., 1973).

The remainder of the western Edwards Plateau (Fig. 6; C) is comprised of an area of dry, high calcium Mollisols, old Aridisols, and Rock Outcrops and miscellaneous soil types. The typical soil series elements found within this area are Ector, Conger, and Rock Outcrop elements. The regolith in this area is similar in structure to the northwestern Edwards Plateau (Godfrey et al., 1973). Relief throughout the area varies from level to steep. Vegetation includes short and midgrasses and scrubby live oak.

Most of the Llano Uplift and a small area to the southeast (Fig. 6; D, E) are classified as Alfisols. These ancient soils are clayey and loamy in texture, and are formed over granite, schist, gneiss, limestone, and sandstone material. Depth to bedrock varies from 25 to 101 cm. The soils in this area were all formed in thermic, dry environments, and often are red in color (Brady, 1974; Godfrey et al., 1973). Soil series common to the Llano Uplift (Fig. 6; D) include Castell, Pontotoc, and Ligon soils, with Castell soils dominating the area. The soil series found within the other Alfisols unit (Fig. 6; E) include Perdenalis, Hensley, and Pontotoc soils, with Perdenalis soils comprising 50 percent of the area. Relief in these areas varies from level to hilly, and these soils support tall and midgrasses, savannah, and shrub vegetation.

Three major soil orders may be found in the extreme southeastern Edwards Plateau (Fig. 6; F). Mollisols dominate within this area, and smaller percentages of Inceptisols and Vertisols occur (Godfrey et al., 1973; Brady, 1974). Vertisols are limited in coverage to the Balcones Escarpment region. Soils common to this area may be classified in the Tarrant, Brackett, and Speck soil series. These soils have a definite calcareous, clay horizon and are formed over limestone. Soils often are stony, and relief includes locally steep slopes. Vegetation supported within this area includes grassland and savannah with oak, juniper, and mesquite (Godfrey et al., 1973).

Soils of the Edwards Plateau may also be ranked according to land capability class. Land capability classes as developed by the United States Soil Conservation Service refer to the suitability of soils to management and agricultural activities. Soils in capability class one are the most suitable to management with soils in class eight being unsuited to management and cropping activities (Brady, 1974). Land in the Edwards Plateau region is generally found in classes five through eight, with 50 to 66 percent being unsuited to agricultural pursuits. Mollisols and Vertisols found in valley areas may be suited to agriculture, especially if these soils are irrigated and fertilized. Some Aridisols are also suited to agriculture if irrigation is available. Most soils of the Edwards Plateau, however, are more suited to range, wildlife, and recreational uses.
VEGETATION

Weniger (1988) summarized much of the early historical (pre-1860) information concerning vegetation upon the Edwards Plateau. His information came mainly from eye-witness descriptions of landscapes and tree data acquired from the Texas Land Office.

Weniger (1988) concluded that the Edwards Plateau was once a link in the discontinuously wooded uplands between woodlands and forests of the eastern United States and northeastern Mexico. He stated that prehistoric regional biogeography also supports this conclusion. Weniger concluded from his research that the Edwards Plateau was a woodland-forest to savannah-grassland vegetation gradient. Forests and woodlands dominated the north and east of the region and extended to near Del Rio, in Val Verde County. This forest graded into the savannah and grassland regions of the Rolling and High Plains farther west and north. Before European settlement, the vegetation ratio of the Edwards Plateau must have consisted approximately of half forests and half grasslands.

Ford and Van Auken (1982) described the Guadalupe River floodplain forests and concluded that the vegetation has remained essentially the same in these forests since the beginning of the twentieth century. These riparian communities exist along major rivers and watercourses on the Edwards Plateau.

Grasslands, like other vegetation on the Edwards Plateau, exist along a gradient running from southeast to northwest across the region. Factors determining the composition and structure of these grasslands seem to be soil depth and type, annual precipitation, climate and
soil temperature, and, in post-settlement times, the effects of herbivory, and management decisions of land owners and land managers (Thomas and Young, 1954; Lynch, 1962; Smeins and Merrill, 1988).

Southern and eastern regions are characterized by midgrass and tallgrass species, such as little bluestem (Schizachyrium scoparium) and red grama (Bouteloua tritida), where they still occur (sometimes only as relict communities). The more arid northern and western regions are dominated by shortgrass species such as buffalo grass (Buchloë dactyloides) and curly mesquite grass (Hilaria berthelotii). Divisions between these types of grasses can be sharply delineated in some areas, depending upon changes of soil types and grassland management practices (Thomas and Young, 1954; Lynch, 1962; Fowler and Dunlap, 1986). Grasslands and other vegetation on the Edwards Plateau exist in dynamic states and many factors contribute to their fluctuations and shifts in species composition over time (Smeins and Merrill, 1988).

Forested and wooded areas of the Edwards Plateau have many unique aspects. Many eastern species of woody plants reach their western limits on the floodplains of rivers dissecting the Edwards Plateau. Also, a few Sonoran and Madrean plants, such as Acacia sp., extend onto the southwestern edge of the Edwards Plateau (Ford and Van Auken, 1982; Riskind and Diamond, 1988).

Gallery forests exist on the Edwards Plateau along major rivers that flow through the area. Numerous investigators have studied the types and quantities of woody species occurring along these waterways (Ford and Van Auken, 1982; Gehlbach, 1988; Van Auken, 1988; Wood and Wood, 1988). In most cases, the canopy cover of the trees is not completely closed, and this property helps to explain the rather high frequency of occurrence of bald cypress (Taxodium distichum) along most rivers of the region. Pecan trees (Carya illinoensis) are also dominant elements in these forests. Both cypress and pecan trees reach their natural western limits on the Edwards Plateau (Ford and Van Auken, 1982; Van Auken, 1988). Other trees found in the gallery forests of the Edwards Plateau are Texas sugarberry (Celtis laevigata), Cedar elm (Ulmus crassifolia), and red mulberry (Morus rubra).

These types of forests are present today only along major rivers and a few of their immediate tributaries of the Edwards Plateau. Although they appear to be at ecological equilibrium at the present time, there is some evidence that species such as bald cypress, black cherry (Prunus serotina), and black walnut (Juglans nigra) are not actively reproducing new generations of trees in this type of plant community. In contrast, other species of trees, such as Texas sugarberry and Ashe juniper (Juniperus ashei) are increasing in population size on the Edwards Plateau (Van Auken, 1988, 1993).

Away from major rivers, woody vegetation grades into what is termed upland forest or woodland. This type of forest on the Edwards Plateau is dominated by such tree species as live oak (Quercus virginiana), cedar elm (Ulmus crassifolia), Texas ash (Fraxinus texensis), and Texas oak (Quercus texana). Canopy cover is more open in these upland woods and savannah areas, with trees more widely dispersed (Gehlbach, 1988). The shift from riparian forest to upland woodland on the Edwards Plateau has been attributed to factors similar to those determining grassland types for the region. Some of these factors are: (1) moisture gradients immediately away from the rivers; (2) changes in soil depths and types; (3) light availability; (4) soil aeration; (5) frequency of flooding; and (6) natural disturbances (Lynch, 1962; Ford and Van Auken, 1982; Wood and Wood, 1988).

A last type of woody vegetation on the Edwards Plateau is the evergreen woodland type. This woodland is dominated by Ashe juniper (Juniperus ashei) and plateau live oak (Quercus virginiana). Both are small evergreen trees and occur in the more arid western and southern regions of the Edwards Plateau. This savannah type of community may also be found in the northern portions of the Edwards Plateau as far as Nolan and Howard counties. There is evidence that Ashe juniper is a colonizing species and is extending its range eastward on the Edwards Plateau (Fonteyn et al., 1988). These evergreen trees occur along the rocky slopes of the region. They may also form what are termed mottes (clumps of trees) in many areas on the Edwards Plateau, and contribute to the savannah-like aspect of many upland areas in the region. A listing of some of the more common plant species found on the Edwards Plateau is given in Table 2.
Table 2. Some common plants found on the Edwards Plateau. Common names are listed in alphabetical order and scientific names follow Gould (1975) and Correll and Johnston (1979).

<table>
<thead>
<tr>
<th>Common name</th>
<th>Scientific name</th>
<th>Common name</th>
<th>Scientific name</th>
</tr>
</thead>
<tbody>
<tr>
<td>Agarita</td>
<td>Berberis trifoliolata</td>
<td>Lotebush</td>
<td>Ziziphus sp.</td>
</tr>
<tr>
<td>American elm</td>
<td>Ulmus americana</td>
<td>Mesquite</td>
<td>Prosopis glandulosa</td>
</tr>
<tr>
<td>Arizona walnut</td>
<td>Juglans major</td>
<td>Mesquite grass</td>
<td>Hilaria berangeri</td>
</tr>
<tr>
<td>Ashe juniper</td>
<td>Juniperus ashei</td>
<td>Mexican hat</td>
<td>Ratibida columnaris</td>
</tr>
<tr>
<td>Bald cypress</td>
<td>Taxodium distichum</td>
<td>Mustang grape</td>
<td>Vitis diversifolia</td>
</tr>
<tr>
<td>Black cherry</td>
<td>Prunus serotina</td>
<td>Pecan</td>
<td>Carya illinoensis</td>
</tr>
<tr>
<td>Black walnut</td>
<td>Juglans nigra</td>
<td>Persimmon</td>
<td>Diospyros virginiana</td>
</tr>
<tr>
<td>Black willow</td>
<td>Salix nigra</td>
<td>Plains bristlegrass</td>
<td>Setaria sp.</td>
</tr>
<tr>
<td>Broomweed</td>
<td>Gutierrezia sp.</td>
<td>Plains lovegrass</td>
<td>Eragrostis sp.</td>
</tr>
<tr>
<td>Buffalo grass</td>
<td>Buchloe dactyloides</td>
<td>Plateau live oak</td>
<td>Quercus fusciflora</td>
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<tr>
<td>Bundleflower</td>
<td>Desmanthus illinoensis</td>
<td>Poison ivy</td>
<td>Rhus toxicodendron</td>
</tr>
<tr>
<td>Canada wild rye</td>
<td>Elymus canadensis</td>
<td>Prickly pear</td>
<td>Opuntia sp.</td>
</tr>
<tr>
<td>Catclaw</td>
<td>Acacia sp.</td>
<td>Prickly poppy</td>
<td>Argemone albaflora</td>
</tr>
<tr>
<td>Cedar elm</td>
<td>Ulmus crassifolia</td>
<td>Red grama</td>
<td>Bouteloua trifida</td>
</tr>
<tr>
<td>Christmas cactus</td>
<td>Opuntia leptocaulis</td>
<td>Red mulberry</td>
<td>Morus rubra</td>
</tr>
<tr>
<td>Cottonwood</td>
<td>Populus deltoides</td>
<td>Sideoats grama</td>
<td>Bouteloua uniflora</td>
</tr>
<tr>
<td>Creosote bush</td>
<td>Larrea tridentata</td>
<td>Silver bluestem</td>
<td>Bothriochloa saccharoides</td>
</tr>
<tr>
<td>Curly mesquite</td>
<td>Hilaria belangeri</td>
<td>Silver-leaf nightshade</td>
<td>Solanum elegiogilum</td>
</tr>
<tr>
<td>Desert sumac</td>
<td>Rhus microphylla</td>
<td>Snow-on-the-mountain</td>
<td>Euphorbia marginata</td>
</tr>
<tr>
<td>Desert yuapun</td>
<td>Schaefferia cuneifolia</td>
<td>Spangletop</td>
<td>Leptochloa sp.</td>
</tr>
<tr>
<td>Dropseed grasses</td>
<td>Sporobolus sp.</td>
<td>Sunflower</td>
<td>Helianthus annuus</td>
</tr>
<tr>
<td>Engelmann-daisy</td>
<td>Engelmannia pinnatifida</td>
<td>Texas ash</td>
<td>Frazinus texensis</td>
</tr>
<tr>
<td>Fall witchgrass</td>
<td>Leptoloma cognatum</td>
<td>Texas barberry</td>
<td>Berberis swaseyi</td>
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<tr>
<td>Foxtail grass</td>
<td>Alopecurus myosuroides</td>
<td>Texas bluebonnet</td>
<td>Lupinus texensis</td>
</tr>
<tr>
<td>Gay-feather</td>
<td>Lithis sp.</td>
<td>Texas needlegrass</td>
<td>Stipa leucotricha</td>
</tr>
<tr>
<td>Greenbriar</td>
<td>Smilax renifolia</td>
<td>Texas sugarberry</td>
<td>Celtis laevigata</td>
</tr>
<tr>
<td>Gumweed</td>
<td>Grindelia sp.</td>
<td>Threeawn grass</td>
<td>Arisida sp.</td>
</tr>
<tr>
<td>Hackberry</td>
<td>Celtis occidentalis</td>
<td>Vine-mesquite</td>
<td>Panicum obtusum</td>
</tr>
<tr>
<td>Hairy grama</td>
<td>Bouteloua hirsuta</td>
<td>Western wheatgrass</td>
<td>Agropyron smithii</td>
</tr>
<tr>
<td>Hooded windmillgrass</td>
<td>Chloris cucullata</td>
<td>White tridens</td>
<td>Tridens albensciens</td>
</tr>
<tr>
<td>Indian blanket</td>
<td>Gaillardia pulchella</td>
<td>Wild carrot</td>
<td>Daucus pusillus</td>
</tr>
<tr>
<td>Indian grass</td>
<td>Sorghastrum avenaceum</td>
<td>Wright Acacia</td>
<td>Acacia wrightii</td>
</tr>
<tr>
<td>Johnson grass</td>
<td>Sorghum halepense</td>
<td>Yucca</td>
<td>Yucca sp.</td>
</tr>
<tr>
<td>Little bluestem</td>
<td>Schizachyrium scoparium</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Live oak</td>
<td>Quercus virginiana</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Plant community classification of the Edwards Plateau has been addressed by numerous researchers (Kuchler, 1964; McHale et al., 1984; Gould, 1975; Diamond et al., 1987; and Riskind and Diamond, 1988). That the region is distinct from surrounding biotic regions has been pointed out by Blair (1950), Gould (1975), Correll and Johnson (1979), and Gehlbach (1991). Most classification systems subdivide the region into grassland areas, savannah areas, woodland areas, and forest areas.

The vegetation classification used herein is primarily based upon the work of McHale et al. (1984). The classification and map, compared to the potential natural vegetation map and classification produced by Kuchler (1964), is found to be congruent in most areas. The most notable exception is found in Val Verde and Crockett counties (association D in Fig. 7). McHale, Frye, and Brown (1984) list the dominant plants as mesquite, juniper, and live oak. No mention is made of creosote (Larrea tridentata) occurring in this association (Kuchler, 1964). I have added the creosote ele-
The assignment of dominant plant species to an association is based upon both quantitative and qualitative assessment and it must be pointed out that all vegetation associations are heterogeneous units. Five physiognomic classes occur on the Edwards Plateau. These classes are grassland, shrub, brush parks, woods, and forest. The physiognomic classes are based upon the types of dominant plants present and percent canopy cover.

McMahan et al. (1984) designate nine major vegetation associations on the Edwards Plateau; whereas Kuchler (1964) designates seven. All researchers point out that the present vegetation types of Texas are the result of past disturbance events and few areas of undisturbed vegetation exist now (Kuchler, 1964; McMahan et al., 1984; Van Auken, 1993).

The northwestern Edwards Plateau is represented by two major vegetation associations. The Mesquite Shrub/Grassland Association occurs around the Midland-Odessa area (Fig. 7; A). Mesquite-Lotebush associations are interspersed in the area in Howard, Sterling, Coke, and Irion counties (Fig. 7; B). The area is characterized by low growing shrubs and grasses.

The western portion of the Edwards Plateau, as far east as Schleicher and Sutton counties, is characterized by two vegetation associations. The Mesquite-Juniper Shrub Association occurs as far east as Concho County and south to Val Verde County (Fig. 7; C). The Mesquite-Juniper-Creosote-Live Oak Brush Association is found in Val Verde County and as far north and east as Crockett and Sutton counties (Fig. 7; D). A small area of this association is found in southern Tom Green County, and this vegetation association comprises all but the extreme southern portion of the Callahan Divide. The creosote element within this association is found primarily in Val Verde and Crockett counties.

A marginal vegetation association occurs in Uvalde and Medina counties in the extreme southern Edwards Plateau. This area is designated as the Mesquite-Live Oak-Bluwood Parks Association (Fig. 7; E). The association contains the dominants listed along with such plants as lotebush (Zaiphus sp.), tasajillo (Opuntia leptocaulis), and desert yaupon (Schaefferia cuneifolia), along with associated grasses.

A single vegetation association is found in the Llano Uplift area of the Edwards Plateau (Fig. 7; F). This association is termed the Live Oak-Mesquite Parks Association. The vegetation is characterized by woody plants usually over nine feet in height, found either in clusters or individually surrounded by a continuous growth of grasses and forbs.

The central to eastern sections of the Edwards Plateau are best described by two vegetation associations. The Live Oak-Mesquite-Ashe Juniper Parks Association is found within the southeastern Callahan Divide and extends as far south and east as Edwards and Mason counties (Fig. 7; G). The second vegetation association found in the central Edwards Plateau is the Live Oak-Ashe Juniper Parks Association. This association abuts the Llano Uplift to the north and south to the Balcones Fault zone, and westward to Val Verde County (Fig. 7; H). These two associations comprise the typical savannah element of much of the Edwards Plateau.

A distinct vegetation association occurs along the Balcones escarpment and in a few hilly regions of the eastern Edwards Plateau. These areas are designated as the Live Oak-Ashe Juniper Woods Association (Fig. 7; I). In addition to the listed dominants, this association contains such species as cedar elm (Ulmus crassifolia), black cherry (Prunus serotina), and little bluestem (Schizachyrium scoparium).

One association omitted from both classifications is one I designate as the Bald Cypress-Pecan-Elm Forest Association. This association is limited to a few major rivers and their immediate tributaries on the eastern Edwards Plateau. These forest associations are limited in extent and to portray them on a map at such small scale would cause a significant misrepresentation of their coverage on the Edwards Plateau. Forest associations in riparian areas are still important, however, because some species such as the swamp rabbit (Sylvilagus aquaticus) are only found within these areas on the Edwards Plateau.
IMPACT OF HUMANS ON THE EDWARDS PLATEAU

The region has a long record of human occupation, possibly due to the ready availability of water from many springs, seeps, and rivers in the central and eastern portions. Evidence of Paleoindian occupation has been documented from caves in Val Verde County at least as early as 10,000 years ago (Graham, 1987), and pictographs from these peoples have been found in Val Verde and Concho counties in the region. Most of the area was occupied by the Comanche Indian tribe during historic times (Stephens and Holmes, 1989). Aside from the remains of mammals found in these people’s middens and the pictographic evidence, Paleoindians left little evidence of their tenure on the Edwards Plateau. Some researchers, however, believe that the extinction of some of the larger Pleistocene animals, such as the mammoth and giant ground sloth, were expedited by increased hunting pressure by humans (Kurten and Anderson, 1980). In addition, the early Spanish explorer Cabeza de Vaca observed that some indians in Texas set fire to the prairie in order to reduce mosquito populations and to obtain game animals (Doughty, 1983).

The first Europeans to enter the Edwards Plateau region were Spanish explorers and missionaries as early as 1535. Two historical figures believed to have traversed parts of the Edwards Plateau during their travels were Cabeza De Vaca and Francisco de Coronado.
Spain attempted to settle the region in the early to middle eighteenth century utilizing the mission and presidio system. Spanish missions and presidios established on the Edwards Plateau during this period include presidio San Luis de los Amarillos in Menard County, San Lorenzo de la Santa Cruz del Canon and Nuestra Señora a la Purisima Concepcion Candelaria del Canon in Edwards County, and missions San Antonio de Valero, Concepcion de Acuna, Xavier de Naxara, San Jose, San Miguel, and San Francisco de la Espada in Bexar County (Stephens and Holmes, 1989). The only mission settlement to have a measure of success was the one established at present day San Antonio, beginning with Mission San Antonio de Valero in 1718. The Edwards Plateau and all of eastern and southern Texas was included within the state of Coahuila, Mexico, when Mexico became an independent nation in 1821. The Spanish missionaries introduced cattle, goats, sheep, and horses into the region, but the European population was so small and limited in extent that, aside from a few exceptions, these introductions probably produced little effect on the Edwards Plateau. The exceptions to the previous statement would be the introduction and assimilation of the horse in the Native-American culture and the introduction of European mice (Mus musculus) and rats (Rattus norvegicus and Rattus rattus) on the Edwards Plateau.

Aside from the Zebulon M. Pike expedition, which was marched under Spanish guard northeast on the Camino Real with a stop at San Antonio in 1807, Anglo-American colonization did not begin on the Edwards Plateau until the government of Mexico initiated the empresario grant system in the years 1821 to 1834 (Stephens and Holmes, 1989). The Department of Bexar retained most of the eastern half of the region from San Antonio north to the San Saba River. The western half of the region was granted to J. L. Woodbury and Company, but this group made no attempt at locating settlers in the region (Pool, 1975). Benjamin R. Milam was awarded a grant that extended into present day Burnet, Hays, and Travis counties, but did not develop his colony (Pool, 1975). Aside from giving settlement rights to Anglo-Americans, no significant settlement of the Edwards Plateau occurred during this period.

The first permanent settlement founded by Anglo-Americans was Fredericksburg in 1847. Settlers followed major rivers into the Edwards Plateau and established other towns in the region. Blanco, in Blanco County, was established in 1854, and, farther west, Kerrville was established by a group of cypress-shingle makers in 1846. Settlement progressed throughout the nineteenth century, with towns being established as the result of ranching enterprises, railroad construction (primarily following the Civil War), buffalo hunting camps on the northwestern edge of the Edwards Plateau, and other reasons (Pool, 1975).

A series of military forts was maintained by the United States Army on the western frontier of the Edwards Plateau in order to provide settlers protection against Indian attacks. Among the most notable were Fort Concho where the city of San Angelo began, Fort Mason at the present site of the city of Mason, Camp San Felipe at Del Rio, and Camp Verde near Kerrville (Stephens and Holmes, 1989). Camp Verde is of special interest because of the novel experiment of the United States Cavalry in the use of camels on the American frontier that took place there in 1857 (Doughty, 1983).

European settlement of the Edwards Plateau region has had a profound effect upon the environment of the area. Europeans have affected the natural flora and fauna of the region by introduction of domestic livestock, elimination or greatly reducing the effects of natural fires on the Edwards Plateau, overhunting and extirpation of some species of native mammals in the region, introduction of pest species into the region, and depletion of water sources in some areas.

The first cattle, goats, and sheep were introduced on the Edwards Plateau by the Spanish, but they were used primarily for consumptive purposes. Angora goats were introduced into the Hays County area by Colonel W. W. Haupt in 1857. Credit for the introduction and instigation of the sheep industry on the Edwards Plateau is given to George W. Kendall, who introduced the animals on his ranch in present-day Kendall County in 1857. Cattle ranching grew in importance on the Edwards Plateau in the 1860's, and included the well-known John Chisum, who founded a ranch in Concho County in 1862 (Pool, 1975). Livestock ranching, with concomitant high stocking rates over this long period of time has depleted much of the understory grasses throughout the region and helped with the spread of many undesirable species of plants upon the Edwards Plateau. The original grasslands composed of bluestem grasses and speargrasses have been replaced in most
localities by shortgrass species such as buffalo grass and curly mesquite or even less desirable three-awn grasses and forbs (Buechner, 1944; Fowler and Dunlap, 1986; Smeins and Merrill, 1988). There is some evidence that, even if livestock pressure on the vegetation is stopped completely, the original vegetation mosaic at a particular location may not regenerate (Smeins et al., 1976).

Researchers have speculated that Ashe juniper has increased its distribution on the Edwards Plateau since the period of European settlement because of a reduction in wildfires across the region (Smeins et al., 1976; Fonteyn et al., 1988). However, because the Edwards Plateau has many broken, rocky areas where Ashe juniper dominates and fires are not effective, the junipers can never be entirely eliminated from the region. Ashe juniper provides escape cover and thermal cover for some species of mammals on the Edwards Plateau (Etheredge et al., 1989; Bryant, 1991).

Europeans have had a considerable impact on the fauna of the Edwards Plateau because of their hunting practices. Deer populations were greatly reduced in the nineteenth century on the Edwards Plateau because of an active trade in deer pelts, and bison were eliminated from the area by around 1880 as a result of over-hunting (Strecker, 1927; Doughty, 1983). Black bears, jaguars, ocelots, gray wolves, and red wolves have been eliminated from the region since European settlement because of over-hunting and habitat losses (Doughty, 1983; Jones, 1993).

Imported red fire ants (*Solenopsis invicta*) were first introduced into the United States in Alabama between 1933 and 1945 and have since spread to Texas (Cokendolpher and Phillips, 1989). Although their full impact upon animal populations is not known as yet, these aggressive ants negatively affect some mammals that occur on the Edwards Plateau (Allan et al., 1994). Mammals known to be affected by these predaceous ants are *Sylvilagus floridanus*, *Peromyscus leucopus*, and *Baiomys taylori* (Allan et al., 1994).

Initial settlement of the Edwards Plateau began along major streams and rivers in the region, as previously mentioned. These watercourses, and especially springs such as Comal Springs in New Braunfels, San Marcos Spring in San Marcos, and Barton Springs in Austin, are the result of the development of the Balcones Fault and subsequent discharge of water from the Edwards Aquifer (Bybee, 1952). Increasing demands for water by metropolitan areas along the Balcones Fault and by agricultural and industrial enterprises have caused water flow to be reduced in Comal Springs and San Marcos Springs (*Dallas Morning News*, 1993). Some species of animals and plants, such as the endangered fountain darter, Texas blind salamander, and Texas wild rice, could lose critical habitats as a result of human demands upon the Edwards Aquifer.
ZOOGEOGRAPHY

LATE PLEISTOCENE AND EARLY HOLOCENE ZOOGEOGRAPHY

Several late Pleistocene and early Holocene faunas have been reported from the Edwards Plateau. Analysis of these faunas may provide clues to the origination and dynamics of the fauna now present on the Edwards Plateau. Four excellent sources for data concerning the Pleistocene on the Edwards Plateau are Kurten and Anderson (1980); Graham, Semkin, and Graham (1987); Wilkins (1992); and Toomey, Blum, and Valastro (1993). Most of the material in this section is based upon these authors' reviews of faunas and climatic conditions prevalent in the region during the late Pleistocene Period (approximately 20,000-10,000 years before present, Y.B.P.) to the beginning of the Holocene Period (approximately 12,000-10,000 Y. B. P.).

Some problems inherent to studies of fossil mammals are the tendency for some species to become fossilized while other taxa are rarely preserved in a fauna at different types of fossil sites, recovery techniques utilized in acquiring the fossil material, and level of identification possible for the material. If a fossil fauna is from an ancient lake or pond site, mammals that require only metabolic water to sustain themselves will rarely be fossilized. If the fauna is from a cave site, as most are on the Edwards Plateau, sometimes the fauna will be biased toward large mammals and carnivores that fell into these natural pitfall traps. In such a case, small mammals may be underrepresented. Many early workers of Pleistocene faunal sites only surveyed the sites visually for larger mammals. Smaller mammals are most often found by screen-washing matrix material from the caves and examining the remains under magnification (Graham and Semkin, 1987), although many may be found by a diligent search of the area in question.

The end on the Pleistocene epoch seems to have been dominated by the extinction of many large mammals such as *Arctodus simus*, *Smilodon floridanus*, *Homotherium serum*, *Mammut americanum*, *Mammuthus columbi*, *Camelops* sp., *Platygonus* sp., and *Equus* sp. Other more montane and mesic species became locally extinct as a result of the progressive decrease in moisture and increase in seasonal temperatures during this time. Examples of these species include *Sorex cinereus*, *Blarina brevicada*, *Synaptomys cooperi*, and *Mustela erminia*. For a more complete listing of fossil taxa and local fauna sites see Table 3.

Toomey, Blum, and Valastro (1993) used a combination of vertebrate remains, fossil pollen, and plant macrofossil records to assess climatic changes on the Edwards Plateau over the last 20,000 years. During the full-glacial period (20,000-14,000 Y. B. P.), extralimital taxa from cooler, moister environments and the now-extinct larger mammals were present, along with taxa which still reside in the area. This non-analogous fauna was interpreted to represent reduced seasonality, with cool and moist summers and winter temperatures that were not very different from the present time. Mammals, such as *Cynomys* sp., *Geomys* sp., *Mylohyus natus*, and *Mammut americanum*, at Friesenhahn Cave in Bexar County, indicated mixed grass upland habitats bordered by riparian woodlands.

Cave faunas from the late-glacial Pleistocene environments of the Edwards Plateau (ca. 14,000-10,000 Y. B. P.) indicated increasing summer temperatures by the disappearance of *S. cinereus* and the appearance of *Sigmodon hispidus* in the fauna of Hall’s Cave in Kerr County (Toomey, Blum, and Valastro, 1993). *Synaptomys cooperi* also disappeared from Hall’s Cave during this time; and the relative abundance of *Notiosorex crawfordi* (a more xeric species) increased over that of *Cryptotis parva* (an eastern and northern species) at Hall’s Cave. Pollen records indicated a decrease in arboreal pollen elements at this time and a corresponding increase in pollen from gramineous species.

Early to middle Holocene environments (10,000-5,000 Y. B. P.) were marked by the absence of many of the large mammals and the gradual reorganization of extant taxa to a more modern aspect. Species requiring more mesic environments, such as *Scalopus aquaticus* and *Blarina* sp. were absent; and species adapted to drier conditions, such as *N. crawfordi* and *Sylvilagus audubonii*, increased in abundance in some faunas (Wilkins, 1992; Toomey et al., 1993). The importance of prairie dogs, badgers and pocket gophers indicated grassland-dominated environments. Western portions
Table 3. Mammals recorded from local faunas on the Edwards Plateau from the late Pleistocene through the Recent period. Local faunas are arranged from oldest to youngest. A, Friesenhahn Cave, Bexar Co. (17,000 -19,000 Y. B. P.); B, Cave Without A Name, Kendall Co. (10,900); C, Longhorn Cavern, red fill, Burnet Co. (late Wisconsin); D, Longhorn Cavern, Breccia, (late Wisconsin); E, Levi Shelter, Travis Co. (10,000); F, Bonfire Shelter, Val Verde Co. (10,000); G, Levi Shelter, zone II, (10,000); H, Schulze Cave, C-1, Edwards Co. (9600); I, Schulze Cave, C-2, (9300); J, Friesenhahn Cave, (9000); K, Schulze Cave, layer B, (6000); L, Bonfire Shelter, Zone 3, (3000); M, Hall's Cave, Kerr Co. (13,000 - modern). After Graham, 1987, and Toomey, 1993.

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**XENARTHRA**

Dasypus bellus

**CARNIVORA**

Canis familiaris
Canis latrans
Canis lupus
Canis dirus
Canis sp.
Vulpes vulpes
Vulpes velox
Urocyon cinereoargenteus
Ursus americanus
Ursus arctos
Ursus sp.
Arctodus simus
Bassariscus astutus
Procyon lotor
Mustela erminea
Mustela frenata
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Percentages of mammalian fossil faunas from the Edwards Plateau that now are extinct, extirpated, or extant in the modern mammalian fauna.

| Number extinct: | 29 | 13 | 0 | 20 | 30 | 29 | 22 | 2 | 4 | 0 | 0 | 0 | 9 |
| Number extirpated: | 20 | 28 | 27 | 33 | 20 | 0 | 11 | 35 | 27 | 17 | 15 | 0 | 22 |
| Modern fauna: | 51 | 59 | 73 | 47 | 50 | 71 | 67 | 63 | 69 | 83 | 85 | 100 | 69 |
of the Edwards Plateau probably contained some shrub elements, and a mixed assemblage of tall and short grasses probably dominated upland vegetation to the east.

The late Holocene, up to about 1000 Y. B. P., was marked by periods of dessication with the return of more mesic conditions by about 1000 Y. B. P. Most of the soil mantle was removed over the region during this time. A period of maximum dryness appeared to have occurred from 5000-2500 Y. B. P., with an increase in effective moisture after this interval. The dominance of xeric adapted species, such as *N. crawfordi* and *S. audubonii*, in faunas with the absence of forms adapted to more mesic conditions (*Microtus pinetorum*, *S. floridanus*, and *C. parva*), with the concomitant return of the mesic taxa after 2500 Y. B. P., tend to support this hypothesis (Toomey et al., 1993). Vegetation cover during this period was probably dominated by grasses and shrubs.

Late Pleistocene mammalian communities contained taxa that are now allopatric in distribution. A possible explanation for this is that western alpine-meadow conditions prevailed on the Edwards Plateau as a result of the presence of the Cordilleran and Laurintide icesheets, and extralimital western species immigrated into the area from the Rocky Mountain region (Dalquest et al., 1969). Hafner (1993) compared *Zapus* fossil material from the Schulze Cave local fauna to western and eastern species of the jumping mouse and found, however, that the Schulze Cave material should be assigned to *Zapus hudsonius*, which is an eastern species. Hafner also stated that a lower jaw previously assigned to *Mustela erminea* may instead belong to *M. nivalis*; also an eastern species (Hafner, 1993). He hypothesized an eastern and northern immigration into the Edwards Plateau for most of the extralimital species present in local faunas.

**CONTEMPORARY ZOOGEOGRAPHY**

Zoogeographic areas are regions with a relatively homogenous fauna which are separated from other adjacent areas by zones of heterogeneity (Hagmeier and Stults, 1964). Because of the homogenous nature of the resident fauna of any particular zoogeographic area, generalizations may be made that apply over large geographic areas (Hagmeier and Stults, 1964). Researchers have long attempted to subdivide the continents into distinct zoogeographic areas, and their efforts have resulted in many types of classification strategies.

The Edwards Plateau has usually been included within one or more zoogeographic areas. Louis Agassiz, in 1854, placed all of Texas, excluding Trans-Pecos Texas, with his Louisiana Fauna (Kendeigh, 1954). J. G. Cooper (1859) placed all except extreme South Texas and the western Trans-Pecos within his Campestrian Province. He divided the Edwards Plateau into two distinct regions called the Comanche Region (western Edwards Plateau) and the Texan Region (eastern Edwards Plateau). Cooper’s provinces were based primarily upon vegetation differences, although he realized that the provinces also were characterized by distinctive animals (Kendeigh, 1954). C. H. Merriam (1890) placed the Edwards Plateau within his Sonoran Province, and divided the area into Upper and Lower Austral life zones (Kendeigh, 1954). Bailey (1905) followed the life zone approach of Merriam in his Biological Survey of Texas. Life zones were delineated primarily by temperature and secondarily by indicator species of plants and animals (Kendeigh, 1954). Allen (1892) included the Edwards Plateau within his Temperate Realm, Arid Province, and Sonoran Subprovince.

Most contemporary researchers (Dice, 1943; Blair, 1950; Hagmeier and Stults, 1964; Hagmeier, 1966) have utilized an approach to zoogeographical classification based upon biotic provinces. Biotic provinces have been defined as contiguous geographic areas characterized by one or more ecologic associations that differ, at least in the proportional area covered, from the associations of adjacent provinces (Blair, 1950). Blair (1950) placed the Edwards Plateau in a distinct province, the Balconian Province. Schmidly (1984a) placed the Edwards Plateau in a large region that he called the Plains Country. The Plains Country also included all of the Panhandle, Edwards Plateau, and Rolling Plains of Texas.

Biogeographers have attempted to demonstrate that distinct zoogeographic areas can be determined by utilizing an objective, numerical approach (Huheey, 1965; Hagmeier, 1966). Hagmeier and Stults (1964) and Hagmeier (1966) used an index of faunal change and, consequently, placed the Edwards Plateau into a Balconian and Tamaulipan mammal province. These researchers separated the Balconian and Texan mammal provinces along the 100th meridian, whereas the
Tamaulipan mammal province included all of southern Texas and part of the southeastern Edwards Plateau.

The geographic distribution of a species may be a consequence of historic accident, physiologic tolerances, and genetic adaptability (Hagmeier and Stults, 1964). The ranges of species tend to be clumped instead of randomly distributed, leading to the conclusion that similar historic accidents, physiologic tolerances, and genetic adaptations have affected groups of species in similar ways. If this is indeed the case, mapping the ranges of species groups provides information about that group’s center of origin and possibly elucidates common routes of movement of numbers of species within an area (Armstrong, 1972). Such groups of overlapping species are termed faunal elements and may encompass a spectrum of ecological potential (Armstrong, 1972). The study of the geographical ranges of species through the use of range maps is called areography. Areographic analysis of an area’s fauna may provide clues to the historical factors of the zoogeography of the area (Armstrong et al., 1986). Analysis of the ecological distributions of mammals resident to an area also provides information concerning the present-day distribution patterns of the mammals within a particular area.

Areal distributions of the 76 extant, native mammalian species, belonging to seven faunal elements (sensu Armstrong et al., 1986), presently residing on the Edwards Plateau, were diagrammed and centers of coincidence were determined in order to elucidate the historical zoogeography of mammals within the area. Distributions of the resident mammals were taken from Hall (1981) and other more recent sources such as Carleton (1989), Sealander and Heidt (1990), Choate (1997), Schmidly et al. (1993), Choate et al. (1994), and Davis and Schmidly (1994). The Edwards Plateau was divided into two quadrats of approximately equal area (Fig. 8) and these quadrats were compared to each other and, also, to adjacent zoogeographic regions by clustering techniques in order to determine if the Edwards Plateau might act as a transition zone for mammalian species within Texas. Blair (1950) stated that the Edwards Plateau (including the Llano Uplift) acted as a transition zone from east to west in regard to the distribution of its resident fauna. Gehlbach (1991) studied the terrestrial vertebrates within a region of Central Texas that included the Balcones Escarpment and a portion of the northeastern Edwards Plateau, and determined that a transition zone existed in this area. In addition, the Edwards Plateau was divided into quadrats based upon rainfall isolines and vegetation associations and data matrices were prepared for the resident, native mammals on the Edwards Plateau.

These matrices provided ecological information concerning the distribution patterns of mammalian species on the Edwards Plateau.

**AREAL DISTRIBUTION**

Mammalian species from seven distinct faunal elements are present on the Edwards Plateau. The seven faunal elements are the Austral, Campestrian, Chihuahuan, Eastern, Local, Neotropical, and Widespread faunal elements. The Austral faunal element is comprised of species from the southeastern United States, and the Campestrian faunal element contains species with distributions centered on the Great Plains of North America. The Chihuahuan faunal element includes species with affinities to areas of Chihuahua, Coahuila, and Durango, Mexico. The Eastern faunal element contains mammalian species from the Ohio Valley and surrounding areas of the United States, whereas the Local faunal element includes species with limited distributions. The Neotropical faunal element is comprised of species with strong tropical affinities, and the Widespread faunal element consists of mammals with sufficiently large distributions that preclude their assignment to a specific, regional faunal element.

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The Austral faunal element of the Edwards Plateau (Fig. 9) contains only two members, *Sylvilagus aquaticus* and *Neotoma floridana*. The center of coincidence for this faunal element includes a wide region of the gulf-coastal states and extends eastward to South Carolina and northward to Missouri and Tennessee (Fig. 10). Both *S. aquaticus* and *N. floridana* reach their western distributional limits on the eastern Edwards Plateau within the center of coincidence (Fig. 9). Each species most commonly inhabits riparian areas and deciduous woodlands. Habitats of this type are found along the rivers and streams of the eastern Edwards Plateau.

The Campestrian faunal element (Fig. 11) is comprised of seven species as follows: *Cynomys ludovicianus*, *Geomys bursarius*, *Chaetodipus hispidus*, *Reithrodontomys montanus*, *Onychomys leucogaster*, *Vulpes velox*, and *Antilocapra americana*. The center of coincidence for this faunal element ex-
tends from the northwestern Edwards Plateau, northward as far as southeastern South Dakota, and westward to northeastern New Mexico (Fig. 12). *G. bursarius* is a peripheral species on the Edwards Plateau, occurring only on the extreme northern and western portions. The range of *C. ludovicianus* within the region is much reduced, and this species presently occurs in small, isolated populations on the Edwards Plateau. *A. americana* occurs in small populations on the western Edwards Plateau, and at least some of the animals may have been reintroduced in the region.

The Chihuahuan faunal element contributes the most species to the fauna of the Edwards Plateau, with a total of 28 as follows: *Notiosorex crawfordi*, *Myotis velifer*, *Myotis yumanensis*, *Pipistrellus hesperus*, *Plecotus townsendii*, *Antrozous pallidus*, *Sylvilagus audubonii*, *Lepus californicus*, *Ammospermophilus interpres*, *Spermophilus mexicanus*, *Spermophilus spilosoma*, *Spermophilus variegatus*, *Thomomys bottae*, *Cratogeomys castanops*, *Perognathus flavus*, *Chaetodipus nelsoni*, *Chaetodipus penicillatus*, *Dipodomys merriami*, *Dipodomys ordii*, *Reithrodonomys fulvescens*, *Reithrodonomys megalotis*, *Peromyscus eremicus*, *Peromyscus pectoralis*, *Onychomys arenicola*, *Neotoma albigula*, *Bassariscus astutus*, *Spilogale gracilis*, *Conepatus mesoleucus* (Fig. 13). The center of coincidence for the Chihuahuan faunal element is located in northwestern Coahuila, Mexico (Fig. 14). Dispersal of these species onto the Edwards Plateau may occur from Coahuila, or from the Trans-Pecos region of Texas. Seven of the species (*M. yumanensis*, *C. nelsoni*, *C. penicillatus*, *D. ordii*, *P. eremicus*, *P. pectoralis*, *O. arenicola*) reach their eastern distributional limits around the Pecos River and its immediate vicinity on the Edwards Plateau. Five
Figure 9. Continental distributions of two Austral species from the Edwards Plateau.

Figure 10. Center of coincidence of Austral species from the Edwards Plateau.
Figure 11. Continental distributions of seven Campestrian species from the Edwards Plateau.

Figure 12. Center of coincidence of Campestrian species from the Edwards Plateau.
Figure 13. Continental distributions of 28 Chihuahuan species from the Edwards Plateau.

Figure 14. Center of coincidence of Chihuahuan species from the Edwards Plateau.
additional Chihuahuan species (A. interpres, S. spilosoma, C. castanops, D. merriami, R. megalotis) have limited ranges on the Edwards Plateau west of the 100th meridian.

The Eastern faunal element (Fig. 15) is comprised of eight species of mammals as follows: Scalopus aquaticus, Pipistrellus subflavus, Lasiurus borealis, Nycticeius humeralis, Sylvilagus floridanus, Sciurus carolinensis, Sciurus niger, Microtus pinetorum. The center of coincidence for this faunal element extends from northern Iowa, southern Wisconsin and southern Michigan, eastward to Ohio, and Virginia. The southern portion of the center of coincidence extends from northern Florida, westward along the gulf-coastal states to central Louisiana and onto the extreme eastern Edwards Plateau (Fig. 16). Three of the species (P. subflavus, L. borealis, N. humeralis) have extensive distributions in the eastern United States. S. carolinensis reaches only the eastern edge of the Edwards Plateau, whereas S. aquaticus and M. pinetorum have limited ranges within the Edwards Plateau and are found only in relictual populations.

The Local faunal element (Fig. 17) includes three species of mammals as follows: Geomys texensis, Peromyscus attwateri, Neotoma micropus. The Local faunal element has two centers of coincidence (Fig. 18), one located on the eastern Edwards Plateau and a second, smaller area in South Texas. The dual centers of coincidence are the result of the distribution of G. texensis within Texas. These pocket gophers occur in relictual populations on the Edwards Plateau and South Texas. Even if G. texensis was not considered, the greatest part of the center of coincidence for the Local faunal element would still be located on the Edwards Plateau and the Rolling Plains of Texas. The other two mammalian species (P. attwateri and N. micropus) both occur throughout most of the Edwards Plateau, but have limited distributions in other regions.

The Neotropical faunal element (Fig. 19) has eight species of mammals as follows: Didelphis virginiana, Mormoops megalophylla, Lasiurus intermedius, Tadarida brasiensis, Dasypus novemcinctus, Baiomys taylori, Sigmodon hispidus, Tayassu tajacu. The center of coincidence for the Neotropical faunal element is found in southern Mexico and Central America (Fig. 20). The area inhabited by all species extends from Veracruz and Guerrero, Mexico, southward to northern Nicaragua. Three of the species (M. megalophylla, L. intermedius, T. brasiensis) are of tropical origin. D. virginiana, D. novemcinctus, B. taylori, and S. hispidus are actively expanding their ranges in North America since the end of the Pleisocene (Jones et al., 1983; Choate et al., 1990).

The Widespread faunal element (Fig. 21) has 20 members as follows: Lasionycteris noctivagans, Eptesicus fuscus, Lasiurus cinereus, Castor canadensis, Peromyscus leucopus, Peromyscus maniculatus, Ondatra zibethicus, Erethizon dorsatum, Canis latrans, Vulpes vulpes, Urocyon cinereogenteus, Procyon lotor, Mustela frenata, Mustela vison, Taxidea taxus, Mephitis mephitis, Lutra canadensis, Felis concolor, Lynx rufus, Odocoileus virginianus. The center of coincidence for the Widespread faunal element includes an area centered in Iowa and Illinois (Fig. 22). The center of coincidence extends from North Dakota southward to southeastern Oklahoma and eastward into Missouri, Illinois, Indiana, and western Ohio.

The Chihuahuan faunal element contributes the greatest percentage (36) of native, resident, mammals to the Edwards Plateau. The route of dispersal onto the region, based upon the center of coincidence, is probably from northern Coahuila, Mexico. Many of the Chihuahuan species of the Edwards Plateau, however, are also resident to the Trans-Pecos region to the immediate west, and these shared species may move onto the Edwards Plateau from that region.

Twenty-six percent of the resident, native mammals belong to the Widespread faunal element. More than half of these species are carnivores that have the ability to disperse over large areas whenever necessary and are found in a variety of habitats throughout their ranges. The white-tailed deer (O. virginianus) adapts quickly to changes in its environment and is found in a wide range of climatic and habitat conditions (Boyd and Cooperider, 1986). Although the center of coincidence of the widespread species is located in the mid-western United States, it would be difficult to hypothesize a route of dispersal onto the Edwards Plateau for these mammals.

The Eastern and Neotropical faunal elements each contribute 11 percent of the total resident, native mam-
Figure 15. Continental distributions of eight Eastern species from the Edwards Plateau.

Figure 16. Center of coincidence of Eastern species from the Edwards Plateau.
Figure 17. Continental distributions of three local species from the Edwards Plateau.

Figure 18. Center of coincidence of local species from the Edwards Plateau.
Figure 19. Continental distributions of eight Neotropical species from the Edwards Plateau.

Figure 20. Center of coincidence of Neotropical species from the Edwards Plateau.
Figure 21. Continental distributions of 20 widespread species from the Edwards Plateau.

Figure 22. Center of coincidence of widespread species from the Edwards Plateau.
malian species of the Edwards Plateau. Based upon the center of coincidence and range limits of some of the eastern species, the most probable route of dispersal onto the Edwards Plateau is from East Texas. The gray squirrel (S. carolinensis) reaches the western limits of its range on the Edwards Plateau, whereas the pine vole (M. pinetorum) occurs in relictual populations within the region. It seems that Neotropical species have migrated onto the Edwards Plateau from Mexico and South Texas. The armadillo (D. novemcinctus) and pygmy mouse (B. taylori) have expanded their ranges on the Edwards Plateau, and elsewhere, within historic times (Bailey, 1905; Choate et al., 1990; Choate, 1991; Jones et al., 1993). Bats included within the Eastern and Neotropical faunal elements are primarily seasonal migrants on the Edwards Plateau.

Nine percent of the resident, native mammals belong to the Campestrian faunal element. The probable route of dispersal, based upon the center of coincidence, is from the Llano Estacado and western Rolling Plains regions of Texas. However, the hispid pocket mouse (C. hispidus) and swift fox (V. velox) have extensive distributions on the Great Plains and within most of Texas. The ranges of all of the Campestrian species have probably decreased in historic times due to reductions in grassland habitats on the Edwards Plateau.

The Local faunal element contributes four percent of the resident, extant, mammalian species to the Edwards Plateau fauna. These autochthonous mammals are all rodents. The llano pocket gopher (G. texensis) exists in relictual, isolated populations on the Edwards Plateau (Block and Zimmerman, 1991), whereas the southern plains woodrat (N. micropus) is a species undergoing an intermediate stage of speciation, probably within the last 200,000 years (Birney, 1973). The Texas mouse (P. attwateri) occurs in suitable habitats throughout the Edwards Plateau and central and eastern Oklahoma eastward to southwestern Missouri and northwestern Arkansas. The fossil record for P. attwateri is limited, thus making it difficult to designate a center of origin for this species.

Three percent of the resident, native mammals on the Edwards Plateau belong to the Austral faunal element. Both austral species, the swamp rabbit (S. aquaticus) and the eastern woodrat (N. floridana), are limited to suitable, riparian habitats on the Edwards Plateau. The probable route of migration onto the Edwards Plateau is from eastern Texas.

THE EDWARDS PLATEAU AS A BARRIER TO MAMMALIAN DISPERSAL

Researchers have stated that the Edwards Plateau is a region with no endemic mammals; rather, the region consists of a mammalian fauna derived from regions surrounding the Edwards Plateau with several species of mammals reaching distributional limits on the Edwards Plateau (Dice, 1943; Blair, 1950; Schmidly, 1984a). Blair (1950) commented on the transitional nature of this region as related to the distribution of mammals within Texas, and Gehlbach (1991) concluded that the Balcones Fault of the Edwards Plateau and Cross Timbers regions acts as a transition zone to terrestrial vertebrates within Texas.

In order to determine if the Edwards Plateau might act as a barrier to the dispersal of mammals within Texas, I divided the Edwards Plateau into two quadrats of approximately equal area around the 100th meridian (Fig. 8). Distributions of native mammals currently residing on the Edwards Plateau were plotted according to the presence or absence of each species within each quadrat (Table 4). The two quadrats were compared using Dice's similarity coefficient. The similarity coefficient of Dice (1943) is given as \(2a/b+c\) where \(a\) equals the number of species shared by both regions, and \(b\) and \(c\) equal the total number of species found within each region. This similarity coefficient does not consider the joint absence of a species from two areas (Sneath and Sokal, 1973). If there was no effect on mammal distributions across the Edwards Plateau, the calculated value of Dice's coefficient should have been one.

The 100th meridian was deemed an appropriate divider for the two quadrats, because (1) it is roughly coincident to the transition area of the eastern deciduous forests and the prairie region of North America (Dice, 1943; Kendeigh, 1954; Jones et al., 1986); (2) other researchers have noted distributional shifts for some vertebrates in the area of the 100th meridian (Bock and Smith, 1982; Bock et al., 1977; Jones et al., 1986); and (3) division around the 100th meridian provided two quadrats large enough to potentially include at least one representative of each species, but not so large that one
Table 4. Distribution of species of mammals on the Edwards Plateau in relation to the 100th Meridian. Ranges that terminate to the west or east of the 100th Meridian are indicated by a single X in the appropriate column. Only extant, native species are included in the analysis.

<table>
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<th>Species</th>
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<th>Species</th>
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<tr>
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The percent similarity of the two quadrats was compared based upon the entire mammalian fauna, only the bats occurring in the two quadrats, only the rodents within the two quadrats, and the combined carnivores and ungulates present in each quadrat. The calculated similarity value for all mammals was 0.83. Similarity values for only the bats and only the rodents were 0.88 and 0.76, respectively. The similarity value for the combined carnivores and ungulates was 0.91. Both quadrats shared 54 out of a total of 76 mammalian species. The two quadrats shared 11 of a possible 14 species of bats.
Twenty-two of a possible 36 rodent species were common in each quadrat. Carnivores and ungulates in the two quadrats shared 15 species out of a total of 18. Based upon these results, environments of the Edwards Plateau appear to act as barriers to the dispersal of some of the species of mammals occurring within its limits. Volant mammals and larger, highly mobile mammals are best able to disperse across the entire Edwards Plateau, whereas the smaller, more sedentary rodents, in some cases, reach distributional limits upon the Edwards Plateau. Nine species of rodents (A. interpres, S. spilosoma, C. nelsoni, C. penicillatus, D. merriami, D. ordii, R. megalotis, P. eremicus, O. arenicola), all of the Chihuahuan faunal element, reach their distributional limits west of the 100th Meridian, whereas four species of rodents (S. carolinensis, G. texensis, N. floridana, M. pinetorum) reach distributional limits east of the 100th meridian.

In order to ascertain which biogeographic region was the most similar in mammalian composition to the Edwards Plateau, the extant, native, mammalian fauna of the Edwards Plateau was compared to the mammalian faunas of surrounding regions within Texas, New Mexico, and Coahuila, Mexico (Table 5). As a consequence of the results of the 100th meridian analysis, an additional analysis was performed utilizing only the rodents of each region. A presence-absence data matrix was prepared for each region from Table 5, and this data matrix was subjected to Unweighted Pair-Group Method of Averages (UPGMA) clustering utilizing calculated Dice similarity coefficients and Euclidean distance measures.

Euclidean distance calculates the distance between two points in Euclidean space utilizing the formula, 
\[ ED = \sum (X_{ij} - X_{ik})^2 \], and emphasizes larger differences in abundance because the differences are summed and squared prior to taking the square root (Ludwig and Reynolds, 1988). The UPGMA method of clustering the data matrices was deemed appropriate due to the presence-absence nature of the data and the difficulties inherent in assigning greater or lesser weights to specific species without sufficient ecological information relating to their distributions within the regions. All subsequent analyses were conducted utilizing the same techniques. Data analysis was performed on an IBM compatible computer utilizing the NTSYS-pc program version 1.80 (Exeter Software, 1993).

Results of the UPGMA clustering, utilizing Dice similarity coefficients and Euclidean distances, of the entire extant, mammalian fauna of the Edwards Plateau with other regional mammalian faunas and clustering of only the rodents of these regions are displayed in Fig. 23. Dice clustering unites the Edwards Plateau most closely with the Rolling Plains of Texas. Similarity of mammals of these two regions is greater than 80 percent. This cluster unites with the Llano Estacado and Panhandle of Texas to form a distinct group at approximately 78 percent similarity. The plains cluster is united with a cluster that combines the mammals of the Trans-Pecos of Texas with Coahuila, Mexico, with East Texas and South Texas forming a distinct, separate cluster away from all of these groups at approximately 66 percent similarity (Fig. 23). The Euclidean distance measure gave slightly different clusters, uniting the Edwards Plateau and Rolling Plains at a distance of approximately 5.1. Coahuila remains unclustered at a distance of approximately 7.9 from the other groups, and East Texas and South Texas remain united at a distance of approximately 6.6 from the plains clusters and the Trans-Pecos region. The cophenetic correlation value of the Dice analysis was 0.69, and the cophenetic correlation value of the Euclidean distance measure was 0.74.

Clustering only the rodents of the regions utilizing Dice similarity coefficients yielded a tree that had identical groupings to the entire mammalian fauna tree (Fig. 24). The rodent fauna of the Edwards Plateau still clustered with rodents of the Rolling Plains and then the Llano Estacado and Texas Panhandle, but at lower percent similarities in all cases. The Edwards Plateau and Rolling Plains formed a cluster at approximately 78 percent similarity, and the Llano Estacado was united with this cluster at approximately 74 percent similarity. Data indicated that rodents of Trans-Pecos, Texas, and Coahuila, Mexico, formed a cluster at an almost identical level of similarity (approximately 79 percent) as in the entire fauna clusters. East and South Texas rodents were united at a much lower similarity value of approximately 52 percent, compared to approximately 66 percent in the complete fauna tree. The cophenetic correlation value of the Dice analysis dendrogram of rodents clustered by region was 0.81. UPGMA clustering of the rodents utilizing Euclidean distance measures resulted in two tied trees. The Edwards Plateau was placed with the Rolling Plains
Table 5. Extant, native, mammals of the Edwards Plateau and surrounding regions of Texas and the state of Coahuila, Mexico. Introduced mammals are excluded. The presence of a mammalian species within a region is denoted by an X. E. P., Edwards Plateau; L. E., Llano Estacado of Texas and New Mexico and the northern Panhandle of Texas; T. P., Trans-Pecos, Texas; E. T., East Texas; S. T., South Texas; R. P., Rolling Plains of Texas; CA, Coahuila, Mexico.

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Figure 23. UPGMA cluster dendrograms for all resident, native mammals. EP, Edwards Plateau; RP, Rolling Plains of Texas; LP, Llano Estacado and northern Texas Panhandle; TP, Trans-Pecos; ET, East Texas; ST, South Texas; CA, Coahuila, Mexico. Cophenetic Correlations are indicated by (r).

Figure 24. UPGMA cluster dendrograms for only rodents. Euclidean distance dendrograms are tied. See Figure 23 for region abbreviations. Cophenetic Correlations are indicated by (r).
and Llano Estacado in one tree, whereas the Edwards Plateau was grouped with the Trans-Pecos and Coahuila, Mexico, in the second tree. The first tree (Fig. 24) placed the rodents of Trans-Pecos and Coahuila in a cluster at a distance of approximately 4.1, and East and South Texas were united in another cluster at approximately 4.8. The second tied tree (Fig. 24) united the rodents of the Llano Estacado and Texas Panhandle with the Rolling Plains region, and combined that clustered pair with South Texas. East Texas was combined with the Llano Estacado and Texas Panhandle, Rolling Plains, and South Texas tree at a distance of 4.8. Considering both of the trees, the rodents of the Edwards Plateau were most similar to rodents of the Rolling Plains (Fig. 24) at a distance of approximately 3.7, whereas rodents of the Edwards Plateau are also similar to rodents of Trans-Pecos, Texas, at a distance close to 4.0. The cophenetic correlation value was slightly higher for the tree that clustered the Edwards Plateau with the Rolling Plains \( (r=0.69) \), as opposed to the tree that united the Edwards Plateau with Trans-Pecos, Texas \( (r=0.61) \).

The most likely source areas for a great deal of the mammalian fauna of the Edwards Plateau seem to be the Rolling Plains and Llano Estacado regions of Texas. These results agree well with those obtained by Choate (1997) in his study of the mammals of the Llano Estacado region. If the entire native mammalian faunas are considered, the Edwards Plateau clusters with the plains regions in both Choate’s study and these analyses. The Edwards Plateau shares a total of 57 mammals with the Rolling Plains and 56 mammals with the Llano Estacado and Texas Panhandle region. The Edwards Plateau shares 25 rodent species with the Rolling Plains and 24 rodent species with the Llano Estacado and Texas Panhandle. The Trans-Pecos region and the Edwards Plateau share 30 rodent species. A difference exists between Choate’s (1991) study and my own because of the clustering of the Edwards Plateau rodent fauna with Trans-Pecos, Texas, in one instance. Choate (1997) indicated that the Edwards Plateau clustered most closely with the plains regions in his study of the small, terrestrial mammals. The results of both studies give at least some support to Schmidly’s (1984a) combining of the Llano Estacado, Rolling Plains, and Edwards Plateau into a plains region.

In order to ascertain where on the Edwards Plateau a barrier to mammal dispersal might be found, if one existed, I utilized distributional data from the two quadrats of the Edwards Plateau divided approximately in half around the 100th meridian (Table 4), and compared the entire mammalian fauna of each quadrat to the previously mentioned regions utilizing Dice similarity coefficients, Euclidean distance values, and UPGMA clustering. Rodents of the regions were clustered together with Dice similarity coefficients, only after a difference in faunal associations was elucidated in the western quadrat of the Edwards Plateau. Each quadrat was compared to the surrounding regions separately after it was determined that the two quadrats clustered with each other before either quadrat was united with a separate biogeographic region. It was reasoned that, if no barrier to dispersal existed, the two quadrats should both cluster with the same outside region.

Clustering all resident, native mammals of the eastern quadrat (Fig. 25) resulted in a dendrogram that placed the eastern half of the Edwards Plateau with the Rolling Plains region at a Dice similarity value of approximately 0.84 (Fig. 25), and at a Euclidean distance value of approximately 4.6 (Fig. 25). The Llano Estacado united with the Dice tree at a similarity of approximately 0.78 and a Euclidean distance value of approximately 5.5. East Texas joined both plains clusters next, and South Texas clustered separately with East Texas at a similarity of approximately 6.5 and a Euclidean distance of 6.6. In both analyses of the entire, regional, mammalian faunas compared to the mammalian fauna of the eastern quadrat, Trans-Pecos, Texas, and Coahuila, Mexico, were united in an independent cluster separated from the remainder of the Texas regions. The cophenetic correlation value of the Dice similarity dendrogram was 0.72, whereas the cophenetic correlation value of the Euclidean distance dendrogram was 0.81.

The likely source area for mammal dispersal onto the eastern Edwards Plateau is from the Rolling Plains region. The eastern quadrat shares a total of 53 species of mammals with the Rolling Plains region. A total of 50 mammalian species are shared with the Llano Estacado and Texas Panhandle region, whereas the eastern quadrat shares 52 species of mammals with the Trans-Pecos region. However, the Trans-Pecos shares 70 species of mammals with Coahuila, Mexico, and, thus is most similar in faunal composition to that biogeographic area.
Figure 25. UPGMA cluster dendrograms for mammals of the eastern quadrat (EM) of the Edward Plateau and surrounding regions. See Figure 23 for region abbreviations. Cophenetic correlations are indicated by \( r \).

Figure 26. UPGMA cluster dendrograms for mammals of the western quadrat (WM) of the Edward Plateau and surrounding regions. See Figure 23 for region abbreviations. Cophenetic correlations are indicated by \( r \).
Slightly different results were obtained by clustering distributional data on mammals of the western quadrant of the Edwards Plateau with the surrounding regions (Fig. 26). UPGMA clustering of Dice similarity coefficients resulted in a dendrogram wherein the mammals of the western Edwards Plateau clustered most closely with the Trans-Pecos region at a value of approximately 0.81. The mammalian faunas of the Llano Estacado and Texas Panhandle region and the Rolling Plains region were clustered together at a value of approximately 0.80, and the four areas formed a united group at a value of approximately 0.77. Coahuila was united with the previous clusters at a similarity value of approximately 0.68. In this analysis, mammals of East and South Texas were united in a cluster at a similarity value of approximately 0.65 and remained separated from all of the previous clusters. Euclidean distance clustering utilizing the UPGMA method resulted in a dendrogram that united the western Edwards Plateau with the Rolling Plains at a distance of approximately 5.1 with the Llano Estacado and Texas Panhandle joining the initial cluster at a distance of approximately 5.3. The Trans-Pecos region was united with the plains regions at a distance of approximately 6.2, and East and South Texas formed a separate cluster at a distance of approximately 6.6. Euclidean distance clustering resulted in mammals of Coahuila clustering alone at a distance of approximately 7.9. The cophenetic correlation value of the Dice cluster analysis of the western Edwards Plateau was 0.74, and the cophenetic correlation value of the Euclidean distance cluster analysis of the western Edwards Plateau also was 0.74.

Clustering only the rodents of the eastern quadrant with only rodents from the surrounding regions produced a dendrogram almost identical to the dendrogram of the entire mammalian fauna of the eastern quadrant compared with the surrounding regions (Fig. 27). The rodents of the eastern Edwards Plateau again clustered most closely with those of the Rolling Plains and this pair united to the Llano Estacado and Texas Panhandle region. The positions and similarity values of the remaining regions were also similar to the entire faunal clustering of the eastern Edwards Plateau. Results of the rodent-cluster dendrogram of the western Edwards Plateau with rodents of the surrounding regions also yielded results which were very similar to comparing the entire mammalian fauna of the western quadrant with the surrounding regions (Fig. 27). Positions and groupings of all clusters were essentially the same in both analyses. The cophenetic correlation value of the dendrogram utilizing rodents of the eastern Edwards Plateau was 0.72, whereas the dendrogram comparing rodents of the western Edwards Plateau was 0.74.

It may be stated, based upon cluster analyses of the two quadrats of the Edwards Plateau, that a barrier to the dispersal of some mammals exists on the Edwards Plateau. The complete mammalian fauna of the eastern Edwards Plateau tends to cluster with the Rolling Plains and Llano Estacado-Texas Panhandle regions. The mammalian fauna of the western Edwards Plateau may cluster with either the Trans-Pecos region or the Rolling Plains region. If rodents alone are considered, the eastern Edwards Plateau is most similar to the Rolling Plains, whereas the western Edwards Plateau is most similar to the Trans-Pecos.

The paradox of the entire mammalian fauna of the western quadrant of the Edwards Plateau clustering with both the Rolling Plains and the Trans-Pecos may be explained in regard to the total number of species that the western and eastern quadrats have in common. The western quadrant, even when considered as a separate geographic area, contains within its fauna all but four mammalian species which are found in the eastern quadrant. The eastern Edwards Plateau shares 53 species with the Rolling Plains, whereas the western Edwards Plateau shares 52 species with the Rolling Plains. However, when considering the entire fauna, the eastern quadrant shares 52 species with the Trans-Pecos region, and the western quadrant shares 62 species with the Trans-Pecos. A rather unidirectional barrier or filter zone appears to exist on the Edwards Plateau allowing most widespread species to inhabit the entire region and some other species to reside in only the eastern or western portions. Rodents are especially sensitive to this filter, with several species being restricted to either the western or eastern quadrant of the Edwards Plateau. The western quadrant has a more diverse rodent fauna with many Chihuahuan species which are lacking to the east, indicating that certain environmental factors within this area impede the spread of some rodent species to the east. Rodent species indigenous only on the eastern Edwards Plateau are primarily limited to riparian areas and migrate onto the Edwards Plateau along rivers and streams found in the Balcones Fault zone and extending farther west and north on the eastern Edwards Plateau. Many of these
Figure 27. UPGMA cluster dendrograms for only the rodents of the eastern and western quadrates of the Edwards Plateau and surrounding regions. See Figure 23 for region abbreviations. Cophenetic correlative correlations are indicated by (r).

Figure 28. UPGMA cluster dendrograms comparing mammals from rainfall isolines on the Edwards Plateau. A, 12-18 in.; B, 18-22 in.; C, 22-26 in.; D, 26-32 in. Cophenetic correlations are indicated by (r).
watercourses have their headwaters east of the 100th meridian, thus creating distributional limits for these species within the eastern quadrat of the Edwards Plateau.

The distributions of resident, native mammals on the Edwards Plateau were plotted against rainfall isocline divisions and combined vegetation associations (Tables 6 and 7) in order to determine possible ecological reasons for the distribution patterns of mammals on the Edwards Plateau. The rainfall and vegetation data matrices were clustered by the UPGMA method with Dice similarity coefficients and Euclidean distance values (Figures 28 and 29). All of the resident, native species of mammals on the Edwards Plateau were included in both analyses, because of difficulties related


Figure 29. UPGMA cluster dendrograms comparing mammals from combined vegetation associations on the Edwards Plateau. A, Mesquite-Lotebush Grasslands; B, Mesquite-Juniper-Creosote; C, Live Oak-Juniper-Mesquite; D, Live Oak-Mesquite; E, Live Oak-Juniper-Mesquite Breaks.
Table 6. Occurrence of mammals on the Edwards Plateau in relation to areas determined by annual rainfall isoclines in inches of precipitation. A, ≤12-18; B, 18-22; C, 22-26; D, 26≥32.

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Dendrograms branching and clusters were essentially the same for the Dice and Euclidean distance analyses of rainfall isocline quadrats versus mammalian distributions (Fig. 28). The far western Edwards Plateau ( ă 12-18 in.) clustered separately from all of the other groups at a similarity value of approximately 0.78 and a Euclidean distance of 5.0. The two central regions of the Edwards Plateau (18-22 and 22-26 in.) clustered together at a similarity value of approximately 0.89 and a Euclidean distance of approximately 3.5. The final rainfall isocline quadrat (26 ă 32 in.) was united with the central quadrats at a similarity value of approximately 0.84 and a Euclidean distance of approximately 3.5. The cophenetic correlation value of the Dice dendrogram for moisture was 0.63 and the cophenetic correlation value of the Euclidean distance dendrogram was 0.70.

The rainfall regimes of the extreme western and eastern Edwards Plateau regions, based upon the results of the cluster analyses, appear to influence the distributions of several mammals in the region. Some species, such as A. interpres, C. castanops, D. ordii, D. merriami, R. megalotis, P. eremicus, and others, are limited to the more xeric western Edwards Plateau, whereas other species, such as Scalopus aquaticus, Sylvilagus aquaticus, S. carolinensis, G. texensis, and others, do not range very far west on the Edwards Plateau. Barriers to dispersal of mammals exist on both the western and eastern Edwards Plateau. The central quadrats of the Edwards Plateau clustered together and are more uniform in their mammalian faunas than the two peripheral quadrats. Fewer species of mammals to the inclusion or exclusion of certain habitat or substrate specific species (which will be discussed below) within both matrices. If such species were all excluded from the analyses, the data sets would be of limited information value, and the inclusion and analysis of all species seemed to be the most conservative approach.

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<td><em>Peromyscus pectoralis</em></td>
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<td><em>Baiomys taylori</em></td>
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<td><em>Onychomys arenicola</em></td>
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reach absolute distributional limits on the central Edwards Plateau than on the peripheral quadrats, and the mammalian fauna of the central quadrats is heavily weighted with widespread species, or species with less specific habitat requirements.

Distribution of mammals related to vegetation associations was similar to mammalian distributions verses rainfall isolines. A high degree of congruence would be expected because of the more-or-less direct effect of precipitation upon vegetative community structure within an area. Clusters and groups of the mammalian distributions based upon vegetation associations were identical in the Dice and Euclidean distance analyses (Fig. 29). The Mesquite-Lotebush-Grasslands Association clustered with the Mesquite-Juniper-Creosote brush Association at a similarity value of approximately 0.87 and a Euclidean distance of approximately 3.8. These western vegetation associations clustered separately from the other vegetation associations at a similarity value of approximately 0.73 and a Euclidean distance of approximately 5.3. The Live oak-Ashe juniper-Mesquite Association and Live oak-Juniper-Mesquite Woods associations of the central Edwards Plateau clustered together at a similarity value of approximately 0.84 and a Euclidean distance of 4.3. These central and southeastern vegetation associations were united with the Live oak-Mesquite Parks at a similarity value of approximately 0.76 and a Euclidean distance of approximately 4.7. The cophenetic correlation values for the Dice and Euclidean dendrograms were 0.74 and 0.77, respectively.

Mammals of the northwestern and southwestern vegetation associations are closely associated with each other and are well separated from the other vegetation associations and their mammalian faunas on the Edwards Plateau. This separation again supports the
hypothesis of a barrier to mammalian dispersal on the western Edwards Plateau. The Live-oak dominated central and southeastern vegetation associations are almost identical in plant community composition, except for riparian areas on the southeastern Edwards Plateau, which contain bald cypress trees. UPGMA clustering united the Live-oak-Mesquite-Parks Association of the Llano Uplift with the central and southeastern Edwards Plateau at a lower level of similarity, but this may be due to a sampling effect over this area. The Live-oak-Mesquite-Parks Association had the lowest total number of native, species of mammals (39) of all vegetation associations on the Edwards Plateau. The Mesquite-Juniper-Creosote Bush Association had the highest total number of native, mammalian species (63), and the The Live-oak-Ashe juniper-Mesquite Association was next with 58 total mammals. The Mesquite-Lotbush-Grasslands of the northwestern Edwards Plateau and the Live-oak-Juniper-Mesquite Woods each had a total of 50 resident, native mammalian species.

Several species of mammals have problematical distributions in relation to their occurrence in the sample quadrats based upon precipitation averages and vegetation associations. Many of these species, as mentioned above, are habitat specialists, habitat generalists, soil substrate limited, or restricted in their distribution by other environmental factors. The eastern mole (S. aquaticus) and all of the species of pocket gophers (T. bottae, G. bursarius, G. texensis, C. castanops) probably are limited most by soil substrate on the Edwards Plateau, rather than simply by moisture or vegetation associations. Some pocket mice and kangaroo rats (C. nelsoni, C. penicillatus, D. merriami, D. ordii) also are probably limited by soil substrate and possibly by moisture. These heteromyid rodents occur in suitable soils on the Trans-Pecos, Llano Estacado, and Rolling Plains of Texas, but are peripheral species of the Edwards Plateau. The rock squirrel (S. variegatus) is a saxicolous species found throughout the southern and central Edwards Plateau but absent on the northern Edwards Plateau. The limiting environmental factors of this species on the Edwards Plateau are unknown. The southern grasshopper mouse (O. arenicola) is found only on the extreme western Edwards Plateau, and may be limited by soil substrate and precipitation levels.

River systems and watersheds also influence the distribution of mammals on the Edwards Plateau. Blair (1950) and Gehlbach (1991) stated that the river systems and Balcones canyonlands provide access to the interior of the Edwards Plateau for some eastern mammals. Some mammals, such as the swamp rabbit (S. aquaticus), eastern woodrat (N. floridana), and the pine vole (M. pinetorum), usually are associated only with riparian areas adjacent to streams and rivers. These mammals rarely are found far from such habitats in any area. Additionally, a few mammals require the aquatic environments provided by rivers and streams in order to reside in an area. Beaver (C. canadensis), muskrat (O. zibethicus), and river otters (L. canadensis) must have aquatic habitats within an area in order to persist, and these species are directly associated with rivers and streams in their distributional patterns on the Edwards Plateau. Beaver and muskrat are especially problematic because they occur in the Pecos and Rio Grande river systems (Hollander et al., 1990) and nowhere else on the western Edwards Plateau, thus giving a wide range to these species in any quadrat analysis. Hollander et al. (1990) noted that the Pecos River had an influence on mammalian distributions in western Texas, and the results of my study support the work of these researchers.

In conclusion, a definite barrier to the distribution of some Chihuahuan and eastern mammals exists on the Edwards Plateau of Texas. The eastern and western faunas undergo distributional shifts on the Edwards Plateau, with several species reaching distributional limits around the 100th meridian. Armstrong et al. (1986) noted a distributional shift of some mammalian species of the Great Plains states around the 100th meridian, with the most pronounced shift occurring among southwestern peripheral species. My research lends some support for the hypothesis that environments found around the 100th meridian constitute a transition zone for some eastern and western mammals in temperate North America. Many bats and other larger, more mobile mammals are not limited in their distributions on the Edwards Plateau, but small rodents and other mammals may be limited in distribution by precipitation, vegetation, soil substrate, river systems and other ecological factors.
Mammals long have been economically important to residents (both Native Americans and Europeans) of the Edwards Plateau. Bison and white-tailed deer furnished food, clothing, and other essentials to humans in the region, and white-tailed deer also were appreciated for sporting and aesthetic reasons (Doughty, 1983). Several trading posts devoted to acquiring deer skins and other mammal pelts were established by the Torrey brothers at Austin, Fredericksburg, Houston, New Braunfels, and San Antonio in the 1840's. George Bernard, a partner of the Torrey's, established a post near Waco, Texas, and exchanged goods primarily for deer skins (Strecker, 1927), but Bernard also handled buffalo hides, bear, beaver, raccoon, and fox skins. Bernard shipped about 75,000 deer skins from his post during the period of 1844 to 1853 (Strecker, 1927).

Deer and exotic ungulates still are economically important to area residents, but the major interest now is in hunting these species for sport, meat, and trophies. Many landowners on the Edwards Plateau lease their properties to game hunters yearly and derive a substantial income by this practice. Costs of deer leases range from $600 to $1200 per person on the Edwards Plateau, depending upon the duration of the lease, size of the property, and other considerations. Other game species, such as upland game birds and waterfowl, may or may not be included in the leasing agreement, depending upon the landowner’s preference.

Furbearing mammals are economically important on the Edwards Plateau and throughout Texas, but data based upon trapper surveys and fur harvest records must be cautiously interpreted. Obbard et al., (1987) stated that factors such as species limits in an area, trapping seasons, protected species, changes in traps and trapping techniques, and animals taken primarily for trophies rather than for sale of pelts need to be considered when evaluating the economic importance or abundance of a species from trapping data. Other factors to consider are variable market demands and subsequent price fluctuations for different furbearers, natural population fluctuations, and trapping intensity for a specific species in an area. Despite these limitations, available trapping data may still be useful in arriving at some conclusions concerning furbearing mammals on the Edwards Plateau region and Texas.

Raccoons and skunks appear to be the most abundant furbearers on the Edwards Plateau, based upon a trapper survey conducted by the Texas Parks and Wildlife Department in 1988 (Perkins, 1989). Gray fox and ringtails were next in abundance, respectively. The Virginia opossum and red fox were estimated to occur in an abundance of approximately one animal per 100 miles, while coyotes were the least abundant of the reported furbearing animals on the Edwards Plateau, being estimated to occur at a density of 0.17 animals per 100 miles (Perkins, 1989). These data on abundances could be suspect due to the relatively high market value in 1988 of raccoon and ringtail pelts ($4.25 and $3.25, respectively). The value for coyote pelts during the same year was $2.75. Additionally, raccoons, ringtails, opossums, skunks, and foxes all are easier to capture by standard trapping methods than are coyotes. No data are available on black bear harvests in Texas, probably due to the fact that *U. americanus* now is protected in this state (Novak et al., 1987). No bobcats were reported from the Edwards Plateau despite a high market price ($32.25) for their pelts (Perkins, 1989). Novak et al. (1987) stated that weasels are not important furbearers for Texas markets and reported numbers throughout the twentieth century are low. Badger, beaver, and nutria numbers have remained relatively constant through the twentieth century after heaviest trapping efforts in the 1940's (Novak et al., 1987; Obbard et al., 1987). With a few exceptions, such as the mountain lion, black bear, and spotted skunk, furbearing mammal populations appear to be either stable or increasing in numbers on the Edwards Plateau.

Domesticated mammals such as cattle, goats, and sheep have been, and still are, economically important to Edwards Plateau residents. Much of the land area of the Edwards Plateau is utilized in ranching enterprises. The Edwards Plateau region is among the leading regions in the United States in the production of mohair and wool and associated products (Pool, 1975). Some of the major mohair and wool markets are located at Del Rio, Kerrville, Rocksprings, San Angelo, San Antonio, and Uvalde (Pool, 1975). Mohair brought $27,428,000 and wool brought $21,473,000 into the Texas economy in 1964 alone.
Introduced animals are also economically important on the Edwards Plateau of Texas. The commensal rodents, *Mus musculus*, *Rattus rattus*, and *R. norvegicus*, cause considerable damage to food supplies, stored grain and agricultural products, equipment, and structures wherever they occur (Jackson, 1982). These rodents (and other native species) have been implicated in the spread of several diseases such as typhus, plague, rabies, hantavirus, and Rickettsial pox (Jackson, 1982; Marshall, 1993). The nutria, *Myocastor coypus*, was introduced into Louisiana in 1938 (Lowery, 1974) and has subsequently spread to Texas and the Edwards Plateau. Lowery (1974) presented evidence that nutria may compete with species, such as muskrat, for living space within a particular habitat. Nutria may benefit an area by eliminating undesirable emergent vegetation, but they also have been reported to destroy young cypress trees and other woody vegetation in an area (Wilner, 1982; Schmidly, 1984b). The reported value of the nutria fur harvest in East Texas from 1976 to 1982 was $1,600,000 (Schmidly, 1984b). In addition, the meat of introduced ungulates, such as bison and axis deer, is sold commercially by some businesses throughout the Edwards Plateau. An example of this type of business is “Venison World” in Eden, Texas, which sells meat and other products from ranch-raised axis deer.
ACCOUNTS OF NATIVE SPECIES

The following accounts are based upon specimens of native mammals obtained on the Edwards Plateau and housed in the mammal collections of universities listed in the methods section. Mammal collection acronymys also may be found in the methods section. Some taxa are also included based upon observations, as well as the records found in scientific literature. Species now extirpated from the region are included in these species accounts, but their status is indicated in the distribution section of the account. The arrangement of taxa and taxonomic nomenclature follows that of Jones and Jones (1992), except where noted in the text. Information concerning the species’ overall distribution, distribution on the Edwards Plateau, identification characters, habitat preference, and other life history information is included in each species account. Measurements given in text are in millimeters and weights are in grams.

KEY TO ORDERS OF MAMMALS ON THE EDWARDS PLATEAU

1 Incisors 1/1 or 2/1 (second upper incisor peglike and set directly behind the first); broad diastema between incisors and cheekteeth; first upper incisor evergrowing and modified for gnawing ............................................................... 2

1’ Incisors variable (never 1/1, 2/1 only in one insectivore and then second upper incisor set normally in toothrow) to absent; first upper incisor, if present, not evergrowing, not modified for gnawing ............................................................... 3

2 Incisors 2/1; maxillary fenestrations present; ears elongated, upright, and lanceolate in shape ................................................................................................... Lagomorpha

2’ Incisors 1/1; no maxillary fenestrations; ears never greatly elongated or lanceolate in shape ........................................................................................................... Rodentia

3 Incisors absent; cheekteeth peglike and supernumerary, cheekteeth lacking enamel, conspicuous dermal scutes ........................................................................... Xenarthra

3’ Incisors present at least in lower jaw; cheekteeth not peglike, composed partly of enamel ............................................................................................... 4

4 Incisors 5/4; angular process of dentary distinctly inflected; marsupium present in females; tail prehensile ............................................................................ Didelphimorphia

4’ Incisors never more than 3/3; angular process of dentary not inflected; marsupium never present; tail not prehensile ........................................................................... 5

5 Upper incisors absent (except Dicotylidae); upper canine absent or, if present, separated from cheekteeth by a modest diastema; postorbital bar present (incomplete in Dicotylidae); terminal digits (except dewclaws) ending in single or clovenhooves ........................................................................... Artiodactyla

5’ Upper incisors present; upper canine present and not separated from cheekteeth by diastema; postorbital bar absent; terminal digits not ending in hooves ..................................................................................... 6

6 Molars 3/3, last upper molar never dumbell-shaped; number of incisors variable; greatest length of skull less than 45 mm ........................................................................... 7

6’ Molars never 3/3; upper incisors always three in number; greatest length of skull usually more than 45 mm; terminal claws well developed and retractile in some members ........................................................................... Carnivora
Canine poorly to modestly developed, never largest tooth in anterior part of toothrow; upper incisors large and procumbent; dorsal profile of skull flattened, braincase not much higher than rostrum; eyes reduced to absent; ear pinnae small to absent; limbs not modified for flight .................................................. Insectivora

Canine well developed, largest tooth in anterior part of toothrow; upper incisors small and not procumbent; dorsal profile of skull not flattened, braincase noticeably higher than rostrum in most members; eyes always present; ear pinnae conspicuous; forelimbs modified for flight ............................................. Chiroptera

ORDER DIDELPHIMORPHIA—OPPOSUMS

Family Didelphidae
*Didelphis virginiana*
Virginia Opossum

*Distribution.*—The opossum ranges from Nicaragua in the south, northward through southern, eastern, and western Mexico. This species ranges northward in the United States from Texas to eastern Colorado and Nebraska, to South Dakota, British Columbia, and Ontario. The opossum ranges eastward from South Dakota at least as far as New Hampshire.

The opossum ranges throughout the Edwards Plateau (Schmidly, 1984b). Specimens of *D. virginiana* in museum collections are from Bexar, Blanco, Coke, Hays, Irion, Kerr, Kimble, Kinney, Llano, Mason, Reagan, Runnels, San Saba, Sutton, Taylor, Tom Green, Travis, and Val Verde counties (Fig. 30).

*Didelphis virginiana* may be recognized by its long, scaly, prehensile tail, and white coloration of the face and toes. Ears are hairless and rounded, and the fur is grayish-white, blending to black around the legs. The pelage is long and coarse. Five toes are present on each foot, and the hallux is clawless, thumblike, and opposable. Females have a marsupium in which to carry the young. The skull has a total of 50 teeth (in adults) and the angular processes of the mandible are inflected.

The opossum occupies a variety of habitats, including riparian areas, deciduous woodlands, grassy valleys, oldfields, prairies, and savannah areas on the Edwards Plateau. The opossum often occurs in close association with humans. Factors limiting opossum distribution include an adequate water supply and, possibly, extremely low winter temperatures. *D. virginiana* can maintain a constant body temperature at ambient temperatures lower than zero degrees Celsius, but extensive frostbite may occur (McManus, 1974).

Opossums are omnivorous in diet (Schmidly, 1983; Davis and Schmidly, 1994). Diet items include fruit, insects, leaf and log litter, acorns, snails, crawfish, bird feathers, carrion, eggs, and various small vertebrates (Jones et al., 1983; Schmidly, 1983). The prehensile tail and opposable toes make the opossum an able climber. *D. virginiana* often forages in the branches of trees, and will also climb trees for refuge from predators. The opossum is nocturnally active.

The opossum is solitary in habit. Social behavior is poorly developed and, except for mating, most encounters between conspecifics elicit antagonistic behaviors (McManus, 1974). Home ranges of the opossum are relatively small and often are located around watercourses through an area (Lay, 1942; McManus, 1974). Populations are heavily weighted toward young of the year, and population turnover is rather rapid (McManus, 1974).

Opossums inhabit the burrows of other animals, live in abandoned buildings, barns, and other deserted structures, and may build arboreal nests of grass, twigs and other vegetation (McManus, 1974). Nest materials are carried by means of the prehensile tail, thus freeing the feet for climbing when the opossum constructs an arboreal nest (McManus, 1974).

The mating season extends from January or February to June or July (McManus, 1974). Two litters of young usually are produced per year. The gestation period is 12 to 13 days, and young are extremely altricial when born. The young attach to the mother's nipples within her marsupium, and remain there for 50 to 65 days (McManus, 1974). Nine to 10 young have been
recorded per litter from Edwards Plateau specimens. Females reach sexual maturity at one year of age (McManus, 1974).

The subspecies of opossum on the Edwards Plateau is *D. v. virginiana* Kerr, 1792. Adult males are larger than females (Gardner, 1973). However, opossums grow throughout life (Gardner, 1982). External measurements of an adult female from the Edwards Plateau are: total length, 783; tail length, 322; length hind foot, 62; ear length, 50. Selected mean cranial measurements of three adult females from the region are: greatest length skull, 118.93; zygomatic breadth, 60.73; interorbital constriction, 22.66; postorbital constriction, 12.43; length maxillary toothrow, 46.17; width across molars, 34.26.

Specimens examined (70).—Bexar Co.: 14 548850E, 3271000N, 1; 14 532400E, 3238700N, 1 (SWTU). Coke Co.: 14 348200E, 3521600N, 1 (ASNHC); 14 364400E, 3514300N, 1 (ASNHC). Hays Co.: 14 601800E, 3312200N, 1 (TNHC); 14 587600E, 3312400N, 1 (SWTU). Kerr Co.: 14 440400E, 3325100N, 1 (WTAM); 4 mi. outside Kerr Wildlife Management Area, 1 (WTAM). Kimble Co.: 14 434400E, 3379000N, 1; 14 404100E, 3394000N, 2 (ASNHC); 14 430200E, 3389500N, 1; 14 429800E, 3377200N, 1 (TCWC); 14 432300E, 3378500N, 1; 14 422300E, 3375400N, 1; 14 425400E, 3372000N, 3; 14 395400E, 3372000N, 1; 14 429800E, 3377200N, 1; 14 439000E, 3372600N, 2 (MWSU); 14 400500E,
ORDER INSECTIVORA—INSECTIVORES

KEY TO INSECTIVORES

1 Zygomatic arch present; front feet broad and paddle-shaped; eyes non-functional and covered with skin; total length more than 150 mm; external ear pinnae absent. ................................................. Scalopus aquaticus

1' Zygomatic arch absent; front feet not paddle-shaped; eyes functional and evident; total length less than 150 mm; external ear pinnae evident ................................................................. Notiosorex crawfordi

Family Soricidae—Shrews

Notiosorex crawfordi
Desert Shrew

Distribution.—The geographic range of the desert shrew extends from central Mexico northward to southern California and southern Nevada, thence eastward throughout most of Arizona and New Mexico, southeastern Colorado, and southern Kansas. The desert shrew’s range extends as far east as western Arkansas, and includes the western two-thirds of Texas.

Records of the desert shrew are spotty on the Edwards Plateau; specimens have been reported from Coke, Howard, Kerr, and Tom Green counties within the region (Fig. 31). The paucity of records likely is a result of trapping difficulty of the desert shrew by standard methods. In most cases, records are more readily obtained by examination of small mammal remains from owl pellets (Jones and Goetze, 1991; Goetze et al., 1991).

Notiosorex crawfordi may be mistaken only for the least shrew (Cryptotis parva) in Texas. The least shrew, however, has not been definitely recorded on the Edwards Plateau. The desert shrew is small in size (average total length 85.5 mm), has distinct ear pinnae, and a long, pointed rostrum. The tail is short and well-haired; overall pelage color is grayish. The appendages are short and feet are pentadactyl. The first upper incisors of this small mammal are procumbant with tips curved backward and possess a second, posterior unicuspilike conule. The teeth are lightly pigmented with red in this species of shrew.

The desert shrew may occur in a variety of habitats within a region. The most common association is semidesert scrub with mesquite, agave, scrub oaks, and...
Figure 31. Distribution of Notiosorex crawfordi on the Edwards Plateau.

other xerophytic vegetation (Armstrong and Jones, 1972). Boyd (1994) stated that N. crawfordi is found in mesquite-juniper, mesquite-juniper-live oak, and mesquite-mixed grass vegetation associations in Tom Green County. Water is not required within the habitat, but water is accepted by captive animals (Armstrong and Jones, 1972).

The desert shrew is quite active. The tail is often arched above the back when N. crawfordi is running. Available data indicate that N. crawfordi forages for food items both diurnally and nocturnally. The desert shrew is insectivorous. Known diet items include mealworms, cutworms, crickets, cockroaches, house flies, beetles, earwigs, centipedes, spiders, and carrion (Armstrong and Jones, 1972). Live rodents, scorpions, and earthworms are avoided. Appendages are removed from prey items first, to immobilize them, and then the skulls are crushed by the desert shrew.

Notiosorex crawfordi is not known to construct burrows, but nests are constructed by both males and females. The desert shrew appears to be more tolerant of conspecifics than other shrew species (Armstrong and Jones, 1972), and individuals may be placed together in captivity. Nests usually are inhabited by a single individual and are constructed from grasses, leaves, and other materials available in a specific area. Runways are not developed around the nest sites, but paths of other small animals are utilized to some extent.

The desert shrew goes into deep sleeps and is not disturbed by external noises and activities when in this state. The shrews are able to reduce their metabolic rate when in this state of torpor (Hoffmeister, 1986).
This mechanism may help *N. crawfordi* to reduce its food requirements for maintenance and reproduction.

The desert shrew has been found in woodrat nests on the Southern Great Plains and in Arizona (Armstrong and Jones, 1972). This species, interestingly, also has been captured in old bee hives. Other cover utilized by the desert shrew includes old logs in floodplains, discarded lumber and building materials, dead agave plants, and even an old, abandoned bathtub (Hoffmeister, 1986). These types of cover often support a moist microhabitat that may be favorable for the invertebrate prey items of the desert shrew.

The reproductive season of the desert shrew apparently extends throughout the warmer seasons of the year (Armstrong and Jones, 1972). Females captured in October and January in Tom Green County evinced no reproductive activity. *N. crawfordi* probably produces litters throughout the year in Arizona (Hoffmeister, 1986). Offspring typically number from three to five. A litter may contain as many as six young, and *N. crawfordi* may produce at least two litters per year (Hoffmeister, 1986). Young shrews grow rapidly and are nearly the size of adults by 40 days after parturition.

The subspecies of desert shrew on the Edwards Plateau is *N. c. crawfordi* (Coues, 1877). Sexual dimorphism is not apparent in *N. crawfordi*. Mean external measurements of four female *N. crawfordi* from Arizona (Armstrong and Jones, 1972) are: total length, 85.5; tail length, 25; length hind foot, 10; ear length, 8. Selected cranial measurements (Hoffmeister, 1986) are: skull length, 15.83; maxillary breadth, 5.00; breadth braincase, 8.36; unicuspid toothrow length, 1.83; complex toothrow length, 4.41; toothrow length, 6.09.

*Specimens examined (5).—Coke Co.: 14 337200E, 3522600N, 1 (ASNHC). Tom Green Co.: 14 355200E, 3452000N, 1 (ASNHC); Head of the River Ranch, 14 357600E, 3449000N, 3 (ASNHC). Additional records.—Howard Co.: 14 267600E, 3570800N. Kerr Co.: 14 476200E, 3326400N. (Davis, 1941).*

**Family Talpidae—Moles**

*Scalopus aquaticus*

**Eastern Mole**

*Distribution.*—The eastern mole is distributed from northeastern Tamaulipas, Mexico northward through the eastern half of Texas and the eastern portion of the Texas panhandle. The eastern mole ranges as far north as southern South Dakota, eastward to Massachusetts, and south throughout Florida. The eastern mole occurs in isolated localities on Trans-Pecos, Texas, and Coahuila, Mexico.

The eastern mole has been reported from Gillespie, Mason, and Travis counties on the Edwards Plateau (Fig. 32). The Pleistocene distribution of this species extended as far west as Edwards County (Yates and Schmidly, 1977), but erosion of the paleosoils at the close of the Pleistocene may have contributed to the elimination of many talpid populations within the region (Toomey et al., 1993).

*Scalopus aquaticus* is adapted for a fossorial existence with a streamlined body, no ear pinnae, and appendages that are short and close to the body. Pelage is short, soft, and is composed of only guard hairs. The dorsum is brown, with silvery hairs interspersed throughout, and the venter is grayish in color. The eyes are completely covered by skin and the rostrum is long, pointed, and devoid of hair. The forefeet are broader than they are long, and are rotated 180 degrees so that the palms face outward. Forefeet are covered by thick skin pads and have well developed claws for burrowing. The hindfeet are small and the tail is short and hairless.

The eastern mole is found in loamy, well-drained soils. Moles prefer soils where burrowing is easy and are usually absent from soils high in clay and stony or gravelly soils. Soil condition, moisture and aeration of the soil, and the availability of food items also are important factors determining the presence or absence of moles in any particular area (Yates and Pederson, 1982). Areas suited for moles on the Edwards Plateau are limited, but would include river and stream valleys (depending upon flooding frequency) and some upland valleys with deeper soils. Water may not represent a significant barrier to dispersal of *S. aquaticus*, as the species is reported to be a good swimmer (Yates and Schmidly, 1978).
Moles are insectivorous in diet, and feed on many types of soil arthropods, earthworms, grubs, and some vegetable matter. *S. aquaticus* has a voracious appetite, and consumes large amounts of food (in comparison to its body weight) daily. Captive moles will eat almost anything that is proffered to them (Yates and Pederson, 1982).

Moles construct two types of burrows. Shallow, surface burrows and tunnels are utilized for foraging and moving through an area. Deeper, permanent tunnels also are constructed. The tunnels are usually interconnected. Some of the surface tunnels, known as mole runs, are utilized only once. Due to a need for large quantities of food, moles range over larger areas than do most other fossorial mammals (Yates and Schmidly, 1978). Nest mounds are also constructed by the eastern mole. The nest mounds are most obvious in the early spring months and are similar in appearance to gopher mounds, excepting the shallow runs that branch out from the nest mound. Nests are sometimes composed of grass and leaves, and are often enlargements of pre-existing deep tunnels (Yates and Pederson, 1982).

Breeding occurs once a year, usually during late winter or early spring (Yates and Pederson, 1982). Except during the breeding season, *S. aquaticus* is solitary in habit. In Texas, the eastern mole may begin breeding as early as January (Yates and Schmidly, 1977). The gestation period is not known, but it is assumed to be four to six weeks. Litter size usually ranges from two to five young (Conaway, 1959).

A single subspecies, *S. a. allenii* Baker 1951, is represented by specimens from the Edwards Plateau.
Sexual dimorphism is common in moles with males averaging larger than females in most characters. External measurements of two males from Travis County are: total length, 155, 142; tail length, 30, 22; length hind foot, 21, 20; ear length, 0, 0. Selected cranial measurements for one of the males (the other skull was not available) are: interorbital breadth, 7.69; zygomatic breadth, 15.82; width maxillary toothrow, 9.59; length maxillary toothrow, 14.58; greatest length skull, 33.92; breadth braincase, 14.27; width skull, 18.49.

Specimens examined (2).—Travis Co.: 14 621950E, 3351500N, 2 (TNHC).

Additional records.—Gillespie Co.: Unspecified Locality. Mason Co.: 14477900E, 3401100N. (Davis and Schmidly, 1994; Yates and Schmidly, 1977).

ORDER CHIROPTERA—BATS

KEY TO CHIROPTERANS

1 Rostrum abruptly upturned; skull profile concave in lateral view; prominent flaps of skin on the chin; tail short and projecting through the dorsal surface of the uropatagium ................................................ Moormoops megalophylla

1' Rostrum not abruptly upturned; skull profile not highly concave in lateral view; no flaps of skin on the chin; tail extending at least the entire length of uropatagium and not projecting through the dorsal surface of the uropatagium .......................... 2

2 Premaxillary notch V-shaped; tail extending conspicuously past interfemoral membrane; tragus not conspicuous; wrinkles of skin present on the upper lips ............................................................................................................................... Tadarida brasiliensis

2' Premaxillary notch rather U-shaped; tail extending even with or just barely beyond posterior margin of interfemoral membrane; tragus conspicuous; no wrinkles of skin on the upper lips ............................................................................................................................... 3

3 Greatest length of skull less than 14.20 mm; total length less than 87 mm ............................................................................................................................................................................. 4

3' Greatest length of skull more than 14.20 mm; total length more than 87 mm .................................................................................................................................................................................. 7

4 Incisors 1/3; dark, chocolate brown dorsum ............................................. Nycticeius humeralis

4' Incisors 2/3; dorsum light tan to yellowish in color .................................................. 5

5 Premolars 3/3; tragus long, straight, and pointed .................................................. Myotis yumanensis

5' Premolars 2/2; tragus short, curved and blunt .................................................. 6

6 Skull nearly straight in dorsal profile; palate extending far behind molars; distinct black facial mask present; dorsal fur not tricolored ................................. Pipistrellus hesperus

6' Skull concave in dorsal profile; palate extending little behind molars; no distinct black facial mask; dorsal fur tricolored, with dark basal band, light middle band, and dark tip .................................................. Pipistrellus subflavus
7 Uropatagium heavily furred on dorsal surface ................................................................. 8
7' Uropatagium sparsely furred on dorsal surface ............................................................. 11

8 Two upper incisors present; first upper premolar not crowded in toothrow; dorsal color black, frosted with white hairs ................................................. Lasionycteris noctivagans
8' One upper incisor present; first upper premolar (when present) crowed to the side of the toothrow; dorsal color yellowish, reddish, or reddish-black and frosted with white ....................................................... 9

9 Greatest length skull averaging 13.71; length maxillary toothrow less than 6 mm; total length averaging 114 mm; dorsal color dull to bright red ................................................................. Lasiurus borealis
9' Greatest length skull averaging greater than 13.71; length maxillary toothrow equal to or greater than 6 mm; total length averaging greater than 114 mm; dorsal color either a pale yellow or reddish-black and frosted with white ....................................................... 10

10 Greatest length of skull usually 17 mm or larger; premolars 1/2; ears rather slender and pointed; only the anterior half of interfemoral membrane heavily furred; dorsal color pale yellow ............................................. Lasiurus intermedius
10' Greatest length of skull less than 17 mm; premolars 2/2; ears rather broad, rounded and with black outer margins; entire interfemoral membrane heavily furred; dorsal color reddish-black and frosted with white ............................................. Lasiurus cinereus

11 Ear length 28 mm or greater; hind foot length 11 mm or greater .................................. 12
11' Ear length less than 28 mm; hind foot length less than 11 mm ..................................... 13

12 Incisors 1/2; premolars 1/2; forearm length 48 mm; no distinct lumps present on sides of the rostrum ................................................................. Antrozous pallidus
12' Incisors 2/3; premolars 2/3; forearm length less than 48 mm; distinct lumps present on both sides of the rostrum ..................................................... Plecotus townsendii

13 Premolars 1/2; tragus short, broad, rounded, and bent distally; keeled calcar; dorsal color yellowish to light brown to chocolate brown; ears black in color ........................................................................ Eptesicus fuscus
13' Premolars 3/3; tragus relatively long, slender, pointed and straight; calcar unkeeled; dorsal color a drab, light gray to dark gray; ears same color as dorsal pelage ................................................................. Myotis velifer

Family Mormoopidae—Mormoopid bats
Mormoops megalophylla  
Ghost-faced Bat

Distribution.—The ghost-faced bat ranges throughout Mexico and, thence, northward to southern Arizona, New Mexico, and Texas. Within Texas, the ghost-faced bat ranges throughout most of the Big Bend region and into southern Texas.

Mormops megalophylla occurs on the extreme southwestern Edwards Plateau, having been collected from caves along the Balcones Fault. Records are available from Bexar, Kinney, Medina, and Uvalde counties (Fig. 33).

This bat is easily recognized by its facial skin folds and ornamentation. It is relatively large, and the pelage is brown in color. The ears are rounded and connected by two high bands to the top of the rostrum. Unlike
Figure 33. Distribution of *Mormoops megalophylla* on the Edwards Plateau.

other bats occurring on the Edwards Plateau, the tail of *M. megalophylla* does not extend the full length of the uropatagium; the end of the tail projects conspicuously through the dorsal surface of the uropatagium. The ror­trum of the skull is sharply upturned in this species.

These bats inhabit caves on the southern Edwards Plateau, and, apparently use them as winter roosts. Specimens have been collected in the months of December, January, February, March, May, September, and November on the Edwards Plateau (Schmidly, 1991). These bats roost colonially, and are often associated with other species of bats in caves.

On the Edwards Plateau, *M. megalophylla* probably forages in riparian areas, around water, and through stands of mature trees. When foraging, the mouth is held open and the skin folds, tubercles, and ears form a funnel to direct food toward the mouth. Little is known of the food habits of this species. The stomachs of two individuals from Big Bend National Park were filled completely with large moths (Schmidly, 1991). Molt­ing of pelage occurs from June through September, begin­ning in patches dorsally and proceeding to the vent­ral side of the bats (Constantine, 1958).

Little is known of reproduction in this species. Females usually carry only a single embryo (Rezsutek and Cameron, 1993). Parturition occurs in the early summer, and lactating females have been recorded from 15 June to 9 August in the Big Bend region (Schmidly, 1991).

The subspecies which occurs on the Edwards Pla­teau is *M. m. megalophylla* (Peters, 1864). Average external measurements of five individuals (all males)
from Uvalde County are as follows: total length, 89; tail length, 26; length hind foot, 10.5; and ear length, 13.5. Average cranial measurements of three males and one female from Uvalde County are as follows: breadth across canines, 4.14; Interorbital breadth, 5.21; zygomatic breadth, 9.48; cranial breadth, 8.94; length maxillary toothrow, 7.54; greatest length skull, 14.46; depth of skull, 10.47; and width across molars, 6.26.

Specimens examined (11).—Uvalde Co.: 14 430700E, 3262900N, 4 (TCWC); 14 431200E, 3268200N, 7 (3, SM; 4 TTU).

Additional records.—Bexar Co.: Haby Cave; Kinney Co.: 14 362700E, 3253700N; Medina Co.: 14 473000E, 3268200N (Schmidly, 1991).

Family Phyllostomidae—Leaf-nosed Bats

**Diphylla ecaudata**

Hairy-legged Vampire

**Distribution.**—This tropical species ranges through eastern Mexico and most of Central America. The species extends as far south as Peru and southern Brazil in South America.

This species is represented in the United States by a single specimen from the extreme southwestern Edwards Plateau (Fig. 34). The bat was collected from an abandoned railroad tunnel in Val Verde County; an extension of approximately 450 miles north of the established range in Mexico (Reddel, 1968).

*Diphylla ecaudata* may be recognized by a much reduced and well haired uropatagium. The hairy-legged vampire has no tail, and is dark brown in coloration. The ears of this bat are short and rounded, and the nose is pugged, with a reduced nose leaf present. The first upper incisors are larger than the canines in this species.

Vampire bats roost primarily in caves, tunnels, and occasionally in hollow trees. This species is found often in association with other types of bats, as was the case with the female collected in Texas. However, even when occupying caves along with other bats, the hairy-legged vampire tends to roost away from other types of bats (Hall and Dalquest, 1963). These bats appear to possess rather poor thermoregulatory ability, and, after feeding, there is a noticeable rise in the mean body temperature (Greenhall et al., 1984).

The hairy-legged vampire feeds exclusively on blood. The tongue of this species has grooves to channel blood, and the saliva contains an anticoagulant to aid in acquiring a blood meal. This bat appears to take blood only from avian species. Hoyt and Altenbach (1981) studied the food habits of captive *D. ecaudata* and found that the bats refused to prey upon rats, rabbits, and defibrinated beef blood. These captive individuals only took meals from the blood of chickens.

Usually a female hairy-legged vampire gives birth to a single young each year. The species does not breed in Texas, and little is known concerning the breeding season of *D. ecaudata*. Vampire bats are believed to be seasonally polyestrous, but the hairy-legged vampire has been reported to have a well-defined breeding season in Tamaulipas and San Luis Potosi, Mexico. In Tamaulipas, pregnant and lactating females have been reported in the month of November (Schmidly, 1991), and in San Luis Potosi, pregnant females were collected in March and half-grown young in July (Dalquest, 1953).

*Diphylla ecaudata* Spix, 1823 is a monotypic species. Average external measurements of two individuals from San Luis Potosi (Dalquest, 1953) are: total length, 83; tail length, 0; length hind foot, 17; ear length, 17. External measurements of the female from Val Verde County are: total length, 83; tail length, 0; length hind foot, 18; ear length, 16. Selected cranial measurements are as follows: breadth across canines, 4.69; interorbital breadth, 6.61; zygomatic breadth, 12.51; cranial breadth, 11.67; condalobasal length, 21.35; and depth of skull, 13.30.

Specimens examined (1).—Val Verde Co.: 14 270800E, 3285900N, 1.

Family Vespertilionidae—Vespertilionid Bats

**Myotis velifer**

Cave Myotis

**Distribution.**—The cave myotis ranges from Honduras northward throughout the central plateau of Mexico and into northern Mexico. The species occurs in southwestern Arizona, southern California and Nevada, and the southern, central, and Trans-Pecos regions of Texas, as well as southwestern New Mexico. A disjunct population of *M. velifer* is found in the Panhandle.
and western Rolling Plains of Texas and extends into western Oklahoma and southern Kansas.

The cave myotis has been reported from all except the far northern and northwestern Edwards Plateau. This bat ranges at least as far north as Tom Green and Coke Counties. Records are available from Bexar, Blanco, Coke, Comal, Crockett, Edwards, Hays, Irion, Kendall, Kerr, Kimble, Kinney, Llano, Mason, McCulloch, Medina, Menard, Real, San Saba, Sutton, Tom Green, Travis, Uvalde, and Val Verde counties (Fig. 35).

*Myotis velifer* may be identified by its large size (for the genus) and dark brown to black coloration. However, coloration varies, and bats living in caves with high ammonia levels may be bleached and paler in color (Constantine, 1957). *M. velifer* does not have a keeled calcar, and the tragus is long and pointed, as opposed to some other vespertilionid bats on the Edwards Plateau. The only other species of *Myotis* occurring on the Edwards Plateau is *M. yumanensis*, which is smaller than the cave myotis, paler in dorsal color, lacks a prominent sagittal crest, and has a pale to buffy venter. The forearm length of *M. velifer* is 37-47 mm, as opposed to 32-38 mm in *M. yumanensis*.

The cave myotis is found in habitats ranging from the arid desert to rather mesic areas on the southern and eastern Edwards Plateau. These bats are tolerant of high temperatures and low humidity throughout their range. The cave myotis is often associated with limestone formations and canyon areas on the Edwards Plateau.
This species is an insectivore, consuming mostly moths and beetles, and may be observed foraging for insects around trees and buildings. The cave myotis is a strong flyer with limited mobility, and forages approximately four to twelve meters above the ground and close to vegetation (Schmidly, 1991). Foraging is conducted in two separate bouts; one soon after emergence from the roost and the second bout prior to return to the roost before dawn (Fitch et al., 1981). The cave myotis may forage over a large area and its opportunistic feeding habits allow it to feed upon any large concentrations of insect prey encountered while foraging (Vaughan, 1980). This bat most often goes directly to a source of water to drink after emerging from the day roost (Fitch et al., 1981).

*M. velifer* roosts primarily in caves and is the most abundant species of myotis on the Edwards Plateau (Schmidly, 1991). This species may also utilize buildings, bridges, culverts, and other structures as roost sites on the Edwards Plateau. The cave myotis also utilizes cave swallow nests as roosts (Buchanan, 1958). *M. velifer* is a year-round resident of the Edwards Plateau region (Manning et al., 1987), and hibernates throughout the winter months in caves. High humidity levels must be found within hibernacula in order for such sites to be suitable for the cave myotis (Fitch et al., 1981). These bats are often found hibernating directly over water within caves. The cave myotis has a relatively poor ability to thermoregulate, and chooses warmer areas within roosts as maternity areas in the summer months. These bats cluster together within a roost site (Schmidly, 1991). The cave myotis is often associated with the Mexican free-tailed bat and the Yuma myotis within a roost (Barbour and Davis, 1969).

Figure 35. Distribution of *Myotis velifer* on the Edwards Plateau.
Although individual *M. velifer* are not territorial, populations of the cave myotis have home ranges that may cover several hundred square kilometers (Fitch et al., 1981). The cave myotis has excellent homing ability and, at localities where this bat migrates in the autumn, they often return to the same roost for multiple years (Fitch et al., 1981). Males are found in the same roosts as females until parturition in late spring or early summer. Most males occupy separate roosts after the birth of young, but return to the maternal roosts by late June (Fitch et al., 1981). Males are more numerous than females during the winter months on the Edwards Plateau; the sexes are almost equal in abundance during other months (Schmidly, 1991).

Copulation occurs in the fall, with subsequent storage of the sperm in the uterus until April (Fitch et al., 1981). Males may also copulate with females during wakeful periods in the winter months. Gestation period ranges from 60 to 70 days (Fitch et al., 1981). The young of *M. velifer* are born in late spring or early summer. Lactating females have been captured in May on the Edwards Plateau. Females commonly give birth to a single offspring (Schmidly, 1991). Young bats grow rapidly, attaining the power of flight by three weeks of age, and foraging for insects by four weeks of age (Fitch et al., 1981).

The subspecies of cave myotis on the Edwards Plateau is *M. v. incautus* (J. A. Allen, 1896). Most measurable characters are not significantly different between males and females (Williams and Findley, 1979). Average external measurements of 10 adults (7 females and 3 males) from the Edwards Plateau are: total length, 95.5; tail length, 42.5; length hind foot, 10; ear length, 15. Selected mean cranial measurements of these same individuals are: greatest length skull, 16.01; zygomatic breadth, 10.38; interorbital constriction, 4.11; cranial breadth, 8.21; length maxillary toothrow, 6.38; width across upper molars, 6.62; breadth across upper canines, 4.60.

Specimens examined (297).—Bexar Co.: Unspecified Locality, 1 (TNHC); 14 549900E, 3277600N, 6 (MWSU). Coke Co.: 14 347000E, 3512400N, 1 (ASNH); 14 331600E, 3509000N, 1 (ASNH). Comal Co.: 14 572000E, 3305700N, 1 (SWTU); 14 568300E, 3300800N, 2 (SWTU). Crockett Co.: 14 265200E, 3373900N, 1. Edwards Co.: 14 396300E, 3324800N, 2 (TNHC). Hays Co.: Waggener Ranch, 1 (SWTU); College Farm Cave, 1 (SWTU); 14 601300E, 3300800N, 10 (SWTU); 14 600500E, 3303700N, 7 (SWTU). Irion Co.: Slenery Ranch (Unspecified Locality), 1 (ASNH); 14 296700E, 3442800N, 1 (ASNH). Kendall Co.: 14 530700E, 3289900N, 1 (SM); 14 530900E, 3289800N, 1 (TNHC). Kerr Co.: Mountain Home, Johnson Fork Creek, 1 (SWTU). Kimble Co.: 14 425400E, 3372000N, 37; 14 418000E, 3372200N, 3; 14 425000E, 3370400N, 2; 14 426600E, 3368900N, 11; 14 425200E, 3364600N, 25; 14 425600E, 3360000N, 20; 14 414900E, 3358800N, 6; 14 257000E, 3344400N, 1 (TNHC); 14 413200E, 3358200N, 2 (TNHC). Llano Co.: 14 531400E, 3401800N, 2 (TNHC); 14 517600E, 3374800N, 1. Mason Co.: 14 472400E, 3393800N, 1 (ASNH); 14 468800E, 3384600N, 11. Medina Co.: 14 447500E, 3269000N, 2 (SM). Menard Co.: 14 399400E, 3414000N, 1 (ASNH). Real Co.: 14 4426300E, 3288500N, 40 (2; TNHC; 38 TTU). San Saba Co.: 14 501500E, 3438800N, 44. Sutton Co.: 14 345100E, 3386300N, 1; 14 318300E, 3382600N, 2 (MWSU); 14 342200E, 3382500N, 1 (MWSU). Tom Green Co.: 14 333200E, 3503900N, 4 (ASNH); 14 337000E, 3502300N, 2 (ASNH); 14 357800E, 3446000N, 3 (ASNH); 14 357800E, 3444400N, 2 (ASNH). Travis Co.: 14 6220000E, 3351500N, 5 (TNHC); Balcones Trail, 1 (TNHC). Val Verde Co.: 14 309900E, 3315200N, 1; 14 307500E, 3303400N, 2; 14 306400E, 3301200N, 10; 14 323000E, 3322900N, 6; 14 289500E, 3303900N, 2 (MWSU); 14 2674000E, 3292700N, 4 (MWSU); Railroad Tunnel on Rio Grande W Comstock, 1 (TNHC); 14 289600E, 3285700N, 2.

Additional Records.—Blanco Co.: Unspecified Locality. Comal Co.: Bracken Cave (TCWC). Crockett Co.: 14 315200E, 3376800N (TCWC); 14 315800E, 3376300N (TCWC); 14 316300E, 3375800N (TCWC); 14 308100E, 3367400 (TCWC). Edwards Co.: 14 352000E, 3321000N. Hays Co.: 14 595600E, 3337000N. Kerr Co.: 14 526400E, 3295600N. Kinney Co.: 14 448200E, 3326100N (TCWC); 14 485800E, 3324600N, 14 474400E, 3320400N (TCWC); 14 476000E, 3312500N (TCWC). Kinney Co.: 14 383500E, 3243100N (TCWC). McCulloch Co.: Unspecified Locality. San Saba Co.: 14 549000E, 3436700N (TCWC). Sutton Co.: 14 375800E, 3347500N. Uvalde Co.: 14 398700E, 3259100N (TCWC); 14 430600E,
Myotis yumanensis
Yuma Myotis

Distribution. — The Yuma myotis ranges from central Mexico, northward through western Texas and the western edge of the Oklahoma Panhandle. This species ranges throughout most of New Mexico, Arizona, and northward into Colorado, and Utah. The Yuma myotis ranges westward through California, western and southern Nevada, Oregon, Washington, Idaho, Wyoming, and western Montana. Its range extends into British Columbia, Canada.

The Yuma myotis is limited to the extreme southwestern portion of the Edwards Plateau. This species has been recorded east of the Pecos River from Val Verde County within the region (Fig. 36).

Myotis yumanensis is a small, pale brown or buff-colored bat, with darker wing membranes, and uropatagium; the venter is pale. This species may be confused occasionally with the western pipistrelle (Pipistrellus hesperus); however, the long, pointed tragus of *M. yumanensis* easily separates it from the western pipistrelle. The western pipistrelle also has a distinctive, black facial mask that the Yuma myotis lacks. The only other representative of the genus *Myotis* resident on the Edwards Plateau is the cave myotis (*M. velifer)*.

*M. yumanensis* is smaller than the cave myotis, and the cave myotis is darker in color and possesses a bare patch of skin between the scapulae. The Yuma myotis lacks a distinct sagittal crest on the skull that is present in *M. velifer*, and the skull of *M. yumanensis* is smaller than the skull of *M. velifer*.

The Yuma myotis is found most commonly in desert areas, and in closer association with open water than many other species of desert-residing chiropterans. This species is found along streams, ponds, irrigation ditches, and other sources of water. In the Trans-Pecos region of Texas, the Yuma myotis is often found along the Rio Grande and its immediate tributaries. The single locality of record for the Edwards Plateau is from the junction of the Rio Grande and Pecos River systems. Open areas are preferred foraging sites. Males forage separately from females after the birth of young in summer.

The Yuma myotis is insectivorous in diet. Diet items include small moths, leafhoppers, midges, flies, caddisflies, crane flies, and other insects (Schmidly, 1991). Foraging is conducted over water or, if in urban areas or around human habitations, around a source of light. The Yuma myotis is an efficient feeder; bats with full stomachs have been collected 15 minutes after they began to forage within an area (Barbour and Davis, 1969). Foraging and other outside activities begin after dark.

The Yuma myotis utilizes buildings, mines, caves, railroad tunnels, rock crevices, and other areas as daytime roosts (Barbour and Davis, 1969). Night roosts are often located in buildings. Females form maternity colonies in the spring and summer months, and adult males are excluded while the young bats mature. Clustering behavior has been reported in buildings during periods of low temperatures. As ambient temperatures increase, individuals separate and move to cooler areas within a roost (Barbour and Davis, 1969).

Parturition is believed to occur from late May to early June. Females give birth to a single young per year (Schmidly, 1991). Disturbance of a nursery colony will often result in movement of many of the bats or the complete abandonment of the colony (Dalquest, 1947). Schmidly (1991) opined that *M. yumanensis* may overwinter in the Trans-Pecos region of Texas, but little is known of the migration patterns of this species throughout its range.

The subspecies of Yuma myotis on the Edwards Plateau is *M. y. yumanensis* (H. Allen, 1864). Average external measurements (Schmidly, 1991) are: total length, 80; tail length, 34; length hind foot, 8; ear length, 14. Selected mean cranial measurements of three adult females from Val Verde County are: greatest length skull, 13.45; breadth rostrum, 5.03; cranial breadth, 7.10; width across molars, 5.29; length maxillary toothrow, 5.07.

Specimens examined (4).— Val Verde Co.: 14 270500E, 3287500N, 4.
Figure 36. Distribution of *Myotis yumanensis* on the Edwards Plateau.

*Lasionycteris noctivagans*

Silver-Haired Bat

*Distribution.*—The silver-haired bat ranges from southeastern Alaska, across the southern provinces of Canada, and southward throughout most of the conterminous United States, excluding Florida. This bat ranges southward into Coahuila, Nuevo Leon, and Tamaulipas, Mexico.

The silver-haired bat reputedly ranges across the entire Edwards Plateau (Schmidly, 1991), but specimens are from scattered localities. Records are available from Bandera, Kimble, Tom Green, and San Saba counties (Fig. 37).

*Lasionycteris noctivagans* is easily identified by the silver hairs interspersed throughout its black, dorsal pelage. The upper surface of the uropatagium is furred, as in the lasiurine bats, but the color pattern is different; this bat is not easily confused with other species of bats upon the Edwards Plateau.

Silver-haired bats utilize trees as roosting sites during the daylight hours and are considered to prefer woodland habitats (Schmidly, 1991). This bat may also roost in buildings, rock crevices, caves, mines, and in hollow trees in the winter months (Kunz, 1982). There are no reports of large numbers of these bats roosting at any particular location (Kunz, 1982).

*Lasionycteris noctivagans* seems to be an opportunistic forager, and consumes a variety of prey items. Known prey items include insects from the orders Lepidoptera, Coleoptera, Hemiptera, Diptera, Isoptera, and Trichoptera (Kunz, 1982). The silver-haired bat be-
gins foraging relatively late, often appearing after other chiropteran species have begun feeding. Where the hoary bat and red bat are sympatric with *L. noctivagans*, the silver-haired bat feeds at differing times. This suggests some form of competition between the silver-haired bat and bats of the genus *Lasiurus*. Reith (1980) found that where the evening bat (*E. fuscus*) and silver-haired bat were sympatric, the silver-haired bat foraged later in the evening hours. In areas where only *L. noctivagans* occurred, foraging began at earlier hours after numbers of *E. fuscus* declined at the foraging site. Each silver-haired bat may have its own hunting route through a foraging area (Kunz, 1982). Foraging flights along hunting routes often consist of many twists and turns within the area, and short, gliding periods.

The silver-haired bat has been described as a rather slow and deliberate flier, and has usually been observed foraging around ponds, along streams, and through forest and woodland areas (Kunz, 1982). Four specimens were netted at the South Llano River on the Texas Tech University Center at Junction as they gleaned insects from under the tree canopy (Manning et al., 1987).

The silver-haired bat is a migratory species and is rather solitary in habit. Females appear to migrate farther than males, and ranges of the two sexes may be separate throughout parts of the year, as in the hoary bat (Findley and Jones, 1964). Migrations appear to be of lesser extent in the western portion of the species’ range, and the silver-haired bat may not be migratory in British Columbia (Kunz, 1982).

Mating probably takes place in autumn, followed by sperm storage in females during the winter months.
A 50 to 60 day gestation period occurs in May and June. Adult females raise one, or possibly two, young per year on the summer range of the species (Schmidly, 1991). Most young males and females attain sexual maturity during their first summer (Kunz, 1982).

*Lasionycteris noctivagans* Le Conte, 1831 is a monotypic species. Sexual dimorphism is not evident in this species of bat, although females show more variation in measurements than do males. Average external measurements of four adult males from Kimble County are: total length, 105; tail length, 42; length hind foot, 8.67; ear length, 15.5. Selected mean cranial measurements of these same individuals are: greatest length skull, 15.77; zygomatic breadth, 9.84; cranial breadth, 8.30; interorbital breadth, 4.19; length maxillary toothrow, 5.66; width across molars, 6.53; breadth across canines, 4.91.


Additional records.—San Saba Co.: 14 548700E, 3434800N. (Schmidly, 1991).

**Pipistrellus hesperus**

Western Pipistrelle

Distribution.—The western pipistrelle is distributed from central Mexico northward through most of Trans-Pecos, Texas, and parts of the panhandles of Texas and Oklahoma. The species ranges from New Mexico, and Colorado, west and north to Idaho, and the Pacific coast states, and southward to Baja, California.

The western pipistrelle occurs on the western portion of the Edwards Plateau. Records of the bat within this region, however, are not common. The species has been reported from Coke, Edwards, Upton, Uvalde, Tom Green, and Val Verde counties on the Edwards Plateau (Fig. 38).

**Pipistrellus hesperus** is the smallest North American bat. It may be distinguished from *Myotis* by a short, blunt tragus. The color ranges from yellow to light gray. The western pipistrelle may be distinguished from the eastern pipistrelle (*P. subflavus*) by the following characters: a black facial mask, keeled calcar, fur not tricolored, wing and tail membranes very dark in *P. hesperus*. Distinguishing characteristics of the eastern pipistrelle are listed in that species’ account.

The western pipistrelle usually roosts in rocky habitats, inside rock crevices, under rocks, within burrows, and inside buildings. Night roosts may include these habitats, trees, bushes, buildings, and other locations within a foraging area (Cross, 1965; Hoffmeister, 1986; Schmidly, 1991). Burrows of kangaroo rats and other animals may be utilized during daylight hours whenever *P. hesperus* is far from favored rocky habitats (Barbour and Davis, 1969).

The western pipistrelle is an insectivore. Diet items include caddisflies, stoneflies, moths, small beetles, leaf and stilt bugs, leafhoppers, flies, mosquitoes, ants, and wasps (Schmidly, 1991). These small bats tend to forage in and around swarms of insects, and often consume a single type of insect during a particular foraging event. They are slow, fluttery fliers, but are highly maneuverable. The western pipistrelle is nocturnally active, but emerges from roosts earlier than most other species of North American bats. These bats sometimes emerge to forage as early as 6 p.m., and they have been observed flying about during the day (Hoffmeister, 1986). Emergence, perhaps, is related more to temperature factors than to light levels.

This bat may form small maternity colonies in the early summer months, but, as a rule, *P. hesperus* roosts singly or in small numbers. The largest maternity colony reported consisted of twelve individuals (Schmidly, 1991). The western pipistrelle hibernates through the winter months, but may awaken and take flight during warm days. Barbour and Davis (1969) reported finding *P. hesperus* hibernating in mines, caves, and rock crevices in scattered locations in Texas.

Parturition occurs from June to July in Texas (Schmidly, 1991). Two young is the most common litter size. The gestation period is approximately 40 days. Newborn bats mature rapidly and become capable of flight when approximately one month of age (Schmidly, 1991).

The subspecies found on the Edwards Plateau is *P. h. maximus* Hatfield, 1936. Findley and Traut (1970) treated geographic variation within this species and found two distinct western and eastern populations that might be readily recognized based upon size. The eastern form, *P. h. maximus*, is the larger of the two. Sexual
dimorphism is apparent, with females larger than males. Average external measurements of specimens from the Big Bend of Texas (Schmidly, 1977) are: total length, 73; tail length, 43; length hind foot, 7; ear length, 11. Selected mean cranial measurements of adult females (Findley and Traut, 1970) are: greatest length skull, 11.98; interorbital breadth, 3.32; cranial depth, 4.13; length maxillary toothrow, 4.17; rostral length, 4.65.


Additional records.— Edwards Co.: Unspecified Locality. Uvalde Co.: Unspecified Locality. (Davis and Schmidly, 1994).

**Pipistrellus subflavus**

Eastern Pipistrelle

*Distribution.*— The eastern pipistrelle ranges from southeastern Mexico, northward throughout most of the eastern conterminous United States. The eastern pipistrelle’s range includes the eastern two-thirds of Texas, most of Oklahoma, eastern Kansas, southeastern Nebraska, almost all of Iowa, and eastern Minnesota. This bat ranges throughout all but southern Louisiana, and northern Maine in the eastern United States, and occurs as far north as southern Ontario and Quebec in Canada.

The eastern pipistrelle ranges over the southern, eastern, and central portions of the Edwards Plateau as far south and west as Val Verde County and at least as far north as Irion and Tom Green counties. Records are
available from Bandera, Bexar, Comal, Edwards, Hays, Irion, Kendall, Kerr, Kimble, Llano, Real, San Saba, Travis, Uvalde, and Val Verde counties (Fig. 39).

Pipistrellus subflavus is easily recognized by its small size and pale, yellow fur. The hair of *P. subflavus* is tricolored; with a dark base, lighter middle band, and dark tip. The eastern pipistrelle may occasionally be confused with *P. hesperus*. However, *P. subflavus* lacks a distinctive dark facial mask, has a hind foot length greater than half as long as the tibia length, has thumbs greater than 4.9 mm, and has a dish-faced skull profile. *P. hesperus* has a dark facial mask, hind foot less than half as long as the tibia, thumbs less than 4.9 mm, and a straight skull profile. The tragus of the genus *Pipistrellus* is short, broad, and curved as opposed to long, pointed, and straight in the genus *Myotis*.

The eastern pipistrelle appears to be a forest-edge species, inhabiting areas of relatively open tree canopy (Schmidly, 1983). This species seldom forages in deep woods or open fields unless there are trees nearby (Barbour and Davis, 1969). The appearance of the eastern pipistrelle above the canopies of trees early in the evening hours, and its tendency to roost in foliage when released during daylight hours suggest that the eastern pipistrelle may roost in trees to some extent (Barbour and Davis, 1969).

The eastern pipistrelle is insectivorous and may be seen foraging among trees or over water. Diet items include carabid beetles, cicadillids, small flies, formicid wasps, and small moths (Fujita and Kunz, 1984). Although primarily nocturnal in activity, *P. subflavus* often begins foraging well before dark (Fujita and Kunz, 1984). A secondary foraging flight may be made before midnight or in the early morning hours before dawn (Sealander and Heidt, 1990). These bats have been collected while foraging under a deciduous tree canopy along the South Llano River in Kimble County. Flight of the eastern pipistrelle is rather slow and erratic.

Eastern pipistrelles roost singly or in small groups in caves, mines, rock crevices, tree foliage, Spanish moss, and occasionally in buildings (Schmidly, 1991). *P. subflavus* may roost in open, abandoned buildings subject to higher light levels than most other species of bats would tolerate (Barbour and Davis, 1969). Summer roosts and winter hibernacula are often in different locations. Males and females are not segregated in hibernacula, but males are initially excluded from maternal roosts of the females in the spring months (Fujita and Kunz, 1984). The eastern pipistrelle selects locations within hibernacula that have relatively constant, high temperatures, low wind movement, and high humidity levels. *P. subflavus* has strong site fidelity within roosting sites and may return to the same location within a roost over multiple years (Barbour and Davis, 1969). Young are initially carried by the female, but are subsequently left within the roost as they mature (Barbour and Davis, 1969).

The eastern pipistrelle is an obligate hibernator over portions of its range in the United States (Barbour and Davis, 1969; Fujita and Kunz, 1984). Fat is deposited by both males and females during the spring and summer months, and weight loss occurs throughout hibernation. Females deposit significantly more fat than males (Fujita and Kunz, 1984). Although sexes are segregated during parturition and early development of the young, both sexes resume communal roosting by August in parts of their range (Sealander and Heidt, 1990). Foraging areas are small in size, and movements and migrations are limited in length. *P. subflavus* populations may move between 50 and 80 miles between their summer and winter haunts (Jones et al., 1983).

Copulation occurs in the autumn months, with subsequent sperm storage and fertilization of ova in the spring (Fujita and Kunz, 1984). The gestation period is approximately 44 days in length. Four ova are usually implanted (two in each uterine horn), but the two medially implanted ova are subsequently reabsorbed (Barbour and Davis, 1969). Young of this species are born in late spring to mid-summer months. Pregnant females have been collected from the Edwards Plateau in the month of May. Litter size is usually two, but may range from one to three (Schmidly, 1991). Young mature rapidly and are foraging by approximately four weeks of age (Fujita and Kunz, 1984).

Two subspecies of *P. subflavus* are found on the Edwards Plateau. *P. s. subflavus* (F. Cuvier, 1832) throughout most of the range on the Edwards Plateau, and *P. s. clarus* Baker, 1954 in Val Verde County. Specimens obtained by Manning et al. (1987) from Val Verde County just west of the Edwards Plateau are intermediate in color between specimens of *P. s. subflavus* from the Panhandle of Texas and specimens from the more
eastern portions of the Edwards Plateau, suggesting the possibility of an east-west cline in color across the range of *P. subflavus* in central Texas. Sizes of the two subspecies of *subflavus* are approximately the same (Manning et al., 1987). Female eastern pipistrelles are larger than males. Average external measurements of nine males from Real County are: total length, 85; tail length, 37; length hind foot, 8; ear length, 13. Selected mean cranial measurements of these same individuals are: greatest length skull, 12.63; zygomatic breadth, 7.91; interorbital constriction, 3.61; cranial breadth, 6.80; length maxillary toothrow, 4.29; breadth across molars, 5.26; breadth across canines, 3.59.


Figure 39. Distribution of *Pipistrellus subflavus* on the Edwards Plateau.
Eptesicus fuscus
Big Brown Bat

Distribution.—The big brown bat ranges from Panama northward throughout almost all of Mexico and the conterminous United States. The range of this bat extends northward into all southern provinces of Canada from Quebec to British Columbia.

Although Hall (1981) maps the range of the big brown bat as occurring throughout the Edwards Plateau, there is a lack of specimens from within this region. Only a single literature record from Bexar County is available to confirm the presence of this species over the entire Edwards Plateau (Fig. 40).

Eptesicus fuscus is a medium-sized vespertilionid bat with rounded, short, black colored ears. The dorsal pelage is tan in color; the uropatagium and wing membranes are black or dark brown. The vent is paler in color than the dorsum. The tragus is broad and narrows toward the tip. The tragus is bent forward slightly at the tip, in contrast to the long, pointed, straight tragus of M. velifer. The face of E. fuscus is dark brown or black in color where sparsely haired. The calcare is keeled in E. fuscus, as opposed to unkeeled in M. velifer. The big brown bat has a single, large upper premolar, as opposed to two upper premolars in M. velifer.

The big brown bat is a habitat generalist. This bat forages around water, over-land, edge, non-edge, canopy covered, open, urban, and rural habitats (Kurta and Baker, 1990). These bats form separate maternity colonies in the spring and summer months after arousal from hibernation. Colonies are often located in barns, houses, churches, hollow trees, and rock crevices.

The big brown bat is an insectivore. Kurta and Baker (1990) reported that small coleoptera are the most common prey. The big brown bat may remove elytra and wings of insects before consuming them. Nonflying prey make up a portion of the diet of this bat, as does vegetation. The vegetation percentage in the diet may result from consumption and subsequent digestion of insect prey. The big brown bat has been reported to prey upon bats of the genus Myotis and Pipistrellus when confined in captivity with these smaller forms (Krutzsch, 1950). In natural situations, E. fuscus roosts separately from other bat species, so predation may result from proximity effects of confinement. This bat forages throughout the night, with greatest activity within the second hour after sunset (Kurta and Baker, 1990).

The big brown bat is a relatively sedentary species. Barbour and Davis (1969) stated that the winter and summer ranges of E. fuscus are identical and lengthy movements are uncommon. Homing ability is well developed in this species. These bats hibernate singly or in small groups in basements, mine tunnels, caves, road culverts, and other underground shelters (Barbour and Davis, 1969).

In Texas, most young of E. fuscus are born from late May to June (Schmidly, 1991). Copulation probably occurs in the fall and ovulation and fertilization are delayed until the female awakens from hibernation (Kurta and Baker, 1990). During the time maternity colonies are formed and the young are born, adult males are scarce. The males return to maternity colonies as the young bats mature. Females of the eastern subspecies of E. fuscus leave their young at the roost as the mothers forage for insects (Barbour and Davis, 1969). Young bats mature rapidly and reach adult size within two months after birth. The western subspecies of E. fuscus has a single young per litter, whereas the eastern subspecies usually has two young per litter.

Although the subspecies of the Bexar County specimen cannot be known for certain, the most likely assignment would be E. f. fuscus (Palisot de Beauvois, 1796). The nearest reported specimen (Schmidly, 1983) is from McLennon County, approximately 140 mi. NE of Bexar County. Sexual dimorphism is present in this chiropteran species with females averaging larger than males. Average external measurements of nine specimens of E. f. fuscus from Louisiana (Lowery, 1974) are: total length, 113.5; tail length, 45.1; length hind foot, 9.8; ear length, 14.6. Selected mean cranial measurements of 16 specimens from eastern Texas (Manning et al., 1989) are: greatest length skull, 20.2; zygomatic breadth, 13.4; mastoid breadth, 10.3; breadth braincase, 8.9; postorbital constriction, 4.4; breadth across canines, 6.4; length maxillary toothrow, 7.3.

Specimens examined (0).

Additional records.—Bexar Co.: 14 541200E, 3284400N. (Schmidly, 1991).
Figure 40. Distribution of *Eptesicus fuscus* on the Edwards Plateau.

*Lasiurus borealis*
Eastern Red Bat

*Distribution.*—The eastern red bat ranges from the southern provinces of Canada, southward throughout all but portions of the Rocky Mountain region of the conterminous United States, into Mexico, and southward to Argentina. Idaho is the only state of the United States where red bats have not been recorded.

The eastern red bat ranges through at least the eastern two-thirds of the Edwards Plateau. This species has been recorded from Bandera, Blanco, Burnet, Coke, Comal, Gillespie, Howard, Irion, Kerr, Kendall, Kimble, Mason, Menard, Real, Schleicher, Sterling, Sutton, Tom Green, Travis, Uvalde, and Val Verde counties on the Edwards Plateau (Fig. 41).

*Lasiurus borealis* may be recognized by its short, rounded ears, heavily furred interfemoral membrane, and reddish-brown coloration. Males are brick-red in color (females are usually paler red in color) and have white hairs interspersed throughout the pelage. The venter is paler in color than the dorsum. The only similar species in Kimble County is the hoary bat (*L. cinereus*), which has a differently colored pelage and is larger than *L. borealis*.

Preferred habitats of *L. borealis* on the Edwards Plateau are riverine and riparian areas. These bats may be found inhabiting areas around woodland and forest edges, and in sites bordered by dense leafy crops such as corn (Barbour and Davis, 1969). This species is rarely found in caves and mines, although the red bat may fly into a cave and become lost; as evinced by the
carcasses and skeletal material found by researchers in some caves (Shump and Shump, 1982).

These bats are insectivorous and often are observed foraging around street lamps and other outdoor lights. _L. borealis_ often emits an audible call when foraging. Prey items include insects of the orders Lepidoptera, Homoptera, Diptera, Coleoptera, Hymenoptera, and Orthoptera (Shump and Shump, 1982). Foraging begins shortly after dark and is conducted over a specific territory (Barbour and Davis, 1969). Foraging activities may be conducted throughout the nighttime hours. In areas where the red bat and hoary bat occur together, _L. borealis_ begins foraging earlier than the hoary bat (Shump and Shump, 1982). Foraging is conducted near the forest canopy at or above the treetop level and progresses to within a few feet of the ground (Barbour and Davis, 1969). Feeding flight is either in straight lines through a territory or in slow, wide circles from higher levels first, then progressing toward the ground.

Eastern red bats utilize trees for daytime roosts. Barbour and Davis (1969) state that _L. borealis_ usually hangs from the petiole of a leaf, a twig, or a branch. When roosting, the bats resemble dead leaves in trees and are well camouflaged from predators. The dense pelage, furred interfemoral membrane, short ears, and other physiological adaptations enable the eastern red bat to hibernate while hanging within the branches of trees (Shump and Shump, 1982). The eastern red bat is considered a solitary species, but may forage through an area and migrate in small groups (Shump and Shump, 1982). Males and females seem to migrate at different times and have different summer ranges.
The eastern red bat breeds in August and September. Copulation apparently is initiated while the male and female are in flight. Viable sperm are held in the uterus throughout the winter months and fertilization occurs the following spring. Gestation period is approximately 80 to 90 days in length (Shump and Shump, 1982). Pregnant *L. borealis* carry three or four embryos, with four being the most common number. However, the average number of young produced per litter is two (Shump and Shump, 1982), indicating a high incidence of intrauterine mortality. Young eastern red bats mature rapidly and are capable of flight within three to six weeks of birth (Shump and Shump, 1982).

*Lasiurus borealis* (Muller, 1776) is a monotypic species (Baker et al., 1988). Female eastern red bats are larger than males. Average external measurements of five adult females from the Edwards Plateau are: total length, 114.2; tail length, 49.4; length hind foot, 8.6; ear length, 13.4. Selected mean cranial measurements from these same individuals are: greatest length skull, 13.71; zygomatic breadth, 10.18; cranial breadth, 8.00; interorbital breadth, 4.30; length maxillary toothrow, 4.86; width across molars, 6.59; breadth across canines, 5.30.


*Lasiurus cinereus* Hoary Bat

**Distribution.**—The hoary bat is the most widespread chiropteran of the Americas. This bat ranges from Chile and Argentina in the south throughout almost all of Mexico, and all of the conterminous United States to near the forest limits in northern Canada.

Despite its widespread distribution in the state of Texas, surprisingly few records exist from the Edwards Plateau region. This bat reputedly ranges throughout the area (Schmidly, 1991). Records are available from Bexar, Blanco, Coke, Comal, Irion, Kerr, Kimble, Sutton, Tom Green, and Travis counties (Fig. 42).

*Lasiurus cinereus* is one of the most colorful bat occurring on the Edwards Plateau, and is not easily confused with any other species. The pelage is red to orange and heavily frosted with silver hair. Ears are short and blunt with black outer margins; the uropatagium is heavily furred. The red bat is smaller in size and possesses a different color of pelage than *L. cinereus*. The northern yellow bat also is colored differently and has more pointed ears than *L. cinereus*.

Hoary bats are similar in habits and habitat preferences to *L. borealis*. *Lasiurus cinereus* is a tree-roosting species, but occasionally may roost in other places. Roosting places other than tree branches include woodpecker holes, caves, squirrel nests, under driftwood, and on the sides of buildings (Shump, 1982). Hoary bats are found in riparian areas, wooded uplands, juniper scrub, and other habitats on the Edwards Plateau. *L. cinereus* is well camouflaged from above and laterally when roosting in trees (Shump, 1982). The hoary bat feeds primarily upon moths, but other insects are included in the diet (Schmidly, 1991). Other diet items include beetles, flies, grasshoppers, termites, dragonflies, and wasps (Shump, 1982). Hoary bats have been reported attacking smaller bats, and may prey upon other species of bats upon occasion (Sealander and Heidt, 1990). The hoary bat feeds upon insects.
while on the wing by engulfing the abdomen and thorax of the prey and biting the insect in half (Shump, 1982). *L. cinereus* emerges to forage after dark and may forage in groups. Hoary bats are strong, swift, and direct fliers (Barbour and Davis, 1969).

I netted a specimen in Blanco County, over a small stream, between 3:00 and 6:00 a.m. Hoary bats have been observed foraging shortly after dark in certain areas (Shump, 1982).

The hoary bat migrates into North America in the early spring. Females appear to migrate prior to males and segregation of sexes occurs throughout most of the hoary bat’s range in the United States (Findley and Jones, 1964). Hoary bats are solitary in nature, except for migration flights and some foraging aggregations (Shump, 1982). The hoary bat evinces little territorial behavior (Schmidly, 1991).

Copulation probably occurs during the autumn migration. Delayed implantation is present in *L. cinereus*. Young are born in late spring and early summer months. The average number of young per litter appears to be two for hoary bats. Gravid females contain from one to four young (Shump, 1982). Young cling to the mother during the day but are usually left behind while she forages at night (Shump, 1982).

The subspecies of hoary bat on the Edwards Plateau is *L. c. cinereus* (Palisot de Beauvois, 1796). Female hoary bats are slightly larger than males (Williams and Findley, 1979). Average external and selected mean cranial measurements of two males and three females from the Edwards Plateau, respectively, are: total length, 135, 142; tail length, 56.5, 54; length hind foot, 11, 11; ear length, 17, 16.67; greatest length skull, 15.91, 16.58; zygomatic breadth, 12.33, 12.59; interorbital constriction, 5.25, 5.16; cranial breadth, 9.97,
10.20; breadth across canines, 7.00, 7.07; length maxillary toothrow, 6.02, 6.22.

**Specimens examined** (17).—**Blanco Co.**: 14 571800E, 3351300N, 1. **Coke Co.**: 14 335500E, 3548600N, 1 (ASNHC); 14 331900E, 3508500N, 1 (ASNHC). **Irion Co.**: 14 336700E, 3455800N, 1 (ASNHC). **Kimble Co.**: 14 444800E, 3392300N, 1; 14 426400E, 3377500N, 1; 14 425400E, 3372000N, 1; 14 426300E, 3288500N, 1. **Sutton Co.**: 14 322800E, 3382900N, 1. **Tom Green Co.**: 14 342100E, 335500E, 3548600N, 1; 14 357800E, 3455800N, 1 (ASNHC); 14 357800E, 3444400N, 1 (ASNHC).


**Lasiurus intermedius**

Northern Yellow Bat

**Distribution.**—The northern yellow bat inhabits the southeastern United States from southern South Carolina westward through central Louisiana and south and east Texas. The northern yellow bat’s range extends southward through eastern, central, and part of western Mexico.

**Lasiurus intermedius** is a marginal species on the Edwards Plateau. The northern yellow bat reaches its western distributional limits in the United States along the Balcones Fault zone of the Edwards Plateau. Specimens are at hand from Bexar and Travis counties (Fig. 43).

The northern yellow bat differs from *L. borealis* and *L. cinereus* in having pale, yellow pelage. In addition, only the proximal half of the uropatagium is furred, as opposed to the entire dorsal surface on the other species of *Lasiurus* on the Edwards Plateau. The ears of this species are usually more pointed than those of *L. borealis* and *L. cinereus*, and the northern yellow bat has only one premolar as opposed to two in the other species of *Lasiurus*.

The northern yellow bat is a tree-roosting species, and has been captured in deciduous and coniferous forests, palm trees, and in Spanish moss hanging from trees. This species has also been captured from buildings (Webster et al., 1980). This bat usually roosts singly, as do other species of *Lasiurus*, but instances have been reported of multiple bats utilizing a roosting site (Lowery, 1974; Nedbal et al., 1994).

This bat is usually found in the vicinity of water, and prefers to forage over open areas and along forest and woodland edges (Schmidly, 1991). In Florida, *L. intermedius* has been reported to form feeding aggregations that are segregated by sex. Males are rarely found in the feeding aggregations, and seem to be rather solitary in habit (Schmidly, 1991). The diet of the northern yellow bat consists of various species of insects.

Breeding in the northern yellow bat occurs in the fall and winter months (Barbour and Davis, 1969). Parturition probably occurs in late May or June in Texas (Schmidly, 1991). Nedbal, Schmidly, and Bradley (1994) captured a female with two pups on 14 June. Litter size is usually two or three young.

The subspecies of yellow bat on the Edwards Plateau is *L. i. floridanus* (Miller, 1902). Sexual dimorphism has been reported in this species, with females averaging larger than males (Webster et al., 1980). Standard external measurements of a female from Bexar County and one from Travis County are, respectively: total length, 152, 131; tail length, 66, 51; length hind foot, 10, 11; ear length, 18, 18.5. Selected cranial measurements for the Bexar County individual are: cranial breadth, 7.68; interorbital breadth, 5.45; length maxillary toothrow, 6.74; greatest length skull, 17.65.

**Specimens examined** (2).—**Bexar Co.**: 14 548700E, 3254600N, 1 (TCWC). **Travis Co.**: 14 622000E, 3351900N, 1 (TNHC).

**Nycticeius humeralis**

Evening Bat

**Distribution.**—The evening bat ranges from Veracruz, Mexico, northward through the eastern portion of Texas as far north as Nebraska, and Iowa. The species’ range extends eastward as far as New Jersey and, thence, southward throughout Florida and includes all of the southeastern states of the United States.
The evening bat has been recorded from the eastern and central portions of the Edwards Plateau. Specimens are scarce, and records are scattered. Records exist from Bandera, Blanco, Burnet, Kerr, Real, San Saba, Tom Green, and Uvalde counties (Fig. 44).

*Nycticeius humeralis* is a rather small vespertilionid with dark brown dorsal pelage and short, rounded, black, leathery ears. The tragus is short, blunt, and curved slightly forward at its tip. Wing membranes and uropatagium are dark in color, whereas the venter is lighter than the dorsum. Only a single upper incisor is present in *N. humeralis*. *Myotis* and *Eptesicus* possess two upper incisors. The evening bat is smaller in size than *E. fuscus* and *M. velifer*, where these three bats might be sympatric upon the Edwards Plateau.

The evening bat is most common in forested habitats of eastern Texas. Lowery (1974) stated that the evening bat is often found roosting in bald cypress trees in eastern areas, and this habitat factor may limit its western distribution on the Edwards Plateau. I have obtained specimens from Blanco County at a small stream bordered by live oak trees, but the location was adjacent to the Perdenalis River; wherein bald cypress habitats occur. The species has been taken in Tom Green and Real counties in closed canopy habitats (Manning et al., 1987; Dowler et al., 1992).

The evening bat is insectivorous in diet. Diet items include true bugs, flying ants, June beetles, pomace flies, Japanese beetles, moths, and other night flying insects (Schmidly, 1991). The evening bat is a nocturnal forager. A bimodal activity pattern is evident with peaks during the early evening hours and the hours immediately preceding dawn. *N. humeralis* initially forages above the tops of trees, and then forages at lower levels as time progresses in the evening (Lowery, 1974).
Figure 44. Distribution of *Nycticeius humeralis* on the Edwards Plateau.

The evening bat normally roosts in hollow trees, beneath loose tree bark, in attics of homes, in barns and other structures, and, rarely, in caves (Watkins, 1972). Maternity colonies are formed and vary in size from a few individuals to as many as 950 bats (Watkins, 1972). Males are segregated from the maternity colonies and are relatively solitary in habits. As in some other vespertilionid bats, clustering has been observed at low ambient temperatures and regular spacing at higher temperatures within the maternity colonies.

Copulation takes place in the fall, with young being born in late May and June in Texas. One female captured on 13 May from Blanco County carried two fetuses. Two young is the most common number of offspring per litter, with three being produced in rare instances (Lowery, 1974). The young bats mature rapidly. Jones (1967) noted definite specificities of adult females for their own young. Young of other females were rejected and repulsed by novel matrons. Young *N. humeralis* attain the ability to fly by about 20 days of age. The evening bat is believed to be migratory within its range in the United States, but little is known concerning migration routes and wintering areas.

The subspecies on the Edwards Plateau is *N. h. humeralis* (Rafinesque, 1818). Females of this species are larger in size than males. Average external measurements of three adult females from the Edwards Plateau are: total length, 99; tail length, 36.67; length hind foot, 7.67; ear length, 13.67. Selected mean cranial measurements for these same individuals are: greatest length skull, 14.12; zygomatic breadth, 10.11; cranial breadth, 8.10; width across canines, 4.79; length maxillary toothrow, 5.28; width across molars, 6.55.

Additional records.—Burnet Co.: 14575700E, 3369700N (TCWC). Kerr Co.: 14461300E, 3322100N (TCWC); 14441700E, 3310800N (TCWC).

Plecotus townsendii
Townsend's Big-eared Bat

Distribution.—Townsend's big-eared bat ranges from southern Mexico, northward throughout much of the western United States. This bat ranges from western Texas, northward into Oklahoma, Colorado, Nebraska, South Dakota, North Dakota, and Montana at the eastern margins of its range. Townsend's big-eared bat occurs as far north as British Columbia, and isolated populations may be found in Arkansas, Missouri, Kentucky, West Virginia, and Virginia.

Townsend's big-eared bat has been taken from the southwestern Edwards Plateau from Edwards, Kimble, and Val Verde counties (Fig. 45).

Plecotus townsendii is a brownish colored bat with large ears. There is a distinctive lump on each side of the rostrum. The large ears identify P. townsendii from most other bats occurring on the Edwards Plateau. The one other large-eared bat in the area lacks the distinctive nose lumps, is pale yellow in color, and has a longer forearm than does P. townsendii.

This species most commonly occurs in western desert scrub and pinyon-juniper regions in west Texas, but is not restricted to specific vegetative associations throughout its range (Schmidly, 1991). The presence of rocky, broken country is consistent with the capture of P. townsendii within an area (Schmidly, 1991).

Townsend's big-eared bat is an insectivore; diet is composed mostly of lepidopterans (Kunz and Martin, 1982). Flies, lacewings, dung beetles, and sawflies also are included in the diet (Schmidly, 1991). P. townsendii emerges from its day roost late in the evening to begin foraging (Kunz and Martin, 1982). Townsend's big-eared bat is versatile in its flight, utilizing both swift, darting movements and hovering movements while foraging (Barbour and Davis, 1969; Hoffmeister, 1986).

Townsend's big-eared bat roosts in caves, abandoned mines, and buildings. Buildings are utilized primarily as night roosts, and caves and mine shafts serve as day roosts and hibernation sites. P. townsendii frequently rolls its large ears backward over the head and shoulders when roosting (Davis and Schmidly, 1994). P. townsendii is a colony-forming species and is rather sedentary. There is little evidence for extensive migrations in this species of bat (Kunz and Martin, 1982).

These bats form colonies of small to moderate size; most colonies number less than 100 individuals (Kunz and Martin, 1982). Females congregate in maternity colonies in late spring and early summer; males are excluded from the maternity roosts during the summer months (Schmidly, 1991). Clustering behavior occurs within the colonies (Barbour and Davis, 1969), presumably as an energy conserving mechanism. P. townsendii folds its ears over the shoulders, folds its wings and interlocks them ventrally, and erects its fur while hibernating (Kunz and Martin, 1982). Townsend's big-eared bat is easily aroused from hibernation and may fly to a different location within a roost (or to another roost) if awakened (Kunz and Martin, 1982).

Copulation in P. townsendii occurs mostly from November through February (Kunz and Martin, 1982). Semen is stored in the uterus of the female and fertilization occurs in the spring. A single young is born in late May to early June (Schmidly, 1991). Young are weaned at about two months of age and the maternity colonies begin to break up. Young bats attain sexual maturity in their first year of life (Kunz and Martin, 1982).

The subspecies of Townsend's big-eared bat on the Edwards Plateau is P. t. pallescens (Miller, 1897). Average external measurements (Schmidly, 1991) are: total length, 98; tail length, 46; length hind foot, 11; ear length, 34. Selected mean cranial measurements of 12 adult female P. t. pallescens from Arizona (Hoffmeister, 1986) are: greatest length skull, 15.72; zygomatic breadth, 8.32; interorbital breadth, 3.40; mastoidal breadth, 8.71; length maxillary toothrow, 5.08.
Figure 45. Distribution of *Plecotus townsendii* on the Edwards Plateau.

*Specimens examined* (4).—Val Verde Co.: 14 325700E, 3297200N, 1; 14 276400E, 3312400N, 1 (TNHC); 14 270400E, 3287500N, 2 (MWSU).


**Antrozous pallidus**  
*Pallid Bat*

*Distribution.*—The pallid bat ranges from central Mexico, northward through approximately the western one-half of Texas, and into western Oklahoma and southwestern Kansas. The species is found westward to Colorado, southern Wyoming, Utah, Nevada, and the Pacific coast states, and as far north as British Columbia.

The pallid bat ranges throughout most of the western and southern portions of the Edwards Plateau. Records of occurrence are rather scattered, and specimens are not especially numerous. Records are available from Crockett, Kerr, Kimble, Kinney, Upton, Uvalde, and Val Verde counties (Fig. 46).

*Antrozous pallidus* may sometimes be confused with *P. townsendii*; however, *A. pallidus* lacks a lump on each side of its nose. Pallid bats are yellowish in color, whereas *P. townsendii* is a smoky, brown color. In *A. pallidus*, the venter is pale yellow or whitish in color. Ears are large, and the tragus is long and lanceolate. The ears of *A. pallidus* are not joined basally, as are those of *P. townsendii*. Other characters that aid in separating the two species are given in the account of *P. townsendii*. 
Figure 46. Distribution of *Antrozous pallidus* on the Edwards Plateau.

Pallid bats are characteristic inhabitants of desert areas and seem to be most abundant in the Sonoran life zones (Hermanson and O’Shea, 1983). Pallid bats inhabit rocky outcrop areas, usually near a source of water. These bats have, however, been collected from areas far from any rocky topographic features (Findley et al., 1975).

Pallid bats are insectivorous and have been observed foraging upon the ground for flightless insects and other invertebrates. Pallid bats are occasionally captured in snap traps intended for rodents (Davis and Schmidly, 1994; Hoffmeister, 1986). Various species of beetles are preferred prey items, with moths being of secondary importance. The pallid bat is also known to prey upon lizards and small rodents (Hermanson and O’Shea, 1983). Prey 25 to 35 mm in body length is preferred, and pallid bats may ignore swarms of smaller insects while foraging in an area (Hermanson and O’Shea, 1983). Pallid bats may feed while in the air or may take prey to a night roost for consumption. Pallid bats are nocturnal and forage in two distinct periods during the night (Hermanson and O’Shea, 1983). These bats usually feed soon after emergence from the day roost, seek a night roost within the area, and, then, forage and feed once more before returning to the day roost.

Pallid bats often visit flowers of cacti and other plants while engaged in foraging activities. The bats thrust their muzzles into the flowers of these plants, and rub against the stamens while foraging, sometimes depositing pollen on the body fur. The pallid bat is an opportunistic forager (Herrara et al., 1993) and probably searches for beetles and other insect prey within the flowers. However, by utilizing this flower-probing method of foraging, *A. pallidus* serves as a pollinator.
of desert plants (Herrara et al., 1993). The foraging pattern of pallid bats may represent an intermediate stage from insectivory to nectivory and frugivory in chiropterans (Hermanson and O’Shea, 1983; Herrara et al., 1993).

Roosts are found in crevices, caves, mine tunnels, beneath rock slabs, and in buildings (Schmidly, 1991). Suitable rocky outcrops along slopes are common throughout all but the extreme northwestern Edwards Plateau. Pallid bats most commonly roost in crevices and structures built by humans and are typically not cavernicolous bats (Hermanson and O’Shea, 1983). Day roosts and night roosts are utilized by pallid bats. I have observed this species roosting in deserted buildings and other structures during the night, and, upon returning the next day, found the bats to be absent from these roosting sites. Many night roosts are exposed to dessicating conditions during the daylight hours, and would be unsuitable diurnal retreats for these bats. Homing ability is not especially well developed in pallid bats. If displaced more than the usual nightly foraging distance (34 to 110 km), pallid bats usually will not return to the original point of release (Hermanson and O’Shea, 1983).

Pallid bats are colonial in social habit. Colonies range in size from a few individuals to 100 or more individuals (Schmidly, 1991). Adult males are often absent from maternal colonies, but are present at some locations (Hermanson and O’Shea, 1983). Bats cluster together within the colony, and body temperatures and metabolism are significantly lower for clustering bats than for solitary individuals (Hermanson and O’Shea, 1983). Brazilian free-tailed bats, big brown bats, western pipistrelles, Yuma myotis, and Townsend’s big-eared bats are sometimes found associated with pallid bats in the same roost site (Hermanson and O’Shea, 1983; Schmidly, 1991). The strongest social ties are between a female and her offspring, but other females within a colony may help to guard and care for young to some extent. A mother may be led to her distressed young by other females within a colony; however, communal nursing of young does not occur (Hermanson and O’Shea, 1983).

Pallid bats are mostly inactive in the winter months and are presumed to hibernate. However, some individuals have been taken during winter months and at cold (2°C) temperatures in Nevada (Hermanson and O’Shea, 1983). Length of hibernation probably varies throughout the range of the pallid bat.

Copulation occurs from October through December, with subsequent storage of sperm in the female’s reproductive tract until the following spring (Hermanson and O’Shea, 1983). Young are probably born in the months of June and July on the Edwards Plateau, but time of parturition varies according to location (Hermanson and O’Shea, 1983). Lactating females have been taken in the month of June on the Edwards Plateau. Juvenile bats have been captured in September on the Edwards Plateau. Litter size ranges from one to four young; most commonly two young are born. In a sample of 24 pregnant females captured in the month of May from Kimble County, Texas, 5 females carried one embryo, 15 females carried two embryos, 3 females carried three embryos, and 1 female carried four embryos. Yearling females may reproduce, but give birth to only a single young (Hermanson and O’Shea, 1983).

The subspecies of pallid bat on the Edwards Plateau is *A. p. pallidus* (Le Conte, 1856). Average external measurements (Schmidly, 1991) are: total length, 106; tail length, 44; length hind foot, 11 ear length, 28. Sexual dimorphism is slight and insignificant in the pallid bat (Martin and Schmidly, 1982). Selected mean cranial measurements of six individuals from the Edwards Plateau (Martin and Schmidly, 1982) are: greatest length skull, 20.66; interorbital constriction, 3.87; zygomatic breadth, 12.48; cranial breadth, 9.86; length maxillary toothrow, 6.81; width across molars, 7.80; cranial depth, 8.64.

**Specimens examined** (116).— Crockett Co.: 14 216800E, 3430700N, 3; 14 216800E, 3431500N, 2. Kimble Co.: 14 425500E, 3372900N, 1; 14 425400E, 337200N, 67; 14 437600E, 3372600N, 6 (MWSU); 14 425300E, 3371300N, 1; 14 425000E, 3371300N, 5; 14 425400E, 3365200N, 6; 14 444900E, 3356200N, 1. Upton Co.: 13 772500E, 3443800N, 8. Val Verde Co.: 14 296300E, 3337300N, 13 (MWSU); 14 248900E, 3343800N, 1 (MWSU); 14 325900E, 3323000N, 1; 14 303300E, 3271600N, 1 (MWSU).

Family Molossidae—Free-tailed Bats

*Tadarida brasiliensis*
Brazilian Free-tailed Bat

**Distribution.** The Brazilian free-tailed bat ranges from south-central, western, and northern South America, northward throughout Central America and Mexico, and into the conterminous United States. This bat ranges throughout the southern regions of the United States northward and east from southern Oregon, Nevada, Utah, northern Nebraska, Arkansas, Alabama, Mississippi, and Georgia.

The Brazilian free-tailed bat ranges throughout Texas during the warmer seasons of the year. This is the most common bat on the Edwards Plateau, especially on the eastern portions of the region (Manning et al., 1987). Records are available from Bandera, Bexar, Blanco, Coke, Comal, Crockett, Ector, Edwards, Hays, Howard, Irion, Kendall, Kerr, Kinble, Kinney, Llano, Mason, Medina, Real, San Saba, Schleicher, Sterling, Sutton, Taylor, Tom Green, Travis, Upton, Uvalde, and Val Verde counties (Fig. 47).

*Tadarida brasiliensis* is easily identified by its tail, which projects conspicuously past the interfemoral membrane. This bat is uniformly dark brown or dark gray in color dorsally, whereas the venter is lighter in color. Scattered white hairs are commonly found in the pelage. The wings are long and narrow, and conspicuous hairs protrude from the toes (Barbour and Davis, 1969). The skin of the upper lips has deep, vertical grooves or wrinkles, and the ears, when laid forward, do not extend beyond the muzzle.

The Brazilian free-tailed bat is found in a variety of habitats throughout its range. These bats may be found in desert, woodland, forest, and marsh habitats in the United States. *T. brasiliensis* is also found in prairie habitats if suitable roosting sites are available.

The Brazilian free-tailed bat is insectivorous and usually takes prey from 2 to 10 mm in length. Insects consumed in the diet include moths, flying ants, June beetles, leaf beetles, leafhoppers, and true bugs (Schmidly, 1991). Whitaker et al. (1996) examined the foraging behavior of *T. brasiliensis* from the James River bat cave in Mason County and found that the bats in this area fed more heavily upon coleopteran insects during evening feeding bouts, whereas moths were taken in greater numbers in early morning foraging episodes. These bats often feed in small groups and prey upon swarming insects. The loose skin around the mouth may help to expand the gape and allow *T. brasiliensis* to feed more efficiently while flying (Wilkins, 1989). The large numbers of these bats may have a negative impact upon insect populations in a given area during the summer months (Schmidly, 1991). The Brazilian free-tailed bat is nocturnal in activity, and usually emerges from the day roost shortly before or shortly after sunset. Average time for bats to be away from the day roost is approximately 3 hr 48 min (Wilkins, 1989).

The Brazilian free-tailed bat most often roosts in large numbers in caves in the region. These bats also utilize hollow trees, cypress trees, rock crevices, buildings, culverts, bridges, railroad trestles, and cave swallow nests as roosting sites (Wilkins, 1989). A feature common to cave roosts is domed ceilings (Wilkins, 1989). Entrances into the caves must be at least 10 m wide; vertical entrance shafts into sinkholes must be at least 10 X 10 m (Wilkins, 1989). Cave roosts are often shared with other species of bats. Because such large numbers of *T. brasiliensis* may inhabit a roost (from four to ten million in some caves), not all Brazilian free-tailed bats inhabiting a roost may leave to forage each night (Barbour and Davis, 1969). *T. brasiliensis* can tolerate high levels of ammonia within a roost with no apparent harm. Carbon dioxide and protein content of the respiratory mucus and carbon dioxide dissolved in blood plasma increase with increasing levels of dissolved ammonia, with a resulting increased pH buffering capacity (Wilkins, 1989). Swarming activity inside the roost also aids in air circulation and helps to dispell some of the gaseous ammonia. The guano from these bats may accumulate in large quantities on the floor of the roosts and has been used for fertilizer since the nineteenth century (Schmidly, 1991).

The Brazilian free-tailed bat is one of the most gregarious of bats, and is colonial during all seasons (Barbour and Davis, 1969). However, adult males migrating north with females in the spring usually form small, separate bachelor colonies (Villa-R and Cockrum, 1962; Wilkins, 1989). *T. brasiliensis* may fly 50 km or more to foraging areas each night and may forage over an area of 400 km (Wilkins, 1989). Homing ability is well developed, and *T. brasiliensis* can home over distances of 525 km (Wilkins, 1989).
The Brazilian free-tailed bat is a migratory species and, as a result, is a rather poor hibernator (Wilkins, 1989). Most Brazilian free-tailed bats migrate from the Edwards Plateau in early fall, but a few probably hibernate in caves on the region throughout the winter months (Villa-R and Cockrum, 1961; Wilkins, 1989). Spring migrations are of longer duration and are in sharp contrast to the more rapid fall migration to the south. *T. brasiliensis* arrives in Texas in March and April (Wilkins, 1989). Cold fronts moving through the region may instigate the fall migrations (Villa-R and Cockrum, 1961).

Brazilian free-tailed bats mate in March and April. Most matings probably occur on the southern portions of *T. brasiliensis*’ range, inasmuch as few adult males migrate northward with the females in the spring (Wilkins, 1989). The gestation period is approximately 77 to 84 days in length (Barbour and Davis, 1969). Pregnant females have been collected in May and lactating females in June on the Edwards Plateau. *T. brasiliensis* females usually give birth to a single young, however, one to three embryos may be produced upon occasion (Wilkins, 1989). Females leave the young within the roost while foraging and, despite the large numbers of young within some maternity colonies, usually return and locate their own young within the roost (Wilkins, 1989).

The subspecies of Brazilian free-tailed bat on the Edwards Plateau is *T. b. mexicana* (Saussure, 1860). The sexes do not differ in appearance externally, and males are only slightly larger than females in some cranial characters (Lowery, 1974). Average external measurements of five females and five males, respectively, are: total length, 95.8, 94.8; tail length, 34.8, 32.8; length hind foot, 8.4, 8.0; ear length, 18.0, 18.8. Selected mean cranial measurements of these same indi-
individuals (females and males, respectively) are: greatest length skull, 16.58, 17.24; zygomatic breadth, 9.67, 9.85; interorbital constriction, 3.86, 3.93; cranial breadth, 9.21, 9.41; length maxillary toothrow, 5.86, 5.97; breadth across canines, 3.90, 3.78.


Family Dasypodidae—Armadillos

*Dasypus novemcinctus*

Nine-banded Armadillo

**Distribution.**—The nine-banded armadillo ranges from southern South America northward through southern and eastern Mexico. The nine-banded armadillo occurs throughout most of Texas, with the exception of parts of the Llano Estacado and Trans-Pecos regions (Schmidly, 1977; Jones et al., 1993). The species ranges as far north as southern Nebraska, and east through parts of Missouri, Arkansas, Louisiana, Mississippi, Alabama, Georgia, and Florida.

The nine-banded armadillo occurs throughout the Edwards Plateau region (Schmidly, 1983). Records are available from Bexar, Blanco, Burnet, Coke, Comal, Crockett, Edwards, Gillespie, Hays, Irion, Kendall, Kerr, Kimble, Llano, Mason, Menard, Nolan, Real, San Saba, Sterling, Sutton, Taylor, Tom Green, Travis, and Val Verde counties (Fig. 48).

*Dasypus novemcinctus* can be mistaken for no other mammal on the Edwards Plateau. These short, stout, burrowing animals are sparsely haired and covered by bony scutes, except on the venter. They have pointed, upright ears; a long tail which drags the ground when the animal is moving at a slow pace; and a long rostrum. Teeth are small and peglike. The front claws are long, and pointed, and are utilized for burrowing. The dorsal surface of the skull, to the level of the jaws, is covered by a bony shield. The overall color is grayish, with the scutes having small areas of ivory color at their edges.

Armadillos occur in varied habitats throughout the Edwards Plateau, ranging from stream and river-side habitats and small, grassy meadows, wooded uplands and rocky, juniper areas, and sandier areas on the far western Edwards Plateau. All permanent habitats must have soil deep enough for the excavation of a burrow. A ready water supply is also an essential requirement of suitable habitats (Taber, 1945). Vegetation within an area is used chiefly for cover by the nine-banded armadillo.

The diet of *D. novemcinctus* consists mostly of insects, but other animal matter is included (Baker, 1943). In addition to animal matter, nine-banded armadillos consume seeds, berries, and other vegetable matter (Fitch et al., 1952). The armadillo uses a probing search method of foraging for insects, utilizing its elongated snout and tongue to unearth grubs, insects and other food items (Taber, 1945). Although insects make up the greater part of the nine-banded armadillo's diet, the animal is known to consume eggs, small reptiles, amphibians, and some plant material. Cultivated crops are consumed in certain instances (Fitch et al., 1952). Armadillos are mostly nocturnal, but are occasionally observed during daylight hours. Armadillos do not hibernate and must seek food throughout the year (Schmidly, 1983).

Burrows are constructed as living quarters and places of refuge. An individual digs several burrows within an area, and, based upon my observations, knows the whereabouts of each while foraging in an area. Dens vary from two to 15 feet in length, and may be only a few inches to four feet in depth (Taber, 1945). Dens are usually branched and may have more than one nest. Nests are made from grasses and other vegetation (McBee and Baker, 1982). Other areas of refuge on the Edwards Plateau include natural caves, cracks, crevices, and rocky areas (Taber, 1945).

Armadillos are not territorial in nature. Several individuals may be observed foraging in an area, with no antagonistic behaviors between them (Taber, 1945; McBee and Baker, 1982). Captive animals of differing sexes show no territorial behaviors even when maintained in the same nest box (Taber, 1945). Home ranges of *D. novemcinctus* range from 1.6 ha to 13.8 ha (McBee and Baker, 1982). A great deal of overlap occurs between the home ranges of all individuals within an area.

The nine-banded armadillo mates from June to August. After mating, a blastocyst forms in five to seven days and development is arrested in the uterus until November (McBee and Baker, 1982). Specific polyembryony occurs and four young are produced. A gestation period of about 120 days follows the period of delayed implantation (Lowery, 1974). Juvenile arma-
dillos have been recorded from the month of May on the Edwards Plateau. The young are all identical in gender, but cytoplasmic differences are evident between offspring (McBee and Baker, 1982).

The subspecies of nine-banded armadillo on the Edwards Plateau is *D. n. mexicanus* Peters, 1864. Male armadillos tend to be slightly larger than females. Ranges of external measurements (McBee and Baker, 1982) are: total length, 615-800; tail length, 245-370; length hind foot, 75-107; and ear length, 40. Selected cranial measurements of two adult males from the Edwards Plateau are: greatest length skull, 95.32, 106.78; zygomatic breadth, 40.44, 43.51; length maxillary toothrow, 24.55, 26.91; postorbital constriction, 24.07; 23.72.

ORDER LAGOMORPHA—RABBITS AND PIKAS

KEY TO LEPORIDAE

1 Interparietal bone indistinct to absent; length of ear from notch more than 100 mm; tail black in color dorsally .............................................................. *Lepus californicus*

1' Interparietal bone distinct; length of ear from notch less than 100 mm; dorsal surface of tail usually brown in color ................................................................................... 2

2 Greatest length of skull 75 mm or more; total length of adults usually from 400 to 500 mm; dorsal surface of hind foot brown in color ........................................................................... *Sylvilagus aquaticus*

2' Greatest length of skull less than 75 mm; total length of adults usually 400 mm or less; dorsal surface of hind foot white in color ....................................................... 3

3 Auditory bullae small and smooth in texture; ear length usually less than 58 mm; nuchal patch reddish in color ............................................................. *Sylvilagus floridanus*

3' Auditory bullae large and coarse in texture; ear length usually 60 mm or more; nuchal patch pale tan in color ............................................................. *Sylvilagus audubonii*

*Sylvilagus aquaticus*

Swamp rabbit

Distribution.—The swamp rabbit ranges from eastern Texas north to Illinois. Its range extends east to South Carolina and, then, south and west to Georgia.

The swamp rabbit is found only in the eastern Edwards Plateau region (Fig. 49). Specimens of this rabbit are available from Blanco, Gillespie, Hays, Kendall, Kerr, Medina, San Saba, and Travis counties.

*Sylvilagus aquaticus* is similar in appearance to *S. floridanus*, but is much larger when mature. The tips of the ears are more rounded in *S. aquaticus* as opposed to *S. floridanus*, and the swamp rabbit is usually washed with more black pelage dorsally than is *S. floridanus*. Nelson (1909) noted, however, that pelage colors in rabbits tended to fade with age and attrition. The swamp rabbit has a distinct, cinnamon-colored eye ring, whereas, the eye ring of *S. floridanus* is whitish or buff in color. The dorsal side of the hind legs is brown.
in color in *S. aquaticus*, whereas, the dorsal side is white in *S. floridanus*.

Swamp rabbits occur primarily in swamps, river bottoms, and lowland areas throughout their range (Chapman and Feldhamer, 1981). Lowery (1974) stated that *S. aquaticus* is found commonly in heavily wooded and marshy areas in Louisiana. The swamp rabbit appears to be restricted to riparian areas along rivers and around ponds on the Edwards Plateau (Baccus and Wallace, 1997). Specimens have been collected from the Guadalupe, Medina, and Perdenalis River bottoms, each of which has forested areas of Bald Cypress and other tree species. Two additional specimens were captured around ponds in Hays County.

Swamp rabbits feed upon a variety of plant species. Various sedges, grasses, and tree seedlings are included in the diet. *S. aquaticus* has been reported to cause damage to bald cypress seedlings in some parts of its range (Chapman and Feldhamer, 1981). Swamp rabbits also are coprophagic in habit.

Swamp rabbits demonstrate a definite social organization, consisting of a hierarchical system of alpha males. Female swamp rabbits are mutually tolerant of members of their own gender (Chapman and Feldhamer, 1981). Dominance displays and avoidance behaviors have been observed in males of this species. *S. aquaticus* also is territorial in behavior. Swamp rabbits are able swimmers and often use this tactic to avoid predators.

Forms are constructed in holes in the ground. The tops of tree stumps, logs, vegetation tangles, and bramble bushes are also selected as form sites (Chapman and Feldhamer, 1981). Nests are constructed mostly of grass and lined with belly fur. Females regularly construct

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Figure 49. Distribution of *Sylvilagus aquaticus* on the Edwards Plateau.
dummy nests at several locations within an area; however, these nests are not lined with belly fur (Chapman and Feldhamer, 1981).

Female swamp rabbits demonstrate synchronized estrous behavior. The breeding season may be year-around in Texas (Hunt, 1959). Davis (1974) reported a breeding peak in the months of February and March. Litter size is usually two or three young (Davis and Schmidly, 1994).

*Sylvilagus aquaticus* (Bachman, 1837) is a monotypic species. No appreciable size differences have been reported between sexes. Average external measurements of three males are: total length, 500; tail length, 58; length hind foot, 103; ear length, 74. Selected average cranial measurements of these same individuals are: length of nasals, 38.22; width of nasals, 16.29; zygomatic breadth, 40.67; parietal breadth, 28.73; breadth braincase, 26.35; basilar length, 68.81; length of bullae, 11.34; length maxillary toothrow, 16.89.


*Additional Records.*—Blanco Co.: 14 581000E, 3365000N. Kerr Co.: 14 472500E, 3330100N; 14 477200E, 3326700N. San Saba Co.: 14 541200E, 3451000N. (Baccus and Wallace, 1997)

*Sylvilagus audubonii*

Desert Cottontail

*Distribution.*—The desert cottontail ranges from central Mexico northward throughout the western half of Texas and the western portions of the Great Plains states, westward to Montana. This species ranges through most of California, south-central Nevada, Utah, and Wyoming.

The desert cottontail ranges through the western portion of the Edwards Plateau. Records are at hand from Coleman, Crockett, Ector, Glasscock, Howard, Midland, Reagan, Tom Green, and Upton counties. Nelson (1909) lists a specimen from Llano County and Davis and Schmidly (1994) list specimens from Edwards, Kerr, and Val Verde counties (Fig. 50). The records from Edwards and Kerr counties are farther east than the range mapped by Chapman, Hockman, and Edwards (1982), but should still be mentioned. All specimens taken from Kerr County in the Texas Cooperative Wildlife Collection have been identified as *S. floridanus*.

*Sylvilagus audubonii* is a small to medium sized rabbit, and may be easily confused with the eastern cottontail (*S. floridanus*), where the two species are sympatric. The desert cottontail differs in having longer ears and a shorter tail with more white on the sides and dorsum than does *S. floridanus*. The nape of the neck is usually tan or pink in color in *S. audubonii*, whereas the nape of the neck is a darker reddish-orange color in *S. floridanus*. The outer margins of the ears are often darker in color in *S. floridanus* than in *S. audubonii*. The auditory bullae are much larger and coarser in texture in the desert cottontail, as opposed to the smaller and smoother auditory bullae of *S. floridanus*.

The desert cottontail occurs in arid habitats throughout its range. This species may be found in oldfield habitats, mesquite pastureland, catclaw thickets and other brushy areas, and in rocky, broken areas on the Edwards Plateau. Old buildings, brush piles and other altered habitats also are favored by the desert cottontail. The desert cottontail and other rabbit species are r-selected animals and rely upon high reproductive rates, escape methods, and protective cover in order to persist within any particular habitat. The desert cottontail occasionally is found in areas with very little cover and must rely upon its ability to escape from predators in order to persist in such an area.

The desert cottontail is herbivorous in diet. The diet varies depending upon availability of preferred plants within an area but includes such items as grasses, mesquite pods, and the fruits of prickly pear. Diet also varies depending upon season, with green vegetation consumed in greater abundance in spring and summer months and more woody vegetation consumed in fall and winter months (Chapman and Willner, 1978). The desert cottontail is able to survive periods of drought by consuming various species of forbs and cactus with high moisture content as a source of water (Chapman et al., 1982). This species is crepuscular to nocturnal in...
activity period. High winds and rain seem to deter movements and foraging of *S. audubonii* and other species of rabbits.

Abandoned skunk and armadillo burrows are sometimes utilized by *S. audubonii* as shelter (Chapman and Willner, 1978). Brush piles, thickets, rockpiles, and burrows underneath buildings are utilized as protective cover by this rabbit. Desert cottontails use forms and areas of bare ground cover for resting places during daylight hours. The habit of “freezing” in place has been observed in *S. audubonii* whenever there is a possible danger. Nests are constructed to shelter young rabbits and are composed of an outer layer of grasses and an inner layer of fur from the venter of the female. The opening to the nest is closed when the mother is absent.

In general, cottontails are not territorial in nature. Different age groups and sexes broadly overlap in home ranges during most of the year. Several rabbits may feed in an area and seem to maintain a sentinel and warning system of communication that is beneficial to the entire group. A dominance hierarchy may be established by adult males in order to reduce antagonistic encounters with conspecifics within an area and, thereby, facilitate reproduction when females are in estrous (Chapman et al., 1982). Various postures and vocalizations have been observed among groups of desert cottontails, including alert postures, submissive postures, approach, dash, marking, boxing, and presentation postures (Chapman et al., 1982).

The breeding season of *S. audubonii* probably extends throughout most of the year (Schmidly, 1977).
Chapman and Morgan (1974), however, noted that the breeding season began in late February and early March in western Texas, and Davis (1974) reported a lack of pregnant females from the months of January, July, and October. Gravid females have been taken in the months of March and May and juveniles in June on the Edwards Plateau. The number of young per litter ranges from one to six, and the gestation period is approximately 26 to 27 days in length (Davis and Schmidly, 1994). Multiple litters may be produced each year, and females become sexually mature at an early age.

Two subspecies of *S. audubonii* may occur on the Edwards Plateau. *S. a. neomexicanus* Nelson, 1907 on the northwestern Edwards Plateau south to Crockett and Tom Green counties, and *S. a. parvulus* (J. A. Allen, 1904) from Llano County and the remainder of the region. Sexual dimorphism is present in cottontails, with females averaging larger than males in most characteristics. Average external measurements (Davis and Schmidly, 1994) are: total length, 418; tail length, 73; length hind foot, 86; ear length, 60. Selected mean cranial measurements (Choate, 1991) are: greatest length skull, 66.93; zygomatic breadth, 34.37; interorbital breadth, 17.74; length maxillary toothrow, 12.58; length of incisive foramen, 16.66.


*Sylvilagus floridanus*  
**Eastern Cottontail**

*Distribution.*—The eastern cottontail ranges from Costa Rica, northward through most of Central America, and into Mexico. Thence from southern Mexico, northward into Arizona, New Mexico, and Texas. The range of this species within the conterminous United States includes almost all of the eastern United States north and east to southern Maine and westward through all of the Great Plains states. The eastern cottontail is also found in southeastern Montana, eastern Colorado, and most of southern New Mexico and Arizona. The eastern cottontail has been introduced into northern Oregon and southern Washington in recent times (Chapman et al., 1982). This rabbit may be found as far north as southern Saskatchewan, Manitoba, Ontario, and Quebec provinces of Canada.

The eastern cottontail ranges throughout the eastern three-fourths of Texas and parts of the Trans-Pecos region (Jones and Jones, 1992). *S. floridanus* occurs throughout the Edwards Plateau. Records are available from Bexar, Coke, Coleman, Crockett, Ector, Edwards, Gillespie, Glasscock, Hays, Howard, Irion, Kendall, Kerr, Kimble, Llano, Mason, McCulloch, Menard, Reagan, Real, San Saba, Schleicher, Sutton, Tom Green, Travis, Uvalde, and Val Verde counties (Fig. 51).

*Sylvilagus floridanus* can be separated from the western cottontail, *Sylvilagus audubonii* by the shorter ears and smaller, smoother auditory bullae of *S. floridanus*. Average ear length is less than 60 mm for *S. floridanus* and 60 mm or greater for *S. audubonii*. The nuchal patch of *S. floridanus* is reddish-orange, whereas the nuchal patch of *S. audubonii* is pale tan. The tail of the eastern cottontail has a narrow, lateral white border on its dorsal side, whereas the lateral white border of *S. audubonii*’s tail is usually broader. The swamp rabbit, *Sylvilagus aquaticus*, is much larger in size and has brown dorsal fur on the hind legs. The dorsal sides of the hind legs of the eastern cottontail are white.

The eastern cottontail rabbit is found in a wide variety of habitats throughout its range on the Edwards Plateau. This rabbit resides in riparian habitats, old fields, grassy valleys, upland woods, agricultural areas, edge habitats, mesquite grasslands, and creosote
Figure 51. Distribution of *Sylvilagus floridanus* on the Edwards Plateau.

The eastern cottontail is usually found not far from water. Cottontail habitat has been improved by interspersion of old fields, brush thickets, the creation of edge habitats, and by breaking up large areas of monotopic habitat (Chapman et al., 1980). Burning of vegetation and heavy livestock grazing, however, adversely affect eastern cottontail habitats (Chapman et al., 1980).

The eastern cottontail rabbit is herbivorous and feeds primarily upon grasses, forbs, and woody browse (Chapman et al., 1980). The eastern cottontail’s diet is seasonally variable, with a greater amount of succulent vegetation consumed in the spring and summer months and more woody browse consumed in fall and winter (Chapman et al., 1980). Diet items include a variety of grasses, curly dock, wild carrot, dandelions, prickly lettuce, giant ragweed, mesquite bark, and other plant materials (Chapman et al., 1980). These rabbits will occasionally cause damage to orchards by girdling stems or cutting down young fruit trees. Digestion of coarse plant material is aided by the cottontail’s coprophagous habits (Chapman et al., 1980). *S. floridanus* is most active during crepuscular and nocturnal hours, although cottontails are active diurnally as well.

Brushpiles are frequently used as refuge and resting cover. Cleared areas or forms may be constructed under herbaceous and shrubby vegetation if brushpiles are lacking (Chapman et al., 1982). A cottontail rabbit often remains motionless within its form whenever a predator approaches. Rabbits undergo bradycardia under such circumstances, and this physiological adaptation may help the rabbit to remain motionless, and thus undetected, for extended periods of time (Kreeger et al., 1990).
Female eastern cottontails give birth to young in a nest. Nests are slanting holes in the ground averaging 125 mm long, 104 mm wide, and 91 mm deep (Chapman et al., 1982). Nests are first lined with leaves and grasses and, then, a layer of fur that the female pulls from herself is added to the nest (Chapman et al., 1982).

Eastern cottontail rabbits are not territorial, and some degree of overlap occurs in the home ranges of individuals throughout the year (Chapman et al., 1980; Althoff and Storm, 1989). Home ranges of males overlap those of females to the greatest extent during mating periods, whereas, the home ranges of females overlap each other in a more stable fashion throughout the year (Althoff and Storm, 1989). Home ranges of males overlap those of females to the greatest extent during mating periods, whereas, the home ranges of females overlap each other in a more stable fashion throughout the year (Chapman et al., 1980). Home ranges of males generally vary in size from 0.95 to 2.8 ha; and home ranges of females vary from 0.95 to 1.2 ha (Chapman et al., 1980). Habitat type and structure, food supply, sex and age of the individuals within the population, season of the year, weather patterns, and other factors affect the size of a rabbit's home range (Chapman et al., 1982). Eastern cottontail rabbits are able to home from at least 3.74 km when removed from their home ranges and released (Hill, 1967; Chapman et al., 1980).

Eastern cottontail rabbits establish dominance hierarchies within an area; dominant males will drive away or displace subordinate males (Chapman et al., 1980). Fighting rarely occurs among cottontails, and usually is conducted between dominant males or dominant males and their immediate subordinates (Chapman et al., 1982). Dominant males mate with most of the females in an area, and the dominant males are more free-ranging and exploratory in habit (Chapman et al., 1982).

The breeding season extends throughout the year in southern Texas (Chapman et al., 1980) and probably extends throughout the year at least on the southern Edwards Plateau. Pregnant females have been collected on the Edwards Plateau in the months of January, February, April, and May. The gestation period ranges from 25 to 35 days. Adult females, on the average, produce three to four litters each year (Chapman et al., 1980). Litters normally range in size from four to eight young (Dalquest and Horner, 1984).
Menard Co.: 14 446900E, 3399900N, 1; 14 412900E, 3425700N, 2. Reagan Co.: Hughes Ranch, Centralia Draw (Unspecified Locality), 18 (ASNHC); Along Hwy 67, W of Texon, 1 (ASNHC); 14 265500E, 3471500N, 8 (ASNHC); 14 255000E, 3456800N, 1 (ASNHC); 14 251000E, 3453500N, 2 (ASNHC); 14 250900E, 3450600N, 1 (ASNHC). Real Co.: 14 400000E, 3494300N, 1; 14 429900E, 3285600N, 1 (ASWHTU). Reagan Co. Line (Unspecified Locality), 3482900N, 1 (ASNHC); 14 355300E, 3466600N, 1 (ASNHC). San Saba Co.: 14 429900E, 3399900N, 1; 14 365700E, 3356700N, 2. Sutton Co.: 14 354900E, 3447500N, 1; 14 362300E, 3447500N, 2; 14 367500E, 3444300N, 1 (ASNHC). Schleicher Co.: 14 395000E, 3410700N, 1. Sutton Co.: 14 362800E, 3356700N, 2. Tom Green Co.: 14 328300E, 3505100N, 1; 14 354900E, 3482900N, 1 (ASNHC); 14 355300E, 3466600N, 1 (ASNHC); 14 362400E, 3447500N, 2; 14 365700E, 3444300N, 1 (ASNHC). Travis Co.: Balcones Research Center, Austin, 1 (TNHC); 14 622000E, 3351400N, 1 (SWHTU). Upton Co.: Near Upton/Reagan Co. Line (Unspecified Locality), 1 (ASNHC); 14 233700E, 34538300N, 5 (ASNHC); 14 219500E, 3456500N, 1 (ASNHC).


**Lepus californicus**

Black-tailed Jackrabbit

**Distribution.**— The black-tailed jackrabbit ranges from Hidalgo and Queretaro, Mexico, northward throughout most of the western conterminous United States. The black-tailed jackrabbit ranges from Arkansas and Missouri in the east, north to south-central South Dakota, and westward to the Pacific coast states; the species reaches its northern and western distributional limits in central Washington.

The black-tailed jackrabbit occurs throughout the Edwards Plateau. Records are available from Bandera, Bexar, Blanco, Burnet, Coke, Crockett, Ector, Edwards, Gillespie, Hays, Irion, Kerr, Kimble, Kinney, Llano, Mason, Menard, Midland, Nolan, Reagan, Real, Runnels, San Saba, Schleicher, Sutton, Tom Green, Travis, Upton, Uvalde, and Val Verde counties (Fig. 52).

*Lepus californicus* is easily distinguished from the various species of cotton-tail rabbits by its larger size, longer ears and legs, and the black colored dorsal surface of the tail. The dorsum of *L. californicus* is brownish to grizzled in color and is washed with black. The sides are brownish and the venter is creamy white. The ears are tipped with black. On the Edwards Plateau, the only rabbit that might be confused with this hare is the swamp rabbit, *S. aquaticus*. The swamp rabbit has shorter ears, is smaller in size and occupies different habitats than *L. californicus*. The skull of *L. californicus* lacks a distinct interparietal bone, as opposed to cotton-tail rabbits.

Black-tailed jackrabbits are primarily animals of arid regions and are found in association with short-grass areas throughout most of the western United States (Dunn et al., 1982). *L. californicus* prefers areas of limited brush and sparse vegetation. Black-tailed jackrabbits are usually associated with vegetation that is no more than one meter in height (Chapman and Willner, 1986). *L. californicus* does not readily inhabit areas of dense, tall vegetation or riparian areas where visibility is reduced (Jones et al., 1983). These hares generally inhabit open, and rocky areas on the Edwards Plateau. Creosote and juniper associations are utilized on the western Edwards Plateau, and *L. californicus* is found in mesquite-juniper-oak pasturelands throughout the region. Agricultural areas also are occupied by the black-tailed jackrabbit. These mammals often become abundant on overgrazed pasturelands (Jones et al., 1983).

Black-tailed jackrabbits are herbivorous and coprophagic in dietary habits. A variety of plants is consumed; the diet of *L. californicus* is seasonally variable. Green, succulent vegetation is preferred whenever available. A greater percentage of grasses and forbs is consumed in the summer months, and woody shrubs are consumed in greater amounts during the winter months (Dunn et al., 1982). Known diet items include mesquite, sagebrush, creosote, globemallow, spiderwort, various grasses, yucca, curly dock, prickly pear, pigweed, buffalo bur, and Russian thistle (Dunn et al., 1982). *L. californicus* also feeds upon various agricul-
tural crops, such as alfalfa, wheat, and barley. Black-tailed jackrabbits regularly utilize mineral licks (Dunn et al., 1982). *L. californicus* seldom drinks water and usually derives sufficient moisture from succulent vegetation consumed in its diet (Jones et al., 1983). Edge areas and clearings are favored feeding grounds. Jackrabbits feed in the early morning and evening hours and throughout the night. Factors known to influence feeding times include cloud cover, moon phase, wind speed, precipitation, and temperature.

Black-tailed jackrabbits utilize forms as resting sites during the daylight hours. These shallow depressions are constructed at the bases of shrubs, trees, other vegetation, and, occasionally, man-made structures. Nests are constructed by females to shelter newly born rabbits for a short time. Nests are made of grasses and are lined with fur. Black-tailed jackrabbits often utilize trails when traveling through an area. Because *L. californicus* inhabits open terrain, it relies upon rapid running to escape predators, speeds up to 40 miles per hour have been recorded (Jones et al., 1983).

Home range size is affected by the pattern of food, cover, and water in the surrounding habitat. Home ranges of adult females tend to be larger than those of adult males. Home ranges of adults are larger than the home ranges of juveniles (Dunn et al., 1982). Black-tailed jackrabbits do not appear to be highly territorial. *L. californicus* exhibits cyclic population densities in some areas, with population highs occurring every five, six, or ten years (Taylor, 1948; Dunn et al., 1982). Population highs are often followed by rapid declines in black-tailed jackrabbit numbers in an area for a few years (Bailey, 1905; Chapman and Willner, 1986).

Figure 52. Distribution of *Lepus californicus* on the Edwards Plateau.
Little is known of the social habits of the black-tailed jackrabbit. *L. californicus* is often observed feeding in groups with no apparent antagonistic behavior between individuals. However, males are frequently involved in fighting, and avoidance behaviors are known to occur between individuals (Dunn et al., 1982; Hoffmeister, 1986). Displacement behaviors, such as feeding and dust bathing, may be observed immediately after an agonistic encounter between two individuals. Females become more aggressive and disperse from each other as their breeding receptivity increases (Dunn et al., 1982).

The breeding season of *L. californicus* extends throughout the year in Texas (Davis and Schmidly, 1994). Male black-tailed jackrabbits are probably polygamous in mating habit. Females are induced ovulators (Dunn et al., 1982). The gestation period ranges from 41 to 47 days (Haskell and Reynolds, 1947). The breeding season usually occurs between individuals (Dunn et al., 1982). However, males are frequently observed with other as their breeding receptivity increases (Dunn et al., 1982). Females become more aggressive and disperse from each other as their breeding receptivity increases (Dunn et al., 1982).

Adult females examined from the month of May carried one or two embryos and one female carried five embryos in February. Larger litters correlate with better nutritional conditions (Jones et al., 1983). Young of black-tailed jackrabbits are born fully furred and precocial. Young black-tailed jackrabbits leave the nest usually within 24 hours of birth (Dunn et al., 1982). *L. californicus* exhibits a relatively well synchronized breeding season. Females do not breed until about one year of age (Jones et al., 1983).

There are three subspecies of black-tailed jackrabbit found on the Edwards Plateau; *L. c. melanotis* Mearns, 1890, in the north; *L. c. merriami* Mearns, 1896 in the south and east; and *L. c. texianus* Waterhouse, 1848, on the western Edwards Plateau. Adult females are slightly larger than adult males (Nelson, 1909). Average external measurements of six adult female *L. c. merriami* are: total length, 588.17; tail length, 76.16; length hind foot, 130.33; ear length, 134.67. Selected mean cranial measurements of ten adult females are: greatest length skull, 100.49; zygomatic breadth, 45.79; length nasals, 42.34; breadth nasals, 20.45; bulla length, 13.27; bulla breadth, 9.52; length maxillary toothrow, 16.75.


ORDER RODENTIA—RODENTS

KEY TO FAMILIES OF RODENTIA

1 Greatest length of skull 110 mm or larger; total length 680 mm or greater ............................................. 2
1' Greatest length of skull less than 110 mm; total length less than 680 mm ............................................. 3

2 Infraorbital foramen larger than foramen magnum; auditory bullae large; guard hairs modified into conspicuous quills; toes of hind feet not webbed; tail short and normal in shape ............................................................................................................................................ Erethizontidae
2' Infraorbital foramen small; auditory bullae small; guard hairs normal in appearance; toes of hind feet webbed; tail long, dorso-ventrally flattened and paddle-like in shape ...................................................................................... Castoridae

3 Cheekteeth 3/3 ............................................................................................................................. Muridae
3' Cheekteeth 5/4 or 4/4 ............................................................................................................................. 4

4 Prominant postorbital processes present; tail distichous or bushy; no external cheek pouches ..................................................................................... Sciuridae
4' No prominent postorbital processes; tail not distichous or bushy; external cheek pouches present ...................................................................................................... 5

5 Infraorbital foramen perforate; mastoid bullae enlarged; ears not valvular; tail well-haired; incisors not protruding through the upper and lower lips; forelimbs not especially modified for digging .............................................................................................................. Heteromyidae
5' Infraorbital foramen not perforate; mastoid bullae not enlarged; ears valvular; tail sparsely haired; incisors protruding through upper and lower lips, allowing mouth to be closed behind the teeth; forelimbs modified for digging .............................................................................................................. Geomyidae

KEY TO SCIURIDAE

1 Length of maxillary toothrow more than 14 mm; upper toothrows strongly convergent posteriorly and teeth laterally expanded; first upper cheektooth (P3) much broader than upper incisor; dorsum a uniform tan color; tail tipped with black ...................................................... Cynomys ludovicianus
1' Length of maxillary toothrow less than 14 mm; upper toothrows not strongly convergent posteriorly; teeth not strongly expanded laterally; P3 present or absent, if present much narrower than upper incisor; dorsum not uniformly tan in color; tail not tipped with black ............................................. 2

2 Greatest length of skull 59 mm or greater; total length 440 mm or greater ............................................. 3
2' Greatest length of skull less than 59 mm; total length less than 440 mm ............................................. 5
Zygomatic plate slanting upward from base to rostrum at an angle of approximately 40 degrees; postorbital breadth noticeably greater than interorbital breadth; premolars 2/1; head and dorsum solid black or brown to the shoulders and remainder of the dorsum black or brown and mottled with white ................................................................. Spermophilus variegatus

Zygomatic plate slanting upward from base to rostrum at an angle of approximately 50 degrees; postorbital breadth about the same as, or only slightly greater than, interorbital breadth; premolars 1/1 or 2/1 (P3, if present, minute); head and dorsum not darker brown or black around the head and shoulders and dorsum uniform in color throughout its length; no white mottling on the dorsum ............................................................................................................................................. 4

Two upper premolars present; bones creamy white in color; dorsal color a salt-and-pepper gray; venter white; lateral edges of tail fringed with white hairs; white eye ring present .................................................... Sciurus carolinensis

One upper premolar; bones reddish in color; dorsum rust colored; venter ferruginous; lateral edges of tail fringed with orange-colored hairs; yellowish eye ring ............................................................................. Sciurus niger

Auditory bulla large, length about one and a half times that of maxillary toothrow; first upper premolar (P3) minute; one white stripe down each side of dorsum; underside of tail white .................................................. Ammospermophilus interpres

Auditory bulla of normal size, length less than (or only slightly greater than) that of maxillary toothrow; first upper premolar (P3) a well-developed, peglike tooth; no white dorsal stripes; underside of tail with banded hairs, whitish at the base and tip and dark brown or black medially .......................................................... 6

Greatest length of skull 43 mm or greater; total length 300 mm or greater; dorsum with conspicuous, squarish, white spots arranged in rows ................................................................. Spermophilus mexicanus

Greatest length of skull less than 43 mm; total length less than 300 mm; dorsum with faint, white spots occurring in no discernible pattern ............................................................................. Spermophilus spilosoma

Family Sciuridae—
Squirrels and Allies
Ammospermophilus interpres
Texas Antelope squirrel

Distribution.—The Texas antelope squirrel ranges from New Mexico, south throughout most of Trans-Pecos, Texas, and eastward onto the Edwards Plateau. This squirrel ranges south through Coahuila, Chihuahua, Durango, and Zacatecas, Mexico.

The Texas antelope squirrel is limited in distribution to the extreme western portion of the Edwards Plateau. The species has been reported from Crane, Crockett, Reagan, Upton, and Val Verde counties of the Edwards Plateau (Fig. 53).

Ammospermophilus interpres is the smallest ground squirrel occurring on the Edwards Plateau, and is not easily confused with other ground squirrels. The dorsal pelage is gray to ruddy-brown in color, and the venter and underside of the tail are white. Two white stripes are present on the lateral sides, extending from the shoulders to the sides of the rump. A white band is present over the eye and two black bands are present on the underside of the tail. Internal cheek pouches are present.
Texas antelope squirrels seem to be limited in distribution on the Edwards Plateau to rocky, broken areas, with little ground cover. This squirrel is often associated with creosote and juniper vegetation. Grasslands and other areas of extensive ground cover appear to present effective barriers to the distribution of *Ammospermophilus interpres* within an area (Best et al., 1990).

As a species primarily of Chihuahuan Desert habitats, *A. interpres* is not dependent upon water for its survival. A captive animal from Trans-Pecos, Texas, maintained at Midwestern State University would not accept water offered to her upon numerous occasions. This squirrel, in fact, would tentatively smell of the water placed in a small dish inside her terrarian and, then, would turn her back to the dish and promptly fill it with sand pushed up with her hind legs.

The Texas antelope squirrel is primarily herbivorous and granivorous in diet. Diet items include a variety of seeds, berries, and occasionally insects. The fruits of various kinds of cacti are consumed when available. Mesquite beans, creosote seeds, and juniper and yucca fruits are eaten (Best et al., 1990).

The Texas antelope squirrel is very active. It is common nowhere and often difficult to obtain by standard trapping methods. This species may be easily recognized by sight because it carries the tail tightly arched over the back while running. *A. interpres* is also well-adapted for climbing (Best et al., 1990).

The Texas antelope squirrel usually inhabits a burrow, but will also den underneath rocks and inside crevices in an area. This squirrel will also make use of the abandoned burrows of other species of rodents. As
is common with most kinds of ground squirrels, there is usually no mound of dirt to mark the entrance of the burrow. Nests are built inside of the burrows; nests are constructed from such materials as rabbit fur, shredded bark, feathers, and dry grasses (Davis and Schmidly, 1994).

*A. interpres* is not known to hibernate and has been sighted in November, December, and February in Trans-Pecos, Texas. These squirrels do become fat in the fall months, and this may allow them to sleep through winter storms throughout their range (Bailey, 1905).

Breeding begins in February. One litter of from five to 14 young is usually raised annually. Davis and Schmidly (1994) reported evidence that two litters per year may be raised by some females.

*A. interpres* (Merriam, 1890) is a monotypic species. Average external measurements of eight males and two females from El Paso, Texas (Best et al., 1990), are: total length, 226; tail length, 74.2; length hind foot, 37.8; ear length (dry), 9.8. Selected cranial measurements given in the same source are: greatest length skull, 39.3; zygomatic breadth, 22.7; cranial breadth, 18.9; interorbital breadth, 9.9; post-orbital constriction, 14.5; nasal length, 12.6; length maxillary toothrow, 6.6.

Specimens examined (1).—Reagan Co.: 14 253400E, 3453600N, 1 (ASNHC).


*Spermophilus mexicanus*  
Mexican Ground Squirrel

Distribution.—The Mexican ground squirrel occurs in two distinct populations in Mexico. One population occurs in central Mexico in the states of Aguascalientes, Guanajuato, Hidalgo, Jalisco, Mexico, Puebla, Queretaro, Tlaxala, and the Distrito Federal; the second population occurs in northeastern Mexico in Coahuila, Nuevo Leon, Tamaulipas, and Zacatecas. This ground squirrel ranges northward into the United States in southern, central, western, and parts of northwestern and northcentral Texas. The Mexican ground squirrel also occurs in southeastern New Mexico.

The Mexican ground squirrel occurs throughout the Edwards Plateau (Davis and Schmidly, 1994). This species is the most common ground squirrel residing on the Edwards Plateau. Records are available from Bexar, Callahan, Coke, Comal, Concho, Crane, Crockett, Edwards, Gillespie, Hays, Howard, Irion, Kerr, Kimble, Kinney, Llano, Mason, McCulloch, Medina, Menard, Midland, Nolan, Reagan, Runnels, Sterling, Sutton, Taylor, Tom Green, Travis, Upton, and Val Verde counties (Fig. 54).

*Spermophilus mexicanus* is tan to light brown in coloration with usually eight rows of squarish, white spots on the dorsal side. The ears are short and rounded, and the belly usually is white. The tail is less than half of the total length, flattened and slightly bushy, with a cylindrical base. The Mexican ground squirrel might be confused with the spotted ground squirrel (*S. spilosoma*) on the Edwards Plateau. The spotted ground squirrel is smaller in size, a pale, cinnamon color, and has an irregular pattern of faint white spots on the dorsum.

The Mexican ground squirrel inhabits level grasslands associated with mesquite, creosote, and cactus (Young and Jones, 1982). Ideal natural habitat is shortgrass prairie. This ground squirrel has adapted well to human alteration of the environment (Young and Jones, 1982). Mexican ground squirrels are now found in highway rights–of–way, parks, cemeteries, and golf courses throughout the Edwards Plateau. *S. mexicanus* favors areas that are now mowed and maintained by humans, and the Mexican ground squirrel may also be found inhabiting overgrazed pasturelands on the Edwards Plateau.

Mexican ground squirrels are herbivorous, but, upon occasion, have been observed feeding upon animal matter (Davis and Schmidly, 1994). Known diet items include Johnson grass, mesquite leaves and beans, agarita leaves and berries, pin clover, cultivated grains, and various insects. *S. mexicanus* is seasonally variable in its diet, and insects may constitute half of its food base by early summer (Edwards, 1946). Mexican ground squirrels may occasionally climb into low shrubs in order to forage for food items (Davis and Schmidly, 1994). *S. mexicanus* is strictly diurnal in activity pe-
period. These squirrels are most active on warm, calm, sunny days. If conditions are cool and overcast, the squirrels will remain within their burrows. Mexican ground squirrels deposit fat in the spring and summer months and utilize the fat stores during the winter months. *S. mexicanus* hibernates through the winter months and becomes active again around the middle of spring.

The Mexican ground squirrel most often inhabits burrows which it constructs, but may occasionally inhabit pocket gopher burrows (Davis and Schmidly, 1994). No mound of earth is evident at the entrance to a burrow, and a burrow may have more than one entrance. Burrows enter the ground at an angle of from 30 to 50 degrees and range in depth from 30 to 125 cm. Females build a brood chamber as an offshoot of the main tunnel. The brood chamber is spheroid in shape and contains a nest of grasses, leaves, and twigs (Young and Jones, 1982). The nesting material is removed to a sleeping chamber and the brood chamber is filled in with soil after the young leave the burrow. Males, immature animals, and nonbreeding females simply enlarge a part of the main tunnel to utilize as a sleeping area (Young and Jones, 1982). Each individual may utilize a home burrow and several surrounding refuge burrows (Young and Jones, 1982). Burrows may be located at the base of mesquite bushes, prickly pear, or other vegetation, or may be found in the middle of grassy plots, or between the vehicle tracks of little-used dirt roads (Young and Jones, 1982).

The Mexican ground squirrel is rather colonial in habit, but tends to be asocial except during the breeding season (Young and Jones, 1982). Home dens are actively defended, and *S. mexicanus* will drive conspe-
specifics from the vicinity of its home den if they approach too closely. Dens are inhabited by solitary individuals, except for a female with young. Home ranges seldom exceed 90 m in diameter and are generally half that size (Young and Jones, 1982; Davis and Schmidly, 1994).

The breeding season is believed to begin in March and April in Texas (Davis and Schmidly, 1994). Social hierarchies related to breeding privileges are probably established between males during the breeding season, as they are in the thirteen-lined ground squirrel (Wistrand, 1974). Length of gestation is not definitely known, but is estimated to be approximately 30 days (Davis and Schmidly, 1994). Females captured in the month of May from the Edwards Plateau carried from two to 10 embryos, with the most common number being six.

The Mexican ground squirrel is known to hybridize with the thirteen-lined ground squirrel within an area of sympatry in western Texas and southeastern New Mexico (Cothran, 1983). These two species of ground squirrels are morphologically distinct, but they have similar karyotypes and a high genetic similarity index (Cothran, 1983; Cothran and Honeycutt, 1984). Possible hybrids have been identified from populations in Taylor and Travis counties on the northern and eastern margins of the Edwards Plateau, but may be the result of hybrid individuals dispersing into established populations of S. mexicanus in these areas (Cothran, 1983). Where hybrids occur, they are always associated with populations of S. mexicanus. All gene flow from hybrids may be into populations of the Mexican ground squirrel in areas of sympatry (Cothran, 1983).

The subspecies of Mexican ground squirrel on the Edwards Plateau is S. m. parvidens Mearns, 1896. Yancey et al. (1993) found Mexican ground squirrels from Kimble County and other parts of the south-central Edwards Plateau to be sexually dimorphic with regard to size. Males are larger than females in most cranial characters. Average external measurements of 19 males and 19 females (Yancey et al., 1993), respectively, are: total length, 327.4, 313.9; tail length, 125.3, 120.9; length hind foot, 43.1, 42.8; ear length, 12.3, 11.5. Selected mean cranial measurements of adult male and female S. mexicanus from the Edwards Plateau, respectively, are: greatest length skull, 47.20, 45.20; zygomatic breadth, 28.77, 27.63; postorbital constriction, 12.85, 12.90; interorbital constriction, 10.43, 9.79; mastoid breadth, 21.78, 20.99; length maxillary toothrow, 8.64, 8.50; breadth across upper molars, 12.01, 11.74 (Yancey et al., 1983).

**Specimens examined (244).—Callahan Co.: 14 475400E, 3554200N, 1 (MWSU). Coke Co.: 14 347200E, 3546500N, 1 (ASNHC); 14 337400E, 3515500N, 1. Comal Co.: 14 552900E, 3290300N, 1 (TNHC). Crane Co.: 13 751700E, 3476300N, 1. Crockett Co.: 14 273700E, 3399300N, 1 (TNHC); 14 289100E, 3398500N, 1. Gillespie Co.: 14 512400E, 3349500N, 4. Hays Co.: 14 602100E, 3306200N, 2 (SWTU). Howard Co.: 14 260900E, 3576600N, 2 (ASNHC); 14 267200E, 3558800N, 1. Irion Co.: 14 296200E, 3475400N, 1 (ASNHC); 14 288300E, 3445900N, 1; 14 292600E, 3438000N, 1. Kerr Co.: 14 486100E, 3324700N, 6 (3 TTU, 3 TNHC). Kimble Co.: 14 444900E, 3393800N, 1; 14 433700E, 3379400N, 1; 14 407300E, 3372700N, 1 (TCWC); 14 425500E, 3372800N, 13; Junction City Park, 6; 14 427000E, 3372800N, 1; 14 425400E, 3372000N, 85 (74 TTU, 11 MWSU); 14 425400E, 3372800N, 3; 14 425700E, 3371800N, 7; 14 425800E, 3372500N, 11; 14 425700E, 3372100N, 1; 14 430900E, 3368200N, 1; 14 437800E, 3364900N, 1 (TCWC). Kinney Co.: Unspecified Locality, 1 (SWTU). Mason Co.: 14 455100E, 3401100N, 1 (SWTU); 14 477900E, 3401100N, 6; 14 477900E, 3399500N, 4; 14 477900E, 3396300N, 8; 14 480300E, 3397100N, 9; 14 464800E, 3391200N, 1 (ASNHC). McCulloch Co.: 14 448300E, 3454400N, 1. Medina Co.: 14 462100E, 3324400N, 1 (TNHC). Menard Co.: 14 424900E, 3420000N, 1; 14 4428700E, 3420000N, 1 (SM). Midland Co.: Unspecified Locality, 2 (SM); 13 764900E, 3513100N, 1. Nolan Co.: 14 368000E, 3592800N, 1 (MWSU); 14 345700E, 3569600N, 2. Reagan Co.: 14 266600E, 3503900N, 1; 14 266600E, 3498700N, 1; 14 266600E, 3480500N, 1; 14 250200E, 3457000N, 1 (SM). Runnels Co.: Hwy. 158 (Unspecified Locality), 1 (WTAM). Sterling Co.: 14 3121000E, 3524000N, 1. Sutton Co.: 14 342200E, 3382600N, 7. Taylor Co.: South Abilene (Unspecified Locality), 1 (MWSU). Tom Green Co.: 14 335100E, 3506100N, 1 (ASNHC); 14 353100E, 3490000N, 2 (ASNHC); 14 345400E, 3460200N, 1. Travis Co.: 14 622000E, 3351500N, 3 (2 TTU, 1 TNHC); Barton Greenbelt in Austin, 12 (MWSU); Zilker Park, Austin, 3 (TNHC); Potter Ranch (Unspecified Locality), 1 (SWTU). Upton Co.: 14 225900E, 3457800N, 1; 13 7651000E, 3447300N, 6. Val Verde

*Spermophilus spilosoma*
Spotted Ground Squirrel

**Distribution.**— The spotted ground squirrel ranges from central Mexico northward through southeastern Arizona, most of New Mexico, and the western one-third of Texas. The range of this species extends northward through western Oklahoma, Kansas, Nebraska, and into southwestern South Dakota. The spotted ground squirrel is found also in southeastern Wyoming, eastern Colorado, southern Utah, and northern Arizona.

The spotted ground squirrel has been collected only from Crane, Glasscock, Howard, Reagan, and Val Verde counties on the Edwards Plateau (Fig 55). This species of ground squirrel seems to be uncommon and restricted to the western portion of the region.

*Spermophilus spilosoma* is a rather small ground squirrel, usually smaller in external measurements than the more common *S. mexicanus*. The dorsum is a cinnamon or pinkish-red color. Faint, squarish, white spots are irregularly spaced over the dorsum; as opposed to the distinct, round, patterned white spots of *S. mexicanus*. The venter is white in color. The tail is short and well-haired. Ears are short and eyes are rather large. The appendages are short and internal cheek pouches are present.

Preferred habitats are areas with dry, sandy soils; usually close to rocks or brush. Vegetation is usually sparse where these squirrels are collected (Streubel and Fitzgerald, 1978). The spotted ground squirrel is sometimes associated with prairie dog towns in an area, as is *S. mexicanus*. Disturbed areas along highways and roads also are utilized by *S. spilosoma*, as well as areas along the sides of arroyos. Overgrazed pastureland also is favorable habitat for the spotted ground squirrel.

**Diet of S. spilosoma** is primarily granivorous and herbivorous. Various grass seeds and the seeds of forbs, such as croton, are eaten by *S. spilosoma*. Selection probably depends a great deal upon what plants are available in a particular area. Insects are included in the diet during times of abundance, as are green grass shoots as they sprout in early spring (Streubel and Fitzgerald, 1978). The spotted ground squirrel has also been observed feeding upon lizards and kangaroo rats.

Burrows are constructed as habitats by the spotted ground squirrel. Burrows are usually dug to a depth of approximately 45 cm and may extend up to 3.5 meters or more in length (Jones et al., 1983). A spherical chamber lined with grass at the end of the burrow serves as the nest chamber. Save for females and their offspring, burrows are usually occupied by only a single ground squirrel. *S. spilosoma* is diurnal in activity, but usually stays inside its burrow during the hottest part of the day, or during cooler, inclement weather.

These squirrels store fat in the autumn months and undergo an incomplete hibernation during the winter months. Young animals seem to be more active than adults during winter months (Jones et al., 1983). *S. spilosoma* also may aestivate during hot, dry periods.

The breeding habits of *S. spilosoma* are not well-known. Males appear to be polygamous. Two litters a year may be born in the southern parts of this species’ range. The usual litter size is five to seven young. Parturition takes place in the spring and again in the late summer after a gestation period of about 28 days (Jones et al., 1983).

Two subspecies of spotted ground squirrel are reported for the Edwards Plateau. *S. s. annectens*, Merriam, 1893 in the extreme southwestern Edwards Plateau in Val Verde County, and *S. s. marginatus* Bailey, 1890 in the remainder of the region. No sexual dimorphism is evident in this species. External measurements of a male from Glasscock County are: total length, 250; tail length, 85; length hind foot, 34; ear length, 5. Average external measurements of eight male...
specimens from north-central Texas (Dalquest and Horner, 1984) are: total length, 245; tail length, 70.1; length hind foot, 33.2; ear length, 9.2. Selected cranial measurements of the Glasscock County specimen are: greatest length skull, 40.44; length nasals, 14.47; interorbital breadth, 8.32; zygomatic breadth, 24.15; mastoid breadth, 19.16; bullar length, 9.98; bullar breadth, 6.17; length maxillary toothrow, 7.90.


Additional Records.—Val Verde Co.: 14 328700E, 3310800N (Personal Communication, T. L. and Doris Zorn); 14 270500E, 3287500N (Hall, 1981).

*Spermophilus variegatus*
Rock Squirrel

Distribution.—The rock squirrel ranges from central Mexico northward to central Texas, and westward through Trans-Pecos, Texas, Colorado, Arizona, and southern California. This species is excluded from all except the far western Llano Estacado (Choate, 1991). The rock squirrel ranges northward onto the panhandle of Oklahoma, and into Colorado, Utah, and Nevada.

The rock squirrel ranges throughout most of the Edwards Plateau. Rock squirrels are found at least as far north as Coke (between the Edwards Plateau and Callahan Divide) and Crockett counties. Records are available from Bandera, Blanco, Comal, Crockett, Edwards, Gillespie, Hays, Kendall, Kerr, Kimble, Llano, Mason, San Saba, Schleicher, Sutton, Tom Green,
Travis, Uvalde, and Val Verde counties on the Edwards Plateau (Fig. 56).

*Spermophilus variegatus* is a large squirrel with solid black or brownish coloration extending from the head to between the shoulders. The posterior portions of the animal’s dorsal and lateral sides are gray, with small white spots. Pelage color, however, is quite variable throughout the range of this species. The tail is rather long and bushy and is carried along the ground when the squirrels are running. Claws are non-retractile and well developed, and large, internal cheek pouches are present. The rock squirrel is sympatric throughout its range on the Edwards Plateau with the Mexican ground squirrel, and to the west with the spotted ground squirrel, but cannot easily be mistaken for either of these species. *S. variegatus* is much larger than Mexican and spotted ground squirrels, occupies different habitats, and pelage color differs between the three species.

Rock squirrels are saxicolous animals; they are found on rocky slopes and hills throughout their range on the Edwards Plateau. These animals have been observed foraging underneath pecan trees at the Texas Tech University Center at Junction at a considerable distance from rocky habitat. They quickly climb trees when startled. Rock squirrels tend to be absent from open plains, wide valley areas, and deserts (Oaks et al., 1987).

Rock squirrels feed upon a variety of vegetation and insects. Diets are seasonally variable depending upon local availability of food sources. Rock squirrels are known to catch and eat small, wild turkeys and other birds (Davis and Schmidly, 1994). Other diet items include nuts, seeds, grain, berries, roots, and green vegetation. Rock squirrels prefer the reproductive parts of plants, if the plants are in flower or fruit, rather than the leaves and stems (Oaks et al., 1987). Mesquite beans, acorns, yucca fruits, cactus fruits, and ragweed tops are utilized as food. Rock squirrels can survive for extended periods of time on diets of succulent foods with no additional water (Oaks et al., 1987). The rock squirrel is active diurnally. Most activity is during the morning and late afternoon hours, but activity period varies according to season. Temperature, wind speed, and rain affect activity periods of *S. variegatus*. Rock squirrels are not active at temperatures below 15°C, in high winds, or heavy rains.

Rock squirrels inhabit burrows. Burrows may be located under large rocks, bushes, trees, or other cover with prominent observation points nearby (Oaks et al., 1987). Burrows may also be excavated underneath buildings and other structures, and rock squirrels occasionally den in trees. Burrows are shallow and are usually short. There is one main tunnel with one to three openings to the outside and a connecting nest chamber (Oaks et al., 1987). Feces are deposited in a latrine tunnel near the nest chamber. Burrows are lined with dried grass, leaves, bark, and seed pods (Oaks et al., 1987). Adults have a home burrow and auxiliary burrows that are used while foraging (Oaks et al., 1987).

Rock squirrels are facultative hibernators. In central Texas, *S. variegatus* hibernates from two to four months, in November to February or March (Oaks et al., 1987). Fat is deposited, and rock squirrels also may store food for winter use. Females generally emerge from hibernation in the spring earlier than males (Oaks et al., 1987).

Populations of rock squirrels tend to be colonial and are organized as maternal aggregations. Colonies consist of breeding females and a dominant male; several subordinate males occupying peripheral areas of the colony (Johnson, 1981). Home ranges are large and much overlap is found within a colony of rock squirrels; home ranges average 0.40 ha for dominant males and 0.15 ha for females (Johnson, 1981). The home ranges of males increase during the breeding season. Females become more territorial during periods of lactation and decrease the size of their home ranges (Johnson, 1981). Many juveniles disperse from the home den in late summer or early fall, and yearlings may disperse from the maternal home range in the spring (Oaks et al., 1987).

Males become capable of breeding after emerging from hibernation. Males are probably polygamous, and breeding territories are actively defended against intruding males (Johnson, 1981). Breeding season extends for about six weeks in March and April in Texas (Oaks et al., 1987). The gestation period is not known for this species. One litter is produced per year. The young are born in late spring and emerge from burrows from the end of May to mid-August. The number of young in a litter ranges from one to seven with an average of four (Oaks et al., 1987).
Two subspecies of rock squirrel are found on the Edwards Plateau. *S. v. buckleyi* Slack, 1861, on the eastern and central Edwards Plateau, and *S. v. grammurus* (Say, 1823) on the far western Edwards Plateau in Crockett and Val Verde Counties. Males are larger than females, but sexual size variation has not been studied extensively in this species. Average external measurements of three individuals (two males and one female) are: total length, 508; tail length, 233; length hind foot, 61; ear length, 27. Selected mean cranial measurements of four adult females are: greatest length skull, 62.90; zygomatic breadth, 39.19; interorbital constriction, 14.98; length nasals, 21.56; breadth rostrum, 11.52; mastoid breadth, 27.61; length maxillary toothrow, 12.05.

Specimens examined (93).—Bandera Co.: 5 mi. S on Park Rd., off Hwy. 16, 1 (SWTU); 14 456900E, 3318400N, 2 (TNHC). Blanco Co.: 14 558700E, 3324200N, 2. Comal Co.: 14 584700E, 3289000N, 1 (SUTW). Crockett Co.: 14 243400E, 3395600N, 1. Edwards Co.: 14 383900E, 3302900N, 1. Hays Co.: 14 587400E, 3347400N, 1 (SUTW); 14 577600E, 3340000N, 1 (SUTW); 14 587400E, 3318600N, 1 (SUTW); 14 599200E, 3306100N, 1 (SUTW). Kendall Co.: 14 524000E, 3320600N, 1; 14 535200E, 3316200N, 1 (SUTW). Kerr Co.: 14 448200E, 3326000N, 1 (WTAM); 14 489900E, 3324700N, 1 (TNHC); 14 502200E, 3329000N, 1 (TNHC). Kimble Co.: 14 422500E, 3374500N, 1; 14 455500E, 3372900N, 1; 14 395400E, 3372000N, 1; 14 407400E, 3372800N, 1 (MWSU); 14 416500E, 3372700N, 1; 14 418000E, 3372900N, 1 (MWSU); 14 427100E, 3372800N, 1; 14 427800E, 3372900N, 1; 14 425400E, 3372000N, 1; 14 437600E, 3372600N, 9 (MWSU); 14 432800E, 3372500N, 3 (MWSU); 14 443400E, 3372800N, 3 (MWSU); 14 423400E, 3372000N, 1;

Figure 56. Distribution of *Spermophilus variegatus* on the Edwards Plateau.
14 427000E, 3371600N, 1; 14 425400E, 3371600N, 2; 14 425500E, 3371400N, 1; 14 423900E, 3372000N, 1; 14 425600E, 3369700N, 1; 14 426700E, 3366800N, 1. Llano Co.: 14 516400E, 3402200N, 1 (TNHC); 14 555800E, 3401100N, 5 (WTAM); 14 518100E, 3388700N, 1 (SM). Mason Co.: 14 475800E, 3443400N, 1 (ASNHC); 14 461300E, 3401200N, 1 (ASNHC); 14 464400E, 3401400N, 2 (SWTU). San Saba Co.: San Saba River (Unspecified Locality), 1 (SM). Schleicher Co.: 14 332000E, 3415200N, 1. Sutton Co.: 14 342300E, 3388800N, 1; 14 318400E, 3382600N, 1 (MWSU); 14 342200E, 3382500N, 2; 14 344200E, 3380500N, 1; 14 365700E, 3361700N, 1 (MWSU). Tom Green Co.: 14 336900E, 3502500N, 1 (SM). Gillespie Co.: Unspecified Locality. Kerr Co.: 14 434300E, 3337500N (TCWC); 14 460100E, 3326100N (TCWC); 14 486100E, 3324800N (TCWC); 14 483200E, 3324800N (TCWC). Uvalde Co.: Unspecified Locality. Val Verde Co.: 14 336200E, 3310700N, 1; 14 306600E, 3315400N, 3; 14 328800E, 3310700N, 1; 14 305600E, 3271600N, 1 (MWSU).


**Cynomys ludovicianus**

Black-tailed Prairie Dog

**Distribution.**—The black-tailed prairie dog ranges from southeastern Arizona eastward through much of southern and eastern New Mexico and into Trans-Pecos, Texas. The black-tailed prairie dog ranges into west-central Texas and throughout the panhandle area of Texas northward through parts of all of the Great Plains states and into southern Saskatchewan, Canada.

Bailey (1905) mapped the previous range of the black-tailed prairie dog throughout the western half of the Edwards Plateau, extending as far east as eastern Mason County. As a result of habitat losses and extermination programs since the early part of the twentieth century, the range of this species has been much reduced on the Edwards Plateau, and only scattered populations remain (Fig. 57). Specimens are available from Crockett, Glasscock, Howard, Midland, Reagan, Sutton, and Tom Green counties. Davis and Schmidly (1994) list additional records from Bexar, Coke, Mason, Schleicher, Taylor, and Upton counties. Save for the Bexar County (Allen, 1896) and Mason County (Bailey, 1905; TCWC) records, the source of Davis and Schmidly's records is unknown to me. Simpson and Maxwell (1989) collected no prairie dogs in their study of the mammalian fauna of Coke County, and opined that the species may no longer occur in that area.

**Cynomys ludovicianus** is the largest ground squirrel that occurs on the Edwards Plateau. Pelage is tan in color dorsally and grizzled with buff and black. The venter is white to buffy white, and the body is short and stocky. The ears are short and rounded and the tail is short, with a black terminal tip. The front feet have well-developed claws to aid in burrowing; a tuft of hair is found in the center of the palm. The head is broad and rounded, and the eyes are moderately large.

The black-tailed prairie dog is most common in plains grassland areas throughout its range. Deep soils for the construction of burrows and open, grassy areas are the most preferred habitats. Overgrazed or denuded pastureland provides good habitat for *C. ludovicianus*.

Black-tailed prairie dogs are herbivorous in diet. Various grasses and forbs constitute the food of this species. Plants are selected from locally available sources. Prairie dogs may prove beneficial during normal years by removing many species of shrubs and other successional forbs from rangeland. However, during years of drought, grazing pressure of both livestock and prairie dogs may completely denude an area of vegetation (Jones et al., 1983). The black-tailed prairie dog is not known to store food in its burrow system, and, aside from remaining below ground during adverse weather, is active throughout the year.

Prairie dogs are highly gregarious, and are diurnal in activity. *C. ludovicianus* inhabits an area termed a "town" with numerous others of its kind. Large colonies may be divided into smaller units called "wards" wherein one to many social groups or "coteries" may exist (Jones et al., 1983). Members of a coterie defend a territory from the encroachment of prairie dogs from a different coterie. Communication within a prairie dog town is carried out by a series of different calls, growls, chirps, screams, and tooth-chattering sounds. Alarm
calls are given if a threat is perceived, and all prairie dogs close to the alarm immediately seek shelter within a burrow. Towns vary from a few individuals inhabiting a small area to many prairie dogs covering an expansive area. Bailey (1905) wrote of a prairie dog town that extended from San Angelo to Clarendon, Texas, and covered approximately 25,000 square miles. Towns of this size are found no more within Texas.

Prairie dogs dig extensive, deep, and permanent burrows (Hoffmeister, 1986). Some burrows may descend vertically more than four meters before leveling off. Nest cavities are located in the deeper parts of the burrow system. A dome-shaped mound is formed at the burrow entrance from excavated soil brought to the surface. Nest chambers are lined with dry grasses and other vegetation. Vegetation between the burrow entrances and within the prairie dog colony is removed by C. ludovicianus by clipping at the base of the plants. This affords a clear, unobstructed view of the area. Females nursing young defend their burrows against other members of the coterie until the pups have been weaned and appear aboveground (Jones et al., 1983).

A single litter of young is produced annually. The young are usually evident aboveground in March and April, depending upon location within the range of C. ludovicianus. Litter size usually ranges from four to five young, however, as many as 10 young have been reported per litter (Jones et al., 1983).

The subspecies of black-tailed prairie dog on the Edwards Plateau is C. l. ludovicianus (Ord, 1815). Average external measurements of two males from Mason County are: total length, 386.5; tail length, 76.5; length hind foot, 63; ear length, 9. Selected mean cr-
nial measurements for these same individuals are: greatest length skull, 65.10; nasal length, 23.92; least interorbital breadth, 14.0; zygomatic breadth, 46.91; cranial breadth, 26.59; length maxillary toothrow, 16.26; buellar breadth, 13.0; cranial depth, 27.54.


**Sciurus carolinensis**

Eastern Gray Squirrel

**Distribution.**—The range of this tree squirrel is centered in the southeastern United States. The western limits of the range extend from eastern Texas, northward to the borders of the Canadian provinces of Saskatchewan, Manitoba, Ontario, and Quebec. Eastern limits extend from Maine in the northeast, southward to Florida.

The gray squirrel has been reported to occur in Hays County of the Edwards Plateau at the extreme western limits of its range (Goodrum, 1961). Aside from this unverified literature record, no specimens of the gray squirrel exist from the Edwards Plateau (Fig. 58). The former range of the species may have included the region immediately west of the Balcones Fault, especially along river bottoms and other drainage systems of the Edwards Plateau, but early researchers and residents make no mention of the species within the region (Allen, 1896; Bailey, 1905).

**Sciurus carolinensis** resembles the fox squirrel (*S. niger*) in external form, but the gray squirrel is smaller in size. The form is squirrel-like and so familiar as to warrant little description. Ears are rather prominent and brownish in color, and the overall dorsal color is gray. The venter, chin, and lateral margins of the rather long, bushy tail are white in color. As opposed to these characters, the venter of the fox squirrel is a rusty, orange color and the dorsum is ferruginous to tan in color. A white eye ring is evident in *S. carolinensis*, and the gray squirrel has an extra, peglike upper premolar that is absent in the fox squirrel.

The gray squirrel occurs in mature forest habitats. This species usually is found in bottomlands of eastern Texas, and would be expected to occur in such habitats on the Edwards Plateau. Dense vegetation with good canopy closure, Spanish moss, grapes, and a variety of hardwood, mast-producing trees provide excellent habitat for gray squirrels (Goodrum, 1961; Lowery, 1974).

*S. carolinensis* is granivorous and frugivorous in dietary habits. Acorns, pecans, and other mast crops are the primary diet items. In some areas, acorns alone comprise as much as 59 percent of the diet (Goodrum, 1961). Other known diet items include seeds from grasses and forbs, grapes, mulberry, elm, and yaupon fruits. The gray squirrel consumes a small amount of animal matter in its diet, as do most other sciurids. Animal foods include insects and insect larvae, frogs, lizards, and bird eggs (Goodrum, 1961; Jones et al., 1983). The gray squirrel also gnaws on shed deer antlers and other animal bones, probably to obtain calcium and other minerals in its diet. Gray squirrels are diurnal in activity and conduct most foraging during crepuscular hours (Lowery, 1974). *S. carolinensis* usually is not as active during the middle of the day as are the fox squirrel and ground squirrels (Jones et al., 1983).

Gray squirrels may den either in tree cavities, at the base of trees, in hollow logs, or in nests in the canopy. Nests are utilized more during summer months when tree cavities are unavailable or become infested with ectoparasites. Nests are constructed of interwoven branches and leaves of trees and are roughly spherical in shape. The nest is located in the bole of a tree or is constructed within the tree’s terminal branches (Goodrum, 1961).

These squirrel horde mast and other food during the summer and fall months, and deposit body fat during these seasons. Several food caches are scattered throughout the home range area of a squirrel. The nuts
are usually buried, but may occasionally be cached in hollow trees. The caches are located subsequently by owners by smell. Gray squirrels are active throughout the year, but may become lethargic and remain inside dens and nests during cold periods of the winter months, sometimes for several consecutive days.

Gray squirrels are solitary in nature, with a single squirrel usually inhabiting each nest or tree den within an area (Jones et al., 1983). Home ranges are centered around the nest, but there is considerable overlap between the home ranges of individuals in a particular habitat. *S. carolinensis* is tolerant of conspecifics when foraging, and only the immediate area around the nests is defended actively (Riege, 1991). Home ranges of males are 2.1 times those of females (Koprowski, 1994a). Large-scale movements involving many individuals have been recorded for *S. carolinensis*, probably due to food shortages, overpopulation, and other factors (Koprowski, 1994a). However, the core area of activity for the gray squirrel is usually no more than two acres (Goodrum, 1961).

Breeding season of *S. carolinensis* extends throughout the year, but two peaks occur in the fall and summer months. The peak periods occur in January to February and May to June. Males are polygamous breeders, and several males may pursue an estrous female (Jones et al., 1983). The gestation period is approximately 40 to 45 days in length (Koprowski, 1994a). Two litters may be produced each year and range in size from one to eight young. Sexual maturity is attained in the first year of life.

The subspecies on the Edwards Plateau is *S. c. carolinensis* Gmelin, 1788. No sexual dimorphism is evident in *S. carolinensis*. Average external measure-
ments (Schmidly, 1983), are: total length, 448; tail length, 209; length hind foot, 60; ear length, 24.

Specimens examined (0).

Additional records.— Hays Co.: Unspecified Locality. (Goodrum, 1961).

Sciurus niger
Eastern Fox Squirrel

Distribution.— The fox squirrel ranges from northeastern Coahuila and northern Neuvo Leon and Tamaulipas, Mexico, northward throughout most of the eastern conterminous United States, west to the Great Plains states. The fox squirrel is absent in New England and much of the northern Great Lakes region (Jones et al., 1983). Fox squirrels have extended their range westward along riparian forests and woodlands, and have utilized shelterbelts, orchards, and tree plantations to extend their range (Koprowski, 1994b). This species also has been introduced in many urban and other areas where it was previously excluded.

The fox squirrel ranges throughout the eastern two-thirds of Texas (Schmidly, 1983). This species' original range included all but the northwestern portion of the Edwards Plateau. Records are available from Bandera, Bexar, Blanco, Coke, Coleman, Comal, Concho, Crockett, Edwards, Gillespie, Hays, Kendall, Kerr, Kimble, Kinney, Llano, Mason, Medina, Menard, Real, San Saba, Sutton, Tom Green, Travis, Uvalde, and Val Verde counties (Fig. 59).

Sciurus niger is a familiar mammal on the Edwards Plateau. These medium-sized, reddish-colored squirrels are easily recognized. The tail is long and bushy, but unlike the rock squirrel, is carried more upright and partially over the back when running or foraging. The ears are rather short and resemble those of S. variegatus, but because of differences in coloration and habitat preferences, these species are rarely confused. The eastern fox squirrel has rusty-brown dorsal fur and an orange or dirty-white colored venter, whereas the dorsum of the gray squirrel (S. carolinensis) is a salt-and-pepper gray and the venter is white. The lateral border of S. niger's tail is edged with buffy-brown fur, whereas the tail of S. carolinensis is edged with white. The eastern fox squirrel has only a single upper premolar, whereas the gray squirrel often has two upper premolars.

The eastern fox squirrel is a resident of open woodlands and bottomland riparian areas along streams and rivers. These squirrels are also at home in edge habitats between open prairie and oak woodlands (Flyger and Gates, 1982). In marginal habitats, fox squirrels may travel long distances across meadows and fields to reach foraging areas (Jones et al., 1983). Motts of live oak and other tree species in the valleys of the Edwards Plateau also are favored habitats of S. niger. The eastern fox squirrel prefers a more open canopy structure than the gray squirrel, and S. niger is usually absent or rare in mature forests (Flyger and Gates, 1982).

The eastern fox squirrel is primarily a vegetarian, and is an opportunistic forager (Flyger and Gates, 1982). S. niger feeds upon a wider variety of items than does the gray squirrel (Jones et al., 1983). The fox squirrel's diet includes pecans, acorns, flowers, osage orange fruits, other fruit crops, bark, and other vegetation (Flyger and Gates, 1982; Jones et al., 1983; Koprowski, 1994b). Arthropods and bird eggs also are included in the diet (Flyger and Gates, 1982; Jones et al., 1983). Water needs are met by consumption of succulent food materials, however, during years of drought, an adequate water supply is essential (Flyger and Gates, 1982). The fox squirrel is arboreal in habit, but also spends a considerable amount of time foraging and moving about upon the ground (Jones et al., 1983). Fox squirrels are active during daylight hours. Activity begins an hour or more after sunrise, decreases by mid morning, and resumes again for a period of time around midday (Sealander and Heidt, 1990). Another period of activity occurs in the late afternoon before sunset. During the spring and summer months, fox squirrels are the most active during the morning hours (Baker, 1944). Fox squirrels become inactive and remain in their nests during periods of inclement weather (Sealander and Heidt, 1990), but are otherwise active throughout the year.

Fox squirrels occupy both tree dens and construct nests of leaves and twigs in the branches of trees. If the number of suitable tree dens is limited within an area, S. niger constructs more leaf nests (Baker, 1944). Leaf nests are utilized more frequently during the summer months (Baker, 1944). More than one tree den and leaf nest may be utilized within an individual's home range (Jones et al., 1983).
Figure 59. Distribution of *Sciurus niger* on the Edwards Plateau.

Home ranges tend to be elliptical in shape instead of circular, and are three-dimensional rather than two-dimensional like those of strictly terrestrial mammals (Jones et al., 1983). Habitat quality, population density, sex and age composition of a fox squirrel population, and food availability are all factors that help to determine the overall size of a home range. The home ranges of males tend to be larger than those of females (Flyger and Gates, 1982).

Fox squirrels are rather solitary in habit (Jones et al., 1983). These squirrels maintain a discrete spacing distance from conspecifics when feeding at a concentrated food source (Flyger and Gates, 1982). A definite social hierarchy exists within populations of fox squirrels, and dominant individuals will drive off subordinate squirrels that approach too close to a den or feeding station (Flyger and Gates, 1982). Males are generally dominant over females within a fox squirrel population. These squirrels are very vocal and often chatter and bark at intruders or disturbances within their territories. Young animals will also emit loud screaming calls that may cause their mother to investigate the cause of their distress (Flyger and Gates, 1982).

Fox squirrels mate in January and February and again in May and June. Males are polygamous in mating habit, and several males may pursue an estrous female for an extended period of time before the dominant male mates with her (Baker, 1944). The gestation period is approximately 45 days in length. Most females produce four offspring each year (Davis and Schmidly, 1994). The number of offspring produced is dependent upon food resources within an area and other factors (Flyger and Gates, 1982). Fox squirrels mature more slowly than most rodents (Flyger and Gates, 1982);
sexual maturity is not attained until the young are approximately 11 months of age.

The subspecies of fox squirrel occurring on the Edwards Plateau is *S. n. limitus* Baird, 1855. Sexual dimorphism is not significant in *S. niger* (Moncrief, 1993). Average external measurements of ten adults (seven females and three males) from the Edwards Plateau are: total length, 462.3; tail length, 208.7; length hind foot, 61.5; ear length, 27.6. Selected mean cranial measurements of these same individuals are: greatest length skull, 59.99; zygomatic breadth, 34.22; interorbital constriction, 18.33; length nasals, 19.96; length maxillary toothrow, 10.39; width across molars, 14.19; length auditory bullae, 10.46; breadth auditory bullae, 9.66.

*Specimens examined* (148).—*Bandera Co.*: 14 466200E, 3292300N, 1 (TNHC). *Blanco Co.*: 14 362100E, 3521400N, 1. *Coleman Co.*: 14 445600E, 3539100N, 1 (TNHC); 14 447700E, 3521900N, 1. *Comal Co.*: 14 578500E, 3304100N, 1 (SWTU); 14 549700E, 3296400N, 1 (SWTU); 14 586600E, 3294400N, 1 (SWTU); *County Rd. 215, 1 mi. N FM 306, 1 (SWTU); 14 584600E, 3285500N, 1 (SWTU). *Concho Co.*: 14 419600E, 3461100N, 1; 14 419600E, 3429300N, 1. *Edwards Co.*: 14 382500E, 3303100N, 3. *Gillespie Co.*: 14 490700E, 3370400N, 1 (TNHC); 14 512700E, 3358600N, 1 (TNHC); 14 508400E, 3346900N, 1 (TNHC); 14 539500E, 3339600N, 1; 14 537000E, 3345000N, 1. *Hays Co.*: 14 583400E, 3347000N, 1 (SWTU); 14 581900E, 3340000N, 1 (TNHC); 14 593800E, 3306600N, 1 (SWTU); 14 600100E, 3306600N, 1 (SWTU); 14 600700E, 3306600N, 1 (SWTU); 14 602900E, 3305900N, 2 (SWTU); *Aquatic Station, SWTSU, 1 (SWTU); 14 587300E, 3318500N, 1 (SWTU); 14 602300E, 3306200N, 9 (SWTU); 14 597300E, 3300700N, 1 (SWTU). *Kendall Co.*: 14 523900E, 3319200N, 3; 14 529500E, 3318900N, 1 (SWTU); 14 527100E, 3310100N, 1 (SWTU). *Kimble Co.*: 14 400100E, 3391100N, 1; 14 417100E, 3397400N, 1; 14 428500E, 3373500N, 6; 14 425500E, 3372800N, 8; 14 418000E, 3372800N, 1; 14 428200E, 3372800N, 1; 14 436000E, 3372800N, 2 (MWSU); 14 436800E, 3372800N, 1; 14 425400E, 3372000N, 3; 14 437600E, 3372800N, 6 (MWSU); 14 440500E, 3372800N, 4 (MWSU); 14 421200E, 3372500N, 2; 14 425500E, 3371300N, 4; 14 425500E, 3370500N, 1; 14 437500E, 3369300N, 3; 14 425500E, 3368200N, 3; 14 441800E, 3358800N, 3; 14 436100E, 3354400N, 1 (TCWC); 14 405000E, 3352600N, 1 (SWTU). *Llano Co.*: 14 527400E, 3402000N, 1 (TNHC). *Mason Co.*: 14 473300E, 3422800N, 1 (ASNHC); 14 464700E, 3401400N, 1 (SWTU); 14 448500E, 3401400N, 1 (SWTU). *Medina Co.*: 14 494600E, 3257000N, 1 (SWTU). *Menard Co.*: 14 394200E, 3410800N, 1. *Real Co.*: 14 400000E, 3298700N, 1; 14 426200E, 3288500N, 1. *Sutton Co.*: 14 342100E, 3382500N, 1; 14 363500E, 3359200N, 1 (MWSU). *Tom Green Co.*: 14 357700E, 3451900N, 1 (ASNHC); 14 357700E, 3450300N, 2; 14 357700E, 3444200N, 1 (ASNHC); 14 393200E, 3445400N, 2. *Travis Co.*: *Bee Cave Rd. (Unspecified Locality), 1 (SWTU); 14 621900E, 3351500N, 26 (6 SWTU, 20 TNHC); *Hwy. 2222 and Mt. Bannel, Austin, 1; *Hwy. 2222 and Dry Creek Rd., Austin, 1; 14 602900E, 3355100N, 1 (TNHC); *West 44 and Red River South, Austin, 1; 14 622000E, 3346800N, 1 (TNHC); 14 608500E, 3344800N, 1 (TNHC). *Uvalde Co.*: 14 402400E, 3263100N, 1. *Val Verde Co.*: 14 307500E, 3314700N, 2.

KEY TO GEOMYIDAE

1 Anterior surface of upper incisor with a single groove; total length usually 257 to 295 mm; feet blackish in color; transverse enamel plate only on first two upper molars ............................................................... Cratogeomys castanops

1' Anterior surface of upper incisor ungrooved or with two grooves; total length usually less than 25 mm; feet whitish in color ........................................................................ 2

2 Anterior surface of upper incisor ungrooved; total length usually 202 mm or less; claws on front feet relatively small (<10mm) ................................................................. Thomomys bottae

2' Anterior surface of upper incisor with two grooves; total length greater than 202 mm; claws on front feet longer than 10 mm .............................................................................. 3

3 Condylobasal length of skull averaging 43.03 mm; total length usually 250 mm or greater; found on the northern and western Edwards Plateau ......................................................... Geomys bursarius

3' Condylobasal length of skull averaging 38.76 mm; total length usually 230 mm or smaller; restricted to the east-central Edwards Plateau .................................................................................. Geomys texensis

Family Geomyidae—Pocket Gophers

Thomomys bottae

Botta's Pocket Gopher

Distribution.—Botta's pocket gopher ranges from Sinaloa and Nuevo Leon, Mexico, northward through central and northern Mexico and into the western and central United States. This pocket gopher is distributed from central and western Texas into western New Mexico, Arizona, and throughout most of California, northward to southwestern Oregon. Botta's pocket gopher ranges eastward into southern and central Nevada, western and southern Utah, and southern Colorado.

Botta's pocket gopher occurs throughout most of the Trans-Pecos region (Schmidly, 1977) and ranges through the western half of the Edwards Plateau at least as far east as Mason County (Wilkins, 1991). Records are available from Concho, Crane, Crockett, Edwards, Irion, Kerr, Kimble, Mason, Menard, Reagan, Schleicher, Sutton, Tom Green, Upton, Uvalde, and Val Verde counties (Fig. 60).

Thomomys bottae is the smallest pocket gopher that occurs in Texas. The dorsum of T. bottae is brown to tan colored; the venter is white. Appendages are short and stout, and claws are rather small when compared to other pocket gophers of the genera Cratogeomys and Geomys. Conspicuous, fur-lined cheek pouches are present. The tail is short and sparsely haired. Eyes and ears are reduced for fossorial existence. The upper incisors are ungrooved in this species of gopher, as opposed to a single groove in the upper incisors of pocket gophers of the genus Cratogeomys and two grooves in the upper incisors of pocket gophers of the genus Geomys. The feet of Thomomys and Geomys are white; whereas the feet of Cratogeomys are black in color.

Pocket gophers are limited in distribution on the Edwards Plateau by the presence of suitable soil conditions. Botta's pocket gopher can tolerate a wider range of soil types and soil conditions than pocket gophers of the genera Cratogeomys and Geomys (Lessa and Thaeler, 1989). Although T. bottae is able to successfully inhabit shallow, rocky soils, these pocket gophers are found mostly along riparian areas, in valleys, parks, and areas of cultivated land on the Edwards Plateau. Pocket gopher distribution on the Edwards Plateau, as a whole, is extremely patchy with isolated populations interspersed within the region (Dalquest and Kilpatrick, 1973).

Botta's pocket gopher is a herbivore. Pocket gophers are opportunistic foragers with seasonally variable diets. Succulent leaves and stems are consumed in the spring and summer months, and a greater percent-
age of roots and tubers are eaten in the winter months (Chase, Howard, and Roseberry, 1982). A variety of 
grasses, forbs, dandelion roots, clovers, prickly pear, 
cultivated crops, and other plants are included in the 
diet (Chase et al., 1982). There is some indication that 
burrowing and feeding activities of pocket gophers help 
to propagate some species of plants. Considerable dam­ 
age may be done to forage crops, such as alfalfa, if many 
*T. bottae* reside in a field. Because of their subterra­ 
nean habits, pocket gophers may be active at any time 
during the day or night. The average activity period is 
of short duration, but pocket gophers may be active as 
many as sixteen periods per day (Vaughan and Hansen, 
1961). Pocket gophers are active throughout the year, 
but reduce their activities during dry and hot periods. 
Burrowing activity also is reduced during the breeding 
season (Miller and Bond, 1960).

Pocket gophers live in burrow systems that they 
excavate. *T. bottae* makes extensive use of its incisors 
to loosen compact, rocky soils while digging a burrow 
(Lessa and Thaeler, 1989). Burrow systems consist of 
relatively shallow, foraging tunnels and deeper tunnels 
that lead to a nest chamber and food storage chambers. 
Depth of the burrows varies with soil conditions in an 
area. Burrows may range from less than 30 cm to 91 cm 
or more in depth (Hoffmeister, 1986). Burrow exits 
are plugged with soil and rarely left open. Nests in the 
deeper tunnels are spherical in shape and are made from 
dried grasses (Chase et al., 1982). Enlarged chambers 
may be found in the shallower tunnel system and probably 
serve the animals as resting and feeding stations 
(Chase et al., 1982). Rejected foods and fecal material 
remain within the burrow system in tunnels that are usu­ 
ally plugged and abandoned by the occupant (Chase et 
al., 1982).
Pocket gophers lead solitary lives, except during brief periods of time while mating and while females raise young. Territories are established by *T. bottae* and are limited to the extent of its burrow system (Chase et al., 1982). In Arizona, burrows (and thus territories) of reproductive males average 60.2 m in length, and burrows of reproductive females average 27.9 m in length (Hoffmeister, 1986). Burrows tend to be shorter in areas of more optimal habitat (Hoffmeister, 1986). The burrows of reproductive males contact those of several females within an area (Hoffmeister, 1986). Pocket gophers have a pugnacious disposition toward both conspecifics and gophers of other species. Fighting occurs between gophers and is not ritualistic; fights often result in the death of one of the combatants (Chase et al., 1982). Young, dispersing animals often travel short distances above the surface of the ground and, thus, are most vulnerable to predation at this time (Hoffmeister, 1986).

Botta’s pocket gopher breeds mostly in the autumn and winter months in Texas (Davidow-Henry and Jones, 1988). Gravid females have been collected in the months of November, December, February, and March and subadult animals have been collected in March, April, and June on the Edwards Plateau. Males are polygamous in mating habitat. The gestation period of *T. bottae* ranges from eighteen to twenty-eight days (Findley, 1987). Whether more than one litter is produced per year is undetermined at present. Old females produce litters averaging five young (Davis and Schmidly, 1994). Factors known to affect the number of young per litter include size of the female, food availability, and elevation of habitat in the mountainous western regions (Chase et al., 1982).

Two subspecies of Botta’s pocket gopher occur on the Edwards Plateau; *T. b. limitaris* Goldman, 1936, just west of the Pecos River on the extreme western Edwards Plateau, and *T. b. confinalis* Goldman, 1936, throughout the remainder of the region. *T. bottae* is sexually dimorphic with males being significantly larger than females (Chase et al., 1982). Average external measurements of five adult female *T. b. limitaris* and seven adult female *T. b. confinalis*, respectively, are: total length, 199, 186.71; tail length, 57.4, 52.57; length hind foot, 26, 25; ear length, 6.4, 6. Selected mean cranial measurements of these same five female *T. b. limitaris* and ten female *T. b. confinalis*, respectively, are: cranylobasal length, 34.79, 33.36; zygomatic breadth, 21.65, 20.77; nasal length, 11.58, 11.00; rostral length, 13.45, 13.24; breadth rostrum, 7.10, 6.67; postorbital constriction, 6.39, 6.36; mastoid breadth, 17.15, 17.59; length maxillary toothrow, 6.86, 6.49.

**Specimens examined** (189).—Concho Co.: 14 396000E, 3445000N, 1; 14 409300E, 3436900N, 1 (TCWC). Crane Co.: 13 752300E, 3467500N, 3. Crockett Co.: 14 265900E, 3433100N, 1; 14 263200E, 3427300N, 1; 14 272000E, 3418900N, 1; 14 273900E, 3421900N, 1; 14 265700E, 3421800N, 1; 14 270300E, 3421800N, 2; 14 275500E, 3410800N, 1; 14 289500E, 3405400N, 3 (TCWC); 14 299300E, 3399400N, 1 (ASNHC); 14 264400E, 3326300N, 1; 14 282900E, 3399100N, 1; 14 290700E, 3399100N, 1; 14 299700E, 3399100N, 1; 14 289100E, 3386900N, 1. Edwards Co.: 14 348700E, 3349100N, 1 (MWSU); 14 388000E, 3420900N, 5 (MWSU); 14 383300E, 3317900N, 1 (MWSU). Irion Co.: 14 294100E, 3455000N, 1 (ASNHC); 14 294100E, 3452600N, 1 (ASNHC); 14 329000E, 3450900N, 1 (ASNHC); 14 292900E, 3451600N, 1; 14 286900E, 3445700N, 1; 14 292100E, 3445700N, 1; 14 292900E, 3443000N, 1 (MWSU). Kimble Co.: 14 440400E, 3393800N, 5 (MWSU); 14 442000E, 3393800N, 1 (MWSU); 14 444900E, 3391500N, 1; 14 444900E, 3390600N, 1; 14 443600E, 3390200N, 3; 14 442900E, 3389600N, 1; 14 448200E, 3390500N, 3 (MWSU); 14 439900E, 3390200N, 1 (MWSU); 14 442100E, 3388000N, 6 (MWSU); 14 444500E, 3389000N, 1 (MWSU); 14 438400E, 3389500N, 2 (MWSU); 14 441200E, 3386200N, 1; 14 438800E, 3382700N, 1 (MWSU); 14 437900E, 3381500N, 8 (MWSU). Menard Co.: 14 393800E, 3433000N, 1. Reagan Co.: 14 257600E, 3474100N, 1; 14 261000E, 3471900N, 1; 14 262400E, 3471100N, 3; 14 265700E, 3464700N, 1 (ASNHC); 14 265700E, 3464000N, 1; 14 265700E, 3456000N, 2 (ASNHC); 14 243100E, 3453500N, 1; 14 247500E, 3453500N, 1; 14 250600E, 3453500N, 1 (ASNHC); 14 253400E, 3453500N, 1 (MWSU); 14 261200E, 3453500N, 5; Salt Lake N of Best on road, 1 (ASNHC); 14 248700E, 3457000N, 1; 14 245200E, 3452400N, 1 (ASNHC); 14 272900E, 3451400N, 1 (ASNHC); 14 265700E, 3451900N, 1; 14 265700E, 3456000N, 1; 14 259200E, 3447500N, 1. Sutton Co.: 14 348700E, 3387200N, 1; 14 328700E, 3385900N, 1; 14 312100E, 3382600N, 6; 14 322700E, 3382600N, 1; 14 342100E, 3382600N, 1 (MWSU); Cemetary, Sonora, 7; Sonora Golf Course, 5; 14 352900E, 3382600N, 8 (TCWC); 14 343100E, 3381700N, 1; 14 342100E, 3379700N, 2; 14 344000E, 3380500N, 1; 14 342100E, 3379500N, 2; 14 342100E, 3378600N, 1; 14 342100E, 3378100N,
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1; 14 342100E, 3378000N, 1; 14 342100E, 3374900N, 2; 14 342100E, 3373300N, 1; 14 342100E, 3372900N, 1; 14 342100E, 3372800N, 1; 14 342100E, 3359200N, 3; 14 331700E, 3360200N, 1; 14 337900E, 3360200N, 1; 14 338000E, 3360200N, 1; 14 338400E, 3360200N, 2; 14 329400E, 3355200N, 6 (MWSU). Tom Green Co.: 14 357700E, 3451700N, 2 (ASNHC); 14 359600E, 3445500N, 2 (ASNHC); 14 357700E, 3444300N, 1 (ASNHC). Upton Co.: 13 773100E, 3466300N, 3; 13 771100E, 3454100N, 1; Schleicher Co.: 14 3321000N.

The plains pocket gopher ranges as far south as Coke County in river valleys, thence northward through western Colorado, Wyoming, southern South Dakota, and western North Dakota. The species ranges eastward throughout parts of Wisconsin, and Indiana, and south through portions of central and western Oklahoma.

The plains pocket gopher is limited in distribution to the northern margin of the Edwards Plateau. The species ranges as far south as Coke County in river valleys. Records are available from Howard, Nolan, and Runnels counties within the region (Fig. 61). The specimens from Coke County are from the Colorado River watershed area between the Callahan Divide and the Edwards Plateau.

*Geomys bursarius* is intermediate in size between *T. bottae* and *Cratogeomys castanops* of the Edwards Plateau. Botta’s pocket gopher is smaller in size and the yellow-faced pocket gopher is larger than *G. bursarius*. *Geomys bursarius* may be separated readily from the other two genera by the presence of two anterior grooves on the upper incisors. Botta’s pocket gopher has no anterior grooves; the yellow-faced pocket gopher has a single anterior groove on the upper incisors. The plains pocket gopher may be confused with the Llano pocket gopher (*G. texensis*) within the region. The Llano pocket gopher, however, is restricted to Gillespie, Kimble, Llano, and Mason counties, and thus is disjunct in range with the plains pocket gopher. The Llano pocket gopher also is smaller than *G. bursarius*.

The overall appearance of *G. bursarius* is as in *T. bottae*, with short, stocky appendages, a relatively short, sparsely haired tail, reduced ears, and external fur-lined cheek pouches. The incisors are yellow and prominent. Lips close behind the incisors and ears are valvular. The eyes are small and the skull is broad and flat in shape. The feet and venter are white in color, and the dorsum is chestnut to tan in color. The skin is relatively loose and pelage is short. The torso is rather elongate and tubular in shape.

The plains pocket gopher has perhaps the most specific substrate requirements of any species of pocket gopher on the Edwards Plateau. Soil types more than vegetation determine the distribution of this species. Clay soils, and stony, shallow soils are unsuitable for habitation. Soils that are poorly drained also are avoided by *G. bursarius* (Jones et al., 1983). Meadow areas, streamside and other alluvial areas, oldfields, and other areas of loamy or sandy soils provide suitable habitats for this species of pocket gopher. The plains pocket gopher had a more extensive distribution on the Edwards Plateau during the Pleistocene, but subsequent topsoil erosion within the area reduced the range of this species almost to the point of exclusion at the present time (Toomey et al., 1993).

The plains pocket gopher is herbivorous in diet. As in *T. bottae*, the plains pocket gopher forages within its burrow by pulling plants into the burrow cavity root-first. Grasses and forbs within an area are consumed. Diet items include various clovers, grasses, leguminous forbs, Johnson grass, and cultivated crops. Food items are clipped into sections and stored in the cheek pouches for transport to food storage tunnels within the burrow system. This pocket gopher occasionally forages on the surface near the entrance of its burrow. Despite its subterranean habitats, *G. bursarius* consumes very little
soil along with the vegetation. The plains pocket gopher carefully cleans food items with its front claws before consuming them (Vaughan, 1966). Because of their subterranean mode of life, gophers may be active during both diurnal and nocturnal hours.

The surface mounds of soil removed from burrows constructed by this species often are quite conspicuous. The entrances to the burrow system are closed if the resident is present. Burrows consist of shallow foraging tunnels approximately six to ten inches below the soil surface, with a deeper main tunnel that connects all of the feeding tunnels (Jones et al., 1983). Foraging tunnels are rather linear in nature and extend through an area in zig-zag fashion (Andersen, 1988). Wilkes (1963) noted that, upon occasion, one gopher may share a part of its burrow system with another gopher, or may utilize another individual’s burrow system to travel through an area. A nest chamber is located in the deeper, main burrow and is usually lined with dry grasses. Food storage chambers and defecation chambers also are constructed.

The plains pocket gopher is solitary in habit, except for brief periods of time during the mating season. Pocket gophers are active throughout the year, although surface-mounding activities may be reduced during winter months and during hot, dry periods. Gophers burrow deeper during these times and backfill old burrow tunnels with soil excavated from new tunnels (Wilkes, 1963; Starks and Andersen, 1988). The home ranges of males and females may overlap to some extent, but home ranges and territories of pocket gophers of the same sex show no, or very little overlap (Wilkes, 1963). Males have larger territories and home ranges than do

Figure 61. Distribution of Geomys bursarius on the Edwards Plateau.
females. Territoriality breaks down during mating periods.

Based upon data available (Schmidly, 1983; Goetze and Jones, 1992; Davis and Schmidly, 1994) it seems that the plains pocket gopher is reproductively active from at least February through November. *G. bursarius* is polygamous in its mating system. Two females taken in March from Runnels County carried three embryos. Litter size ranges from one to six young. Two litters may be produced in rapid succession every year (Schmidly, 1983), indicating the presence of a postpartum estrous in *G. bursarius*. The female exclusively cares for young and may forcibly eject them from her burrow after weaning.

The subspecies of plains pocket gopher on the Edwards Plateau is *G. b. major* Davis, 1940. Average external measurements of four adult females from Runnels County are: total length, 253.25; tail length, 75.25; length hind foot, 31.5; ear length, 6.75. Selected mean cranial measurements of these same four animals (Goetze and Jones, 1992) are: condylobasal length, 43.03; zygomatic breadth (2 specimens), 27.3; mastoid breadth, 25.23; rostrum length, 19.15; rostrum breadth, 10.4; postorbital constriction, 6.85; length maxillary toothrow, 8.43.

Specimens examined (24).—Howard Co.: 14 268200E, 3575300N, 1; Big Spring Area, 1 (ASNH); 14 267100E, 3562200N, 1 (MWSU); 14 267100E, 3559200N, 1 (MWSU); 14 267100E, 3557700N, 1 (MWSU); 14 267100E, 3557700N, 1 (MWSU). Nolan Co.: 14 368000E, 3588000N, 1. Runnels Co.: 14 409400E, 3508900N, 3 (ASNH); 14 407100E, 3508100N, 14.

**Geomys texensis**
Llano Pocket Gopher

Distribution.—The Llano pocket gopher is found in only a few counties in central and southern Texas. Records are available from Blanco, Gillespie, Kimble, Llano, Mason, McCulloch, and San Saba counties on the Edwards Plateau (Fig. 62).

*Geomys texensis* is larger in size than *T. bottae*, and smaller in size than *C. castanops*. The overall external appearance is similar to that of *G. bursarius* (described in a previous species account) from the northern and western Edwards Plateau. The Llano pocket gopher is smaller in size, both externally and cranially, than *G. bursarius*. However, morphology alone may not always separate these two species of *Geomys* because of a high degree of convergence due to habitation of similar soil types by both species, and the Llano pocket gopher is accorded specific status based upon fixed allelic differences between *G. texensis* and other species of *Geomys* in Texas (Block and Zimmerman, 1991). Gophers inhabiting denser soils containing greater percentages of clay tend to be smaller in size than pocket gophers inhabiting sandy or loamy soils (Davis, 1938; Smith and Patton, 1988).

*Geomys texensis* may be found inhabiting valley areas and fluvial soils at the margins of rivers and streams. Llano pocket gophers also may be taken in city parks, lawns, and roadside drainage ditches. *G. texensis* is excluded from stony, shallow soils on the Edwards Plateau, which may still be utilized by *T. bottae*. The populations of *G. texensis* found on the Edwards Plateau inhabit loamy sands or gravelly, sandy loam soils and are effectively isolated by unsuitable soils from other populations of *Geomys* within Texas (Block and Zimmerman, 1991).

Little is known of the natural history of the Llano pocket gopher. *G. texensis* is herbivorous, and, presumably, feeds upon most of the same plants as do *Thomomys* and *Cratogeomys*. Grasses and various forbs make up the majority of the diet of *G. texensis*. Reingestion of fecal pellets occurs in *G. bursarius* (Wilks, 1962), and probably in *G. texensis*. Foraging activities are conducted from within a burrow system similar to that of other species of pocket gophers. The Llano pocket gopher may be active during both diurnal and nocturnal hours and remains active throughout the year.

*G. texensis* digs burrow systems and tunnels similar to those of *Geomys bursarius*. Each burrow system is inhabited by a single resident except during the breeding season and rearing young. Territories and home ranges are limited to the immediate system of tunnels of an individual pocket gopher throughout an area. For a more complete description of burrow systems, social habits, and territories see the account of *G. bursarius*.

Reproductive physiology and behavior is probably similar to that of *G. bursarius*. The gestation pe-
period of *G. texensis* is not definitely known. Gestation periods of *G. bursarius* range from as few as 18 to as great as 51 days in length (Nowak, 1991: 621). Pregnant females and females with uterine scars are recorded from the month of June. Scrotal males have been captured in the month of April. The number of young per litter, based upon counts of fetuses appears to be three. Whether females give birth to more than one litter of young per year is at present unknown.

An isolated population of *G. texensis* was recently discovered in Medina, Uvalde, and Zavala counties. Smolen et al. (1993), using both molecular and cranial morphology data, concluded that this isolated population was distinct from populations of *G. texensis* on the Edwards Plateau, and the two distinct populations warranted subspecific designations. The subspecies proposed for the Edwards Plateau is *G. t. texensis* Smolen, Pitts, and Bickham, 1993. Males are significantly larger than females (Smolen et al., 1993). Average external measurements of five adult females from the Edwards Plateau are: total length, 213.6; tail length, 53.1; length hind foot, 26.1; ear length, 4.6. Selected cranial measurements of 10 adult females are: condylobasal length, 38.76; zygomatic breadth, 23.67; length rostrum, 17.18; breadth rostrum, 9.19; postorbital constriction, 5.84; mastoid breadth, 21.89; length maxillary toothrow, 7.44.

Specimens examined (81).— Gillespie Co.: Fredericksburg City Limits, 2 (WTAM); 14 509500E, 3349500N, 2; 14 498800E, 3349500N, 1 (TNHC); 14 520000E, 3349500N, 3 (SWTU). Llano Co.: 14 515100E, 3414700N, 1 (SWTU); 14 531700E, 3416700N, 1; 14 506800E, 3400500N, 3; 14 504300E, 3395700N, 3; 14 504100E, 3396300N, 3; 14 527700E, 3404800N, 2; 14 518200E, 3402200N, 3; Lake Buchanan, 7 (WTAM); West Side Lake Buchanan, 2 (WTAM); 14 549800E, 3378000N, 4; 14 552800E,
GOETZE—MAMMALS OF THE EDWARDS PLATEAU

3376800N, 1; 14 553900E, 3375700N, 2; 14 558100E, 3406700N, 2. **Mason Co.**: 14 477900E, 3422800N, 1 (ASNC); 14 477900E, 3419400N, 9 (MWSU); 14 475800E, 3406400N, 1; 14 470400E, 3403300N, 2; 14 476300E, 3402600N, 4; 14 477900E, 3401100N, 4; 14 464400E, 3401100N, 1 (SWTU); 14 463800E, 3401100N, 1; 14 475600E, 3400700N, 3; 14 476500E, 3400700N, 1; 14 476900E, 3400700N, 1; 14 500800E, 3395300N, 3; 14 499100E, 3394900N, 2; 14 499700E, 3393300N, 1; 14 499600E, 3392400N, 1; 14 477900E, 3393600N, 1 (MWSU).

**Additional records.**—**Blanco Co.**: Unspecified Locality. **Gillespie Co.**: 14 512500E, 3350900N (TCWC); 14 512500E, 3350600N; 14 518400E, 3349400N; 14 512800E, 3349000N (TCWC). **Kimble Co.**: Unspecified Locality. **Llano Co.**: 14 503800E, 3396400N; 14 504700E, 3396400N; 14 511200E, 3396400N; 14 531200E, 3397600N (TCWC). **McCulloch Co.**: 14 468400E, 3429000N. **Mason Co.**: 14 477900E, 3421200N (TCWC); 14 477900E, 3419600N (TCWC); 14 477900E, 3416400N (TCWC); 14 475100E, 3404700N; 14 477900E, 3401100N (TCWC); 14 462900E, 3401100N; 14 500400E, 3396500N; 14 479500E, 3401100N (TCWC); 14 464400E, 3391000N; 14 477900E, 3367900N. **San Saba Co.**: 14 528000E, 3427400N. (Dalquest and Kilpatrick, 1973; Block and Zimmerman, 1991).

**Cratogeomys castanops**

**Yellow-faced Pocket Gopher**

**Distribution.**—This rodent ranges from north-central Mexico, northward through the western one-third of Texas, and through the extreme northwestern portion of the Oklahoma Panhandle and into Colorado and Kansas. The yellow-faced pocket gopher reaches its western distributional limits in south-central New Mexico, and Chihuahua, Mexico.

This pocket gopher occurs on the extreme northwestern and western portions of the Edwards Plateau. The species has been recorded from Crockett, Glasscock, Howard, Irion, Reagan, Sterling, Upton, and Val Verde counties within the Edwards Plateau region (Fig. 63).

**Cratogeomys castanops** may be distinguished from the other three species of pocket gophers on the Edwards Plateau by its larger size (adults), dark-colored feet, and single groove on the anterior face of the upper incisors. The pelage is brown to buffy in color on the dorsum and gray to white, or buffy on the venter of the yellow-faced pocket gopher. The tail is short to moderate in length, and is sparsely haired. Ears are short, naked, and valvular. Body conformation and shape are as in other pocket gophers, with *C. castanops* being well-adapted to burrowing and fossorial existence.

Ideal habitat for the yellow-faced pocket gopher seems to be determined more by suitable soil substrate than by vegetation. Areas with shallow or poorly drained soils are not favored habitats for this species of pocket gopher. This species prefers sandy or loamy soils that are relatively free of rocks. However, where *C. castanops* is parapatric with *G. bursarius*, the yellow-faced pocket gopher is restricted to denser, shallower, and rocky soils (Davidow-Henry et al., 1989). A minimal topsoil depth of approximately 175 to 200 cm is required, or the yellow-faced pocket gopher will be excluded from an area (Davidow-Henry et al., 1989). The yellow-faced pocket gopher is a generalist in habitat choice when necessity demands and has the ability to survive in many types of habitat provided an adequate topsoil depth for burrowing (Hollander, 1990).

The yellow-faced pocket gopher is a strict herbivore in diet. These gophers feed upon plant roots, tubors, bulbs, stems, leaves, and even the outer bark of trees. Plants are pulled into the burrow root-first and then cut into sections small enough to accommodate the cheek pouches. Clovers, hay crops, and lechugilla are known to be consumed by this rodent. Most foraging is done while the species is underground. Because of its subterranean habits, the activity pattern of *C. castanops* varies, and the rodents may be active either diurnally or nocturnally. The yellow-faced pocket gopher is active throughout the year.

This species constructs and lives entirely within subterranean burrow systems. Burrows and tunnels occur at several levels beneath the surface. Shallow, more extensive burrows are constructed primarily for foraging within an area, and deeper tunnels usually lead to a nest and food chambers. No special defecation chambers are constructed within the burrow system, and...
burrows range from 42 to 104 m in length (Davidow-Henry et al., 1989). Burrows normally are occupied either by a single gopher or by a female and her offspring. However, plural occupancy of burrow systems has been recorded; especially during breeding seasons (Chase et al., 1982). Mormon crickets and tiger salamanders are known to coinhabit active burrows.

Gophers are highly territorial and asocial toward congeners and conspecifics. Placing gophers together usually results in fighting and death of one of the individuals (Chase et al., 1982). Juveniles disperse after being weaned, and a high vagility has been noted for the yellow-faced pocket gopher (Davidow-Henry et al., 1989). The young animals, and occasionally adults, are sometimes observed dispersing above ground.

The yellow-faced pocket gopher breeds throughout the year in Texas (Davidow-Henry and Jones, 1988). Females are polyestrous and males are polygynous. At least two litters, and perhaps more depending upon location, are produced annually. Litters range in size from one to four, with two being the average number of young (Davidow-Henry and Jones, 1988).

Hollander (1990) indicated three subspecies of yellow-faced pocket gopher on the Edwards Plateau of Texas. These three subspecies are *C. c. purplanus* Nelson and Goldman, 1934 in Howard County on the northern Edwards Plateau; *C. c. dalquesti* Hollander, 1990 in the central portion of the species' range; and *C. c. clarkii* (Baird, 1855) in Crockett and Val Verde counties. Sexual dimorphism is known to occur in pocket gophers with males being larger than females. Average
external measurements of five females from Glasscock County are: total length, 247.4; tail length, 64.8; length hind foot, 34.6; ear length, 5.8. Selected cranial measurements (Hollander, 1990) of the holotype of *C. c. dalquesti* from Sterling County are: condylobasal length, 51.79; zygomatic breadth, 32.88; mastoid breadth, 28.86; breadth rostrum, 10.59; length rostrum, 21.64; nasal length, 16.97; interorbital constriction, 6.62; length maxillary toothrow, 9.02.

Specimens examined (91).—Glasscock Co.: 14 273900E, 3541600N, 1(MWSU); 14 265300E, 3549000N, 1(MWSU); 14 265300E, 3546600N, 1(MWSU); 14 265300E, 3544300N, 1(MWSU); 14 265300E, 3542500N, 1(MWSU); 14 265300E, 3542400N, 2(MWSU); 14 265300E, 3539300N, 2(MWSU); 14 265300E, 3538000N, 1(MWSU); 14 265300E, 3534800N, 1(MWSU); 14 265300E, 3534000N, 1(MWSU); 14 265300E, 3530400N, 1(MWSU); 14 265300E, 3529000N, 1(MWSU); 14 265300E, 3526800N, 2(MWSU); 14 265300E, 3525000N, 2(MWSU); 14 265300E, 3523000N, 1(MWSU); 14 265300E, 3520500N, 1(MWSU); 14 265300E, 3518000N, 1(MWSU); 14 265300E, 3515000N, 1(MWSU). Irion Co.: 14 293400E, 3483600N, 1(MWSU); 14 294600E, 3478400N, 1(MWSU); 14 294600E, 3476800N, 2(MWSU); 14 294600E, 3477400N, 1(MWSU); 14 294600E, 3469000N, 1(MWSU). Reagan Co.: 14 263700E, 3478800N, 1(MWSU); 14 265600E, 3480800N, 1(MWSU); 14 265600E, 3479500N, 1(MWSU). Sterling Co.: 14 306500E, 3538000N, 1(MWSU); 14 300700E, 3531500N, 1(MWSU); 14 303500E, 3531800N, 1(MWSU); 14 307000E, 3536900N, 1(MWSU); 14 307000E, 3536300N, 1(MWSU); 14 307500E, 3527700N, 2(MWSU); 14 306600E, 3529700N, 1(MWSU); 14 306600E, 3529000N, 1(MWSU); 14 306600E, 3528000N, 1(MWSU); 14 306600E, 3528000N, 1(MWSU). Upton Co.: 14 219700E, 3458200N, 2(MWSU); 14 222600E, 3458200N, 1(MWSU); 14 231700E, 3458200N, 1(MWSU). Additional records.—Crockett Co.: 14 241400E, 3395600N; 5 mi. S Howard Springs. Val Verde Co.: 14 326300E, 3337400N. (Hollander, 1990).

**KEY TO HETEROMYIDAE**

1 Width across mastoid bullae greater than width across zygomatic arches; interparietal much reduced; length hind foot usually 39 mm or greater; body modified for saltatorial locomotion; white rump strips present ......................................................... 2

1' Width across mastoid bullae less than width across zygomatic arches; interparietal not much reduced; length of hind foot less than 39 mm; body not modified for saltatorial locomotion; white rump strips absent................................................................. 3

2 Five toes present on hind foot; outer fifth toe greatly reduced in size .................................................................................................................... Dipodomys ordii

2' Four toes present on hind foot ........................................................................................................ Dipodomys merriami
3 No conspicuous rump spines present; tail not penicillate; tail length less than head and body length ......................................................................................................... 4

3' Conspicuous rump spines present; tail penicillate; tail length greater than head and body length ........................................................................................................ 5

4 Greatest length of skull 26 mm or greater; total length 180 mm or greater; ochraceous lateral stripe present; no white patches present behind the ears ................................................................. Chaetodipus hispidus

4' Greatest length of skull less than 26 mm; total length less than 180 mm; no ochraceous lateral stripe present; white patches present behind the ears ......................................................... Perognathus flavus

5 Spines on rump weakly developed and not black-tipped; soles of hind feet pale in color; dorsal color cinnamon, washed with white. .......... Chaetodipus penicillatus

5' Spines on rump strongly developed and black-tipped; soles of hind feet dusky in color; dorsal color grayish, washed with black. ......................... Chaetodipus nelsoni

Family Heteromyidae—Pocket Mice and Kangaroo Rats

Perognathus flavus
Silky Pocket Mouse

Distribution.—The silky pocket mouse occurs from central Mexico northward throughout the western two-thirds of Texas, and western Oklahoma, Kansas, and Nebraska. The range of the silky pocket mouse extends as far north as southwestern Nebraska, eastern Wyoming, and westward through eastern Colorado, most of New Mexico, eastern Arizona, and southern Utah.

The documented range of the silky pocket mouse includes the entire Edwards Plateau (Schmidly et al., 1993). Specimens are not especially numerous, and the species seems to be more common on the western Edwards Plateau. Records are available from Bandera, Bexar, Burnet, Coke, Concho, Crane, Crockett, Edwards, Howard, Kerr, Kimble, Kinney, Mason, Nolan, Reagan, Real, Schleicher, Sterling, Sutton, Tom Green, Travis, Upton, and Val Verde counties (Fig. 64).

Perognathus flavus is the smallest species of pocket mouse occurring on the Edwards Plateau. The silky pocket mouse is easily identified from the other heteromyids on the Edwards Plateau by size alone. The dorsal color is rather golden, with black hairs interspersed throughout the pelage. No distinct, dark mid-dorsal strip is evident in the silky pocket mouse. Small, white auricular patches are present, and external cheek pouches are evident. The upper incisors are grooved in pocket mice and kangaroo rats, but heteromyids have four cheek teeth, whereas harvest mice (which also have grooved upper incisors) have three cheek teeth.

Silky pocket mice are found in rocky habitats with interspersed midgrass species, such as sideoats grama. They may also be found in grassland valley habitats on the Edwards Plateau. Silky pocket mouse are found in soil substrates varying from sandy, deep soils to clayey, shallow soils (Best and Skupski, 1994). I have captured these pocket mice in areas of sparse ground cover and short to mid-grasses on the Edwards Plateau. Habitats with dense ground cover and rank vegetation are usually avoided.

The diet of P. flavus consists primarily of seeds of various weeds and grasses. Juniper seeds and other fruits are consumed if available (Davis and Schmidly, 1994). Insects make up a minor percentage of the diet. Items consumed in the diet vary by availability and season in any particular habitat. The silky pocket mouse obtains the water it needs from its diet and metabolic water that is salvaged from the tissues. Seeds are carefully shelled and only the endosperm is consumed (Jones et al., 1983). Like other heteromyids, P. flavus is nocturnally active.

During cold periods, these small mice become torpid in their burrows (Findley, 1987). The silky pocket mouse, however, does not hibernate; P. flavus is able to
remain in torpor for only about 24 hours. Seed stores within the burrow are utilized during periods of cold weather (Hoffmeister, 1986), and silky pocket mice also feed upon stored seeds before emergence from burrows in the evening hours (Wolff and Bateman, 1978).

Silky pocket mice are solitary in habit; save for a female and her offspring. Burrows are constructed underneath brush, rocks, and cacti. Each burrow usually has more than one entrance. The entrances are closed during daylight hours if the burrow system is occupied (Bailey, 1905). Burrows may be dug to a depth of 38 cm, and a nest of grasses is located somewhere in the passageway (Schmidly, 1983). Several burrows may be utilized by an individual within its home range (Best and Skupski, 1994).

Figure 64. Distribution of *Perognathus flavus* on the Edwards Plateau.

Silky pocket mice are rather sedentary in nature and have small home ranges. Males seldom move more than 38 m from their home burrows and females seldom move more than 29 m (Schmidly, 1983). Juveniles move farther than adults, suggesting that the juveniles disperse to areas at the margins of the population (Schmidly, 1983).

Silky pocket mice breed from early spring until late fall (Schmidly, 1983). Gravid females are present on the Edwards Plateau in the months of June and July. Some females may produce two or more litters annually (Schmidly, 1983). In more northern portions of their range or in inhospitable habitats, the silky pocket mouse may reproduce only once annually (Jones et al., 1983; Hoffmeister, 1986). The gestation period is 26 days or longer in duration (Eisenberg, 1993). Litter
size ranges from three to six young. The average litter size is four (Eisenberg, 1993).

Two subspecies of silky pocket mouse occur on the Edwards Plateau. *P. f. merriami* J. A. Allen, 1892 on the eastern Edwards Plateau to Howard and Edwards counties; and *P. f. gilvus* Osgood, 1900 on the western Edwards Plateau. Some researchers (Lee and Engstrom, 1991) propose the elevation of *merriami* to specific rank based upon genetic differences and lack of introgression in areas of sympathy, as elucidated by protein electrophoresis. However, no distinct morphological differences are evident between *flavus* and *merriami* within areas of sympathy. No significant sexual dimorphism is present in *P. f. gilvus* (Best, 1993). Average external measurements (Schmidly, 1983) are: total length, 105; tail length, 48; length hind foot, 15; ear length, 6. Selected mean cranial measurements of 11 individuals (six males, five females) from the Edwards Plateau are: nasal length, 7.48; interorbital breadth, 4.74; zygomatic breadth (7 only), 9.61; occipitonasal length (10 only), 20.27; interparietal width, 3.32; length mastoid bullae, 6.83; mastoid breadth, 10.96; frontonasal length (10 only), 13.49.


**Chaetodipus hispidus**

Hispid Pocket Mouse

**Distribution.**—The hispid pocket mouse ranges from central Mexico northward throughout the Great Plains states to North Dakota. This pocket mouse ranges as far east as Louisiana, and westward through eastern Colorado, New Mexico, and southeastern Arizona.

The hispid pocket mouse is a ubiquitous species on the Edwards Plateau (Schmidly, 1983), but is rarely taken in great numbers at any single locality. Records are available from Bexar, Burnet, Callahan, Coke, Crane, Crockett, Edwards, Glasscock, Howard, Kinney, Llano, Mason, McCulloch, Menard, Reagan, Runnels, Schleicher, Taylor, Tom Green, Travis, Upton, and Val Verde counties (Fig. 65).

*Chaetodipus hispidus* is larger in size than the silky pocket mouse. The dorsal pelage is harsh and ochraceous in base color, interspersed with black. An orange lateral line is present and the underparts are white. The ears of *C. hispidus* are small and external cheek pouches are present. Appendages are short. The tail is darker dorsally and distinctly bicolored. Besides its smaller size, the tail of the silky pocket mouse is indistinctly colored, and the silky pocket mouse has no distinct lateral line on its sides.

The hispid pocket mouse is found in a variety of dry, grassland habitats. This pocket mouse is an inhabitant of mesic valleys, watercourse vegetation, rocky, juniper habitats, and pasturelands throughout the Edwards Plateau. This species often occurs in habitats with mesquite, juniper, cactus, yucca, and ocotillo (Paulson, 1988). I have also taken the hispid pocket
Figure 65. Distribution of Chaetodipus hispidus on the Edwards Plateau.

The hispid pocket mouse is herbivorous and granivorous in diet. Seeds make up as much as 81 percent of the diet during part of the year (Paulson, 1988). Seeds seem to be selected rather than simply gathered by random foraging, and the diet of C. hispidus is seasonally variable. A few insects also may be consumed by the hispid pocket mouse. Major foods in winter include the seeds of sunflower, mesquite, and cacti. Important food items in the summer months include seeds and leaves of mesquite, blanket flower, cactus seeds, and bluestem grass leaves and seeds (Paulson, 1988). Seeds are stored in caches within the burrow and are consumed during periods of food shortage (Jones et al., 1983). Foraging is conducted nocturnally; the hispid pocket mouse is active throughout the year.

Burrows vary from single tunnels to branched tunnel systems with two or three entrances. Immature individuals usually construct single-tunnel burrows, and adults construct more complicated burrow systems (Paulson, 1988). A small amount of soil may be mounded about the entrance of the burrow (Jones et al., 1983), but I have often found burrows to be either level with the surface of the ground or dug into embankments with no obvious mounding activity. Burrows usually are plugged during daylight hours.

A single pocket mouse occupies each burrow. C. hispidus, like most heteromyids, is unsocial and solitary during most of the year. The hispid pocket mouse enters torpor at low temperatures (about 5°C or lower), but the beginning of torpor depends upon the food sup-
The hispid pocket mouse probably breeds throughout the year when conditions are favorable (Choate and Jones, 1989). Females are polyestrous and more than one litter may be produced per year. Pregnant females have been taken in the months of June and July, and juvenile individuals in May on the Edwards Plateau. Little is known about the growth and development of *C. hispidus*. The number of young per litter varies from two to nine with an average of six (Schmidly, 1983).

Two subspecies of hispid pocket mouse reside on the Edwards Plateau. *C. h. hispidus* (Baird, 1858) is found on the eastern and central Edwards Plateau as far west as Howard and eastern Val Verde counties; *C. h. paradoxus* (Merriam, 1889) is found on the remainder of the region to the west. *C. h. paradoxus* is larger in size than *C. h. hispidus* (Glass, 1947). Sexes are not significantly different in external or cranial dimensions (Jones et al., 1983). Average external measurements of five adult males and two adult females (combined) from Schleicher County are: total length, 189; tail length, 89.5; length hind foot, 24; ear length, 11. Selected mean cranial measurements of these same individuals are: greatest length skull, 28.65; zygomatic breadth, 14.68; interorbital constriction, 7.10; length rostrum, 11.47; width across auditory bullae, 14.74; length maxillary toothrow, 3.99.


**Chaetodipus nelsoni**

Nelson's Pocket Mouse

**Distribution.**—Nelson's pocket mouse ranges from central Mexico north through Trans-Pecos, Texas. The species reaches its distributional limits in the United States in southeastern New Mexico.

This species of pocket mouse reaches eastern distributional limits on the western Edwards Plateau. Nelson's pocket mouse has been taken from Upton, and Val Verde counties on the Edwards Plateau (Fig. 66).

*Chaetodipus nelsoni* is intermediate in size between the larger *C. hispidus* and smaller *P. flavus*, and is not easily mistaken for either of these pocket mice. The only other species of pocket mouse which *C. nelsoni* may be mistaken for is the similar appearing desert pocket mouse (*C. penicillatus*). Both of these species have harsh pelage; although the pelage of *P. nelsoni* is usually mixed with more black hairs dorsally than is that of the more pinkish, buffy *C. penicillatus*. Nelson's pocket mouse has numerous, black-tipped hairs projecting past the rump; *C. penicillatus* lacks these black tipped hairs. The soles of the hind feet of Nelson's pocket mouse are black in color; the soles of *C. penicillatus* hind foot are naked and white in color. The
venter of both species is white in color, and both have rather long, penicillate tails with terminal tufts of hair. Tails of both species are indistinctly bicolored. External cheek pouches are present in both Nelson’s pocket mouse and the desert pocket mouse.

*Chaetodipus nelsoni* is a saxicolous species (Baker, 1956; Davis and Schmidly, 1994). This species is most frequently trapped in rocky areas, or in habitats with stony, gravelly soils. Vegetation in an area does not appear to be as critical a factor to habitat selection as does substrate (Schmidly, 1977). Sandy areas seem to be avoided by this species of pocket mouse. Nelson’s pocket mouse may be found in association with creosote brush and rocky slopes on the Edwards Plateau, but does not appear to be a common species in any area within the region.

Diet of *C. nelsoni* is composed almost exclusively of seeds. Seeds of creosote, wild buckwheat, mesquite, and prickly pear are included in the diet (Schmidly, 1977). Insects also may be consumed in the diet (Best, 1994). Water is not required in the diet of *C. nelsoni*. These mice are nocturnal in foraging activity.

Nelson’s pocket mouse lives in burrows, which are usually found near the base of rocks or shrubs. This pocket mouse stays in the burrow during daylight hours, and the entrance is usually plugged. Several entrances may be constructed around a series of tunnel systems radiating out from a central tunnel.

Nelson’s pocket mouse is solitary. Males and females have definite home ranges, with the male’s home range being slightly larger than that of the female (Best, 1994). The home ranges of females do not overlap

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**Figure 66.** Distribution of *Chaetodipus nelsoni* on the Edwards Plateau.
(Schmidly, 1977). *C. nelsoni* does not hibernate during winter months as does *C. penicillatus*, and is active throughout the year. Activity may be reduced during periods of high moonlight, high to moderate winds, or other inclement conditions.

Mating in *C. nelsoni* begins as early as February and continues through July. Apparently only a single litter is born each year. The number of young per litter ranges from one to five (Best, 1994). The annual population turnover in Trans-Pecos, Texas, was estimated to be as high as 86 percent (Schmidly, 1977).

The subspecies which occurs on the Edwards Plateau is *C. n. canescens* (Merriam, 1904). Sexual dimorphism may occur in this species, as both individual and sexual dimorphism has been found within other species of heteromyid rodents. External measurements of the holotype (a young adult male from Jaral, Coahuila) are as follows: total length, 193; tail length, 117; length hind foot, 22; length ear (dry), 8. Cranial measurements of the holotype (Williams et al., 1993) are: occipitonasal length, 25; basilar length, 17.5; interorbital breadth, 6.1; width mastoid bullae, 13.5; length interparietal, 3.7; width interparietal, 7.2; nasal length, 9.3.

**Specimens examined** (4).—Upton Co.: 13 772500E, 3454400N, 1. Val Verde Co.: 14 307500E, 3303400N, 1; 14 309100E, 3292000N, 1 (ASNHC); 14 289600E, 3299400N, 1 (ASNHC).


**Chaetodipus penicillatus**

*Desert Pocket Mouse*

**Distribution.**—The desert pocket mouse ranges from central Mexico north into Trans-Pecos, Texas, and adjacent areas. Its range extends westward through southern New Mexico, Arizona, and southern California. The range extends as far north as southern Nevada and the southwestern corner of Utah.

Distribution of the desert pocket mouse is limited to the extreme western edge of the Edwards Plateau. The species has been recorded east of the Pecos river from Crane and Val Verde counties within the region (Fig. 67).

*Chaetodipus penicillatus* may be confused with *C. nelsoni* in areas where the two species may be sympatric. Characters separating the two species are given in the account of *C. nelsoni*. Generally, *C. penicillatus* lacks black-tipped rump spines, is more of a cinnamon color dorsally than is Nelson’s pocket mouse, and the soles of the hind feet of *C. penicillatus* are not black as in *C. nelsoni*. Overall sizes are similar for both species of pocket mice.

The desert pocket mouse favors habitats and areas which have sandy substrates and sparse vegetation. Rocky and gravelly soils are generally avoided by this species. Sandy arroyos and drainage areas are utilized as burrowing, foraging, and dust-bathing sites by *C. penicillatus*. These types of habitats are found along the Pecos and Rio Grande rivers and their immediate tributaries within the region. The desert pocket mouse has been trapped in association with mesquite, creosote, cholla and other cacti, yucca, sparse grasses, and other vegetation.

The desert pocket mouse is primarily granivorous. Green vegetation may be consumed during seasons when seeds are scarce within a foraging area. Seeds from mesquite, creosote, and broomweed have been found in *C. penicillatus*’ cheek pouches. Seeds are stored in shallow caches around the burrow. A captive individual that I have maintained makes a habit of frequently moving his seed caches to different locations within his terrarium, sometimes moving the seeds to different locations each night. Water is not required in the diet of this species; sufficient moisture being obtained from seeds and occasional green vegetation. *C. penicillatus* is strictly nocturnal, and remains within a burrow during daylight hours. The desert pocket mouse enters periods of torpor during winter months, and may remain in torpor for several days during inclement weather conditions (Schmidly, 1977).

Burrows are constructed in loose soils at the base of rocks, bushes, or other vegetation. The desert pocket mouse also may burrow into hard-crusted soils by chewing its way through the hard soil crust (Hoffmeister, 1986). Nest chambers are constructed within the burrow, and are lined with dry grasses and other plant materials. Burrow entrances usually are plugged by the occupant during the daytime. This helps to maintain higher humidity levels inside the burrow, as opposed to the external environment.
The desert pocket mouse is unsocial. Adults live alone in separate burrows and maintain separate home ranges (Jones, 1993). Females and young reside in a burrow until the young are able to disperse. There is no appreciable size difference between the home ranges of adult males, females, and juvenile animals (Schmidly, 1977).

Reproduction periods are bimodal in *Chaetodipus penicillatus*. One period peaks in the spring months, and the second period peaks in June and August. Eisenberg (1993) gave the gestation period of *C. penicillatus* as 26 or more days in length. Litter size ranges from three to six young. This species breeds early when conditions are favorable, and it is not uncommon for young females to become pregnant while still in juvenile pelage (Schmidly, 1977). In Trans-Pecos, Texas, the annual population turnover of *C. penicillatus* is almost 95 percent. Most individuals survive less than 12 months in natural populations. With such a high mortality rate, an early-breeding strategy would be advantageous to the desert pocket mouse.

The subspecies on the Edwards Plateau is *C. p. eremicus* (Mearns, 1898). Hoffmeister (1986) indicated that significant sexual dimorphism may occur in this species of pocket mouse. Average external measurements (Schmidly, 1977) are: total length, 175; tail length, 94; length hind foot, 23; ear length, 7. Selected mean cranial measurements of eight males and five females from Coahuila, Mexico (Baker, 1956) are respectively: occipitonasal length, 26.1, 25.6; frontonasal length, 18.0, 17.9; mastoid breadth, 13.3, 12.9; length auditory bullae, 8.0, 7.9; least interorbital constriction, 6.7, 6.4; interparietal breadth, 7.1, 7.2; length maxillary toothrow, 3.7, 3.7.
Specimens examined (2).—Crane Co.: 1375000E, 3470200N, 1. Val Verde Co.: 14 258600E, 3341600N, 1.

_Dipodomys merriami_
Merriam's Kangaroo Rat

_Distribution._—Merriam's kangaroo rat ranges from central Mexico northward through Trans-Pecos and adjacent areas of Texas into New Mexico. This species occurs in southern Arizona north and westward to southern California and northwestern Nevada.

Merriam's kangaroo rat is found in the extreme western portion of the Edwards Plateau. Records of this species are available from Crane, Crockett, Midland, Upton, and Reagan counties within the region (Fig. 68).

Merriam's kangaroo rat may be distinguished from _D. ordii_ by the presence of only four toes on the hind feet of _D. merriami_; whereas _D. ordii_ has five toes on the hind feet. Pelage is buffy in color dorsally with a white stripe on the lateral sides of the hips. The tail is relatively long and has a dusky, tufted tip, and white, lateral stripes. The underparts are white in color. Ears are short and rounded and the front feet are reduced. The hind legs of kangaroo rats are modified for saltatorial locomotion. Conspicuous external cheek pouches are present in kangaroo rats. Auditory bullae are greatly enlarged in kangaroo rats.

_Dipodomys merriami_ apparently prefers open environments, although it does not significantly favor any single microhabitat (Schmidly et al., 1993). Soil substrate may influence the distribution of _D. merriami_ within the Edwards Plateau. This species is not found in areas where soils are very rocky or contain a high percentage of clay. Densely packed soils also are avoided; perhaps because of the difficulty encountered by _D. merriami_ in constructing burrows in such soils. Merriam’s kangaroo rat seems to avoid habitats with dense grasses and other ground cover. Perhaps these habitats present difficulties to locomotion of kangaroo rats.

Kangaroo rats are primarily granivorous in diet. Green vegetation and insects are consumed in minor percentages in the diet of _D. merriami_. Seeds are apparently not selected entirely at random by kangaroo rats (Reichman and Price, 1993). Seeds must be of the proper size (neither too large nor small) and contain enough nutrients to meet the species’ dietary needs. However, because kangaroo rats and other heteromyid species are often found inhabiting areas with unpredictable environments, diets also reflect the food resources that are available within a particular area. Cheek pouches allow seeds to be gathered and stored and help to reduce the kangaroo rat's foraging time outside of a burrow. Seeds are often stored in caches around the vicinity of _D. merriami_’s burrow (Reichman and Price, 1993). Water is not needed in the diet of _D. merriami_. Foraging is conducted during nocturnal hours.

Burrows of _D. merriami_ are usually simple in design, shallow, and with openings near the base of shrubs (Davis and Schmidly, 1994). Usually only a single adult, or a female and her offspring, inhabit each burrow system in an area. Burrows must be deep enough to insulate _D. merriami_ from temperatures in excess of 37°C or below 7°C (Hoffmeister, 1986). Merriam's kangaroo rat has a limited ability to withstand cold temperatures, as do most heteromyid rodents.

Kangaroo rats are solitary in social habit. When conspecifics are encountered, antagonistic displays and fighting often take place. Females drive males away from their burrows except for short periods of postpartum estrous (Hoffmeister, 1986). Males take no part in raising young.

Breeding may begin in February and continue through August in Merriam’s kangaroo rat. The number of young per litters ranges from one to five (Schmidly, 1977). The gestation period of _D. merriami_ is approximately 29 days, and sexual maturity of young is usually attained in 60 days (Eisenberg, 1993).

The subspecies of Merriam’s kangaroo rat on the Edwards Plateau is _D. m. ambiguus_ Merriam, 1890. Average external measurements of two male and two female specimens (combined) are: total length, 242; tail length, 147.5; length hind foot, 38.5; ear length, 12. Selected mean cranial measurements for these same specimens are: greatest length skull, 35.42; nasal length, 13.37; least interorbital breadth, 13.25; greatest length bullae, 14.53; length maxillary toothrow, 3.85.

Specimens examined (37).—Crane Co.: 13 759800E, 3491200N, 18 (ASNHC); 13 754300E, 3470200N, 2. Crockett Co.: 14 241400E, 3420000N, 1; 14 227400E, 3418400N, 1; 14 230200E, 3409500N,
Ord’s kangaroo rat is a peripheral species of the northwestern Edwards Plateau. Records are common in many counties bordering the region within this area, but actual records on the Edwards Plateau are scarce. Records are on hand from Crane, Crockett, and Upton counties within the region (Fig. 69).

*Dipodomys ordii* is very similar in external appearance to *D. merriami*. Merriam’s kangaroo rat was described in the previous account. The surest way to separate the two species is by examination of the toes of the hind feet. *D. ordii* possesses five toes on each hind foot, whereas, *D. merriami* has only four toes. The fifth toe of *D. ordii* is reduced and is located on the exterior side of the foot. Ord’s kangaroo rat averages larger in most cranial and external characteristics when compared to Merriam’s kangaroo rat.
Figure 69. Distribution of *Dipodomys ordii* on the Edwards Plateau.

Ord’s kangaroo rat is found predominantly inhabiting areas of sparse vegetation and sandy soils. This species of kangaroo rat does not favor gravelly substrates, and this factor may limit the distribution of *D. ordii* over most of the Edwards Plateau. In areas where *D. ordii* and *D. merriami* occur together, Ord’s kangaroo rat usually is taken in the more sandy areas, whereas, *D. merriami* is more tolerant of gravelly soils. Vegetation associated with most habitats includes mesquite, yucca, broomweed, sand sage brush, and shin oak (Garrison and Best, 1990).

Ord’s kangaroo rat is primarily granivorous in diet. Winter diets consist of seeds gathered in rough proportion to their availability within a habitat. The kangaroo rats are more selective in seed selection in spring months, possibly because of an overall increase in seed abundance. Seeds of mesquite, blanketflower, ragweed, sunflower, croton, and bluestem grasses are among some food items selected by *D. ordii*. Insects constitute a small percentage of the diet in both winter and spring months. Kangaroo rats can survive indefinitely without water, meeting their water requirements from metabolic water produced during oxidative metabolism (Jones et al., 1983). Foraging and other activities are conducted during nocturnal hours. Hours and nights of bright moonlight are periods of low activity for *D. ordii* (Kaufman and Kaufman, 1982).

Burrows are constructed at the base of shrubs or clumps of grasses, and in banks or other eroded areas, with loose, sandy soils. Burrows may become quite complex, but always consist of separate nest and food-storage chambers (Jones et al., 1983). Ord’s kangaroo rat may defecate anywhere within the burrow system, except the nest chamber. Urination takes place in one
area of the burrow (Jones et al., 1983). Nests are built of plant fibers found locally within an area.

Ord's kangaroo rat is solitary in habit. Each burrow system is inhabited by a single, adult animal. Garner (1974) noted a nonrandom activity and home range center for this species in western Texas. This researcher reported that the kangaroo rats at his study site demonstrated temporal differences in foraging times that allowed multiple individuals to utilize portions of similar home ranges at different times. This allows for population increases within a habitat, while reducing such factors as antagonistic encounters between conspecifics.

Garner (1974) found a continuous period of reproductive activity in female *D. ordii* from August through May in western Texas. Peaks occurred in early autumn and late winter months. Reproductive quiescence occurred for three or four months in late spring and summer. Two litters may be produced annually by adult *D. ordii*. Gestation usually lasts 29 to 30 days (Jones et al., 1983). Litters may range in size from one to six. Females examined from the months of January, October, and November carried three embryos. One female captured in March carried two embryos. Premating courtship rituals were observed by Allen (1944), and included genetalia nudging, reciprocal chasing, and pushing behaviors. Males apparently establish a dominance hierarchy wherein only dominant males will mate with females within a specific area of overlap.

The subspecies on the Edwards Plateau is *D. o. medius* Setzer, 1949. Geographic variation and sexual dimorphism has been demonstrated by numerous researchers (Schmidly, 1971; Kennedy and Schnell, 1978; Baumgardner and Kennedy, 1993). Selected mean external and cranial measurements of six male *D. o. medius* from the type locality at Santa Rosa, New Mexico (Setzer, 1949) are: total length, 258.5; tail length, 143.3; length hind foot, 38.0; greatest length skull, 39.5; bul- lae breadth, 25.2; breadth across maxillary arches, 21.4; rostrum width, 4.1; nasal length, 14.2; interorbital width, 12.9; basilar length, 24.8.

*Specimens examined* (13). — *Crane Co.*: 13 752000E, 3493300N, 6 (ASNHC); 13 759800E, 3491600N, 4 (ASNHC). *Upton Co.*: 13 756300E, 3481500N, 3.

*Additional records.* — *Crockett Co.*: 14 223200E, 3431900N. (Chapman and Spencer, 1987).

**Family Castoridae**— Beavers

*Castor canadensis*

**American Beaver**

*Distribution.* — The beaver is found from Chihuahua, Coahuila, and Tamaulipas, Mexico, northward throughout all except the most arid regions of the contiguous United States, southern Florida, most of South Carolina, and parts of Tennessee, Kentucky, Indiana, and Ohio. The beaver ranges north into the Northwest Territories of Canada and to the north slope of Alaska.

Beavers are found throughout all of the Edwards Plateau, except the extreme northwestern portion. Records of occurrence are available from Bexar, Blanco, Crockett, Edwards, Hays, Kimble, Real, Travis, and Val Verde counties on the Edwards Plateau (Fig. 70). The beaver is probably found along all of the Colorado River and its immediate tributaries on the Edwards Plateau, and along all of the major rivers and streams throughout the region. The beaver has been taken in Tom Green and Coke counties in tributaries of the Colorado River off of the Edwards Plateau (Simpson and Maxwell, 1989; Boyd, 1994). Beavers occur on the extreme western Edwards Plateau, along the Pecos and Rio Grande rivers and their immediate tributaries. The northwestern Edwards Plateau and most of Val Verde and Crockett counties have no permanent rivers and streams to support populations of beavers.

*Castor canadensis* is the largest rodent on the Edwards Plateau. *C. canadensis* has chestnut brown pelage, webbed feet, and a nearly hairless, flat, and scaley tail. The venter, flanks, and cheeks are usually lighter in color. Valvular ears and a nictitating membrane covering the eyes are present. The only mammal on the Edwards Plateau likely to be confused with *C. canadensis* is the nutria (*Myocastor coypus*). However, beavers are larger than nutria (average weights 20.4 and 9.1 kg, respectively), and possess a flat, broad tail, whereas the nutria's tail is long and rounded. The beaver's two inside toes of each hind foot have doubled nails utilized in grooming. The front feet are smaller than the rear, and are well-clawed. Beavers utilize the front feet for digging and object manipulation, and, thus, are quite dexterous.
Beavers are restricted to areas around permanent water. They occur commonly in large rivers, impoundments, and large lakes with relatively stable water levels (Hill, 1982). Smaller streams and tributaries may also be inhabited, provided that high water conditions and flooding are rare events. Beavers seem to prefer flat terrain and valley areas with an abundance of winter food sources (Hill, 1982).

The beaver’s diet is exclusively plant material, with much bark and cadmium of willow and cottonwood trees included. Other diet items include cattails, rushes, and sedges (Sealander and Heidt, 1990). Diet varies by season, with green vegetation, other aquatic vegetation and bulbs, willow leaves, and other food consumed in the spring and summer months. Bark and cadmium of trees are cached close to the lodge and are consumed in greater quantities in the autumn and winter months (Jenkins and Busher, 1979). *C. canadensis* is coprophagic, and is able to digest approximately 30 percent of the cellulose consumed in its diet. Reingested feces are not encapsulated as in lagomorphs and are chewed before being swallowed (Buech, 1984). Passage time of food materials through the digestive tract (with reingestion) is about 60 hours (Jenkins and Busher, 1979; Buech, 1984). Fat is stored in the tail of beavers, and, in the southern portion of their range, is utilized during the spring and early summer months. Activity is reduced during this time, possibly because of seasonal physiological changes (Hill, 1982). Beavers are primarily crepuscular and nocturnal in activity (Hill, 1982), but I have observed beavers moving about in early morning or late afternoon hours.

Beavers build either lodges in small ponds or lakes or burrow into the sides of river and stream banks for

Figure 70. Distribution of *Castor canadensis* on the Edwards Plateau.
The ability of beavers to cut down trees is unique, and enables them to build mud and wood lodges and dams even in fast-flowing streams (Jenkins and Busher, 1979). Lodges usually have more than one entrance leading into the structure from beneath the water level. A central chamber is elevated a few inches above the water level within the lodge. The central chamber is lined with grasses and bark and serves as a nest (Jones et al., 1983). Bank dens may have entrances that are accessible only from the water and no building material may be added to the den; or a smaller house of sticks and logs may be constructed around the bank den (Jones et al., 1983).

The social unit is a colony and usually consists of four to eight related individuals (Findley, 1987). Some disagreement is present over the structure of the colony, with some researchers of the opinion that the adult male and female are co-dominant, and other researchers opining that the adult female is dominant over the male partner (Jenkins and Busher, 1979). Territories and activity center around the lodge or den. Adult females tend to be more sedentary than males in their movements (Jenkins and Busher, 1979). Longest movements are made by dispersing young and are usually less than 10 miles in distance (Jenkins and Busher, 1979). Mud and vegetational debris are placed in piles near territorial boundaries and marked with urine, castoreum, and anal gland secretions (Hill, 1982).

Beavers are monogamous in mating habit (Hill, 1982). One litter of kits is produced per year. Breeding may occur from late November to February (Hill, 1982). The gestation period is about 107 days in length (Schmidly, 1984b). Litter size is usually three to four young. Offspring typically stay with their parents until about two years of age; at which time sexual maturity is attained and the young will disperse (Hill, 1982; Schmidly, 1984b).

Two subspecies of beaver occur on the Edwards Plateau; *C. c. texensis* Bailey, 1905, on the northern and central Edwards Plateau, and *C. c. mexicanus* Bailey, 1905, along the Rio Grande and its tributaries on the western Edwards Plateau. Sexual dimorphism is not evident in this species. Ranges of external measurements (Sealander and Heidt, 1990) are: total length, 875-1212; tail length, 230-440; length hind foot, 156-192; ear length, 33-37. Selected cranial measurements of an adult male and female from Edwards County, respectively, are: nasal length, 50.94, 49.49; width rostrum, 31.81, 34.55; postorbital breadth, 27.38, 25.90; zygomatic breadth, 94.51, ——; mastoid breadth, 58.41, 62.70; occipitonasal length, 133.58, 129.94.

Specimens examined (10).—*Edwards Co.:* 14 412800E, 3344700N, 1 (TCWC); 14 412800E, 3347000N, 1 (TCWC); South Llano River, 1 (TCWC). *Hays Co.:* 14 6013000E, 3306500N, 1 (SWTU); Campus Southwest Texas State University, 2 (SWTU). *Kimble Co.:* 14 4362000E, 3354400N, 2 (TCWC); 14 4254000E, 3372000N, 1; 14 4251000E, 3355100N, 1 (TCWC).

Additional records.—*Bexar Co.:* Northwest of San Antonio; Along Medina River (Unspecified Locality). *Blanco Co.:* 14 5719000E, 3360900N. *Crockett Co.:* Along Pecos River (Unspecified Locality). *Edwards Co.:* 14 4129000E, 3355300N (TCWC); 14 4257000E, 3343300N (TCWC); 14 4232000E, 3299400N. *Kimble Co.:* 14 4255000E, 3368200N (TCWC). *Real Co.:* 14 4274000E, 3290100N. *Travis Co.:* 14 6212000E, 3347900N. *Val Verde Co.:* Along Pecos River, Rio Grande River, and Devils River (Unspecified Locality). (Bailey, 1905; Davis, 1940; Davis and Schmidly, 1994).

### Key to Muridae

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<td>1'</td>
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Greatest length of skull more than 52 mm; cheekteeth prismatic; toes of hind feet webbed at their base; tail hairless and laterally compressed.......................................................................................................... *Ondatra zibethicus*

Greatest length of skull 52 mm or less; cheekteeth cuspidate or only semiprismatic; toes of hind feet not webbed; tail haired and round in cross-section ........................................................................................................ 3

Enamel folds of cheekteeth forming an S-shaped pattern; dorsal pelage coarse and black basally with hair tipped with light brown or tan distally; venter grayish; feet grayish in color ................................................................. *Sigmodon hispidus*

Cheekteeth semiprismatic, enamel folds not forming an S-shaped pattern; dorsal pelage not especially coarse and hairs not black distally; venter white in color (at least in part); feet white in color ........................................ 4

Septum between anterior palatine foramina complete; anterior palatine spine bifurcated; anteriointernal reentrant angle of first upper molar (M1) relatively well-developed and deep; dorsal color olivaceous, lateral sides buffy in color; tail not sharply bicolor ed ................................................................. *Neotoma floridana*

Septum between anterior palatine foramina complete or perforate; anterior palatine spine pointed; anteriointernal reentrant angle of first upper molar (M1) poorly developed and shallow; dorsal color steel gray or buffy brown; lateral sides gray or brown in color; tail distinctly bicolor ed ........................................................................................................ 5

Nasal septum usually with maxillovomerine notch; zygomatic breadth 25.40 mm or less; posterior palatal spine usually absent or inconspicuous; dorsum washed with buffy hairs, gular hairs white at the base ......................... *Neotoma albigula*

Nasal septum usually lacking maxillovomerine notch; zygomatic breadth 25.40 mm or greater; posterior palatal spine moderately to well-developed in adults; dorsum steel gray; gular hairs dark at base ............................................................................................................. *Neotoma micropus*

Greatest length of skull less than 20 mm; length of maxillary toothrow less than 3.2 mm; total length 115 or less ................................................................. *Baiomys taylori*

Greatest length of skull more than 20 mm; length of maxillary toothrow more than 3.2 mm; total length greater than 115 mm .............................................. 7

Cheekteeth prismatic; temporal ridges and mastoidal crest well-developed; tail length about one-quarter or less of body length ................................................................................................. *Microtus pinetorum*

Cheekteeth cuspidate; temporal ridges and mastoidal crest weakly developed or absent; tail longer than one-quarter of body length ........................................ 8

Cheekteeth noticeably hypsodont; coronoid process of lower jaw long, high, and pointed; tail length less than 60 percent of head and body length ........................................................................ 9

Cheekteeth not noticeably hypsodont; coronoid process of lower jaw short and blunt; tail length usually more than 60 percent of head and body length ........................................................................ 10
GOETZE—MAMMALS OF THE EDWARDS PLATEAU

9 Length of maxillary toothrow 4 mm or more; tail about two and one-half times length of hind foot; dorsal color buffy cinnamon ................................. *Onychomys arenicola*

9' Length of maxillary toothrow less than 4 mm; tail about twice the length of hind foot; dorsal color steel gray ................................. *Onychomys leucogaster*

10 Upper incisors with single, conspicuous groove on the anterior face; greatest length of skull less than 22.4 mm; insides of ears with conspicuous fringe of brown hairs along outer edge ........................................ 11

10' Upper incisors ungrooved on the anterior face; greatest length of skull more than 22.4 mm; insides of ears without a conspicuous fringe of hairs along the outer edge, hairs inside of ears white ........................................ 13

11 Greatest length of skull 19.19 or shorter; length of rostrum 6.70 mm or shorter; tail length shorter than head and body length; tail with a narrow, distinct, dorsal stripe ......................................................... *Reithrodontomys montanus*

11' Greatest length of skull greater than 19.19 mm; length of rostrum greater than 6.70 mm; tail length about equal to or greater than head and body length; tail without a noticeable dorsal stripe or with a broad, indistinct dorsal stripe ................................................................ 12

12 First primary enamel fold of upper third molar (M3) as long as or longer than the second primary fold; each fold usually extends more than halfway across the tooth; occlusal surface of upper third molar E-shaped; lower third molar (m3) major enamel fold as long as or longer than first primary fold; occlusal surface of lower third molar S-shaped; dorsum a golden brown color; tail much longer than head and body length; tail sparsely haired with no evident dorsal stripe .................................................. *Reithrodontomys fulvescens*

12' First primary enamel fold of upper third molar (M3) distinctly shorter than second primary fold; occlusal surface of upper third molar C-shaped; lower third molar major enamel fold shorter than first primary fold; occlusal surface of lower third molar C-shaped; dorsum tan to light brown in color, with little or no buffy pelage; tail about equal in length to head and body; tail well-haired with a broad, indistinct, dorsal stripe .................................................. *Reithrodontomys megalotis*

13 Interorbital constriction 9.97 mm or less; tail distinctly shorter than head and body length with a narrow, distinct mid-dorsal stripe; hind foot length usually 20 mm or less ............................................................... *Peromyscus maniculatus*

13' Interorbital constriction greater than 9.97 mm; tail about equal to or longer than head and body length with either a broad mid-dorsal stripe or no distinct mid-dorsal stripe; hind foot length greater than 20 mm ................................................................ 14

14 Length of rostrum 9.40 or less; soles and heels of hind feet naked; tail longer than head and body length, tail sparsely haired and lacking a terminal tuft of hairs .......................................................... *Peromyscus eremicus*

14' Length of rostrum greater than 9.40 mm; soles and heels of hind feet well-haired; tail equal to or shorter than head and body length, or, if tail is longer than head and body length, a terminal tuft of hairs present on tail ........................................................................................................ 15
Tail about equal to head and body length or only slightly shorter; tail not
tufted; no buffy lateral line on the sides ........................................................... *Peromyscus leucopus*

Tail longer than head and body length with a conspicuous terminal tuft
of hairs; buffy lateral line present on the sides .................................................... 16

Length of maxillary toothrow 4.0 mm or greater; hind foot length
22 mm or greater; tail well haired; ankle of hind foot gray or brownish
in color ................................................................................................. *Peromyscus attwateri*

Length of maxillary toothrow less than 4.0 mm; hind foot length
22 mm or smaller; tail sparsely haired, with annulations conspicuous;
ankle of hind foot white in color ............................................................ *Peromyscus pectoralis*

**Family Muridae—Rats and Mice**

*Reithrodontomys fulvescens*  
Fulvous Harvest Mouse

*Distribution.*—The fulvous harvest mouse ranges
from Honduras and El Salvador northward throughout
most of Mexico and westward to New Mexico and Ari­
izona. This species ranges through most of Trans-Pecos
and the eastern half of Texas northward to southern Kan­
sas, and thence, eastward to Missouri, and south to Mis­
issippi and Louisiana.

The fulvous harvest mouse is widespread on the
Edwards Plateau, ranging through the southern and east­
er portions of the region. The species, however, is not
usually collected in great numbers at any locality within
its range. Records exist from Bexar, Callahan, Comal,
Hays, Kerr, San Saba, Travis, and Val Verde counties
(Fig. 71).

*Reithrodontomys fulvescens* may be distinguished
from the other two species of harvest mice occurring on
the Edwards Plateau (*R. megalotis* and *R. montanus*)
by its more golden dorsal pelage and a tail length that
exceeds the body length. The venter and feet are white
or pale buff in color. The tail of *R. fulvescens* is more
sparingly haired than that of *R. megalotis* and *R.*
*montanus*. Characteristics of the upper third molar help
to separate *R. fulvescens* from *R. megalotis* and are
given in the account of the latter species. *Reithrodontomys*
may be distinguished from *Peromyscus* by the presence of anteriorly grooved inci­
sors in harvest mice.

The fulvous harvest mouse favors weedy and over­
grown habitats. Soil substrate seems not as important
a factor in habitat selection as is dense vegetation and

The fulvous harvest mouse is relatively tolerant
of conspecifics. There is some evidence of pair bond­
ing in *R. fulvescens*. Many nests, when examined, are
occupied by two harvest mice (Spencer and Cameron,
1982). Multiple captures reported by researchers in
one study involved a significant number of male-female
captures in one or two traps adjacent to each other, sug-
gesting pair bonding between males and females (Spencer and Cameron, 1982).

Female fulvous harvest mice appear to be diestrous with a tendency toward polyestry in more southern areas. A bimodal breeding season in Texas has been proposed, with peaks in late spring and early autumn months (Spencer and Cameron, 1982). Peak population densities have been reported in July and December through February. Litter size ranges from two to four young.

The subspecies on the Edwards Plateau is *Reithrodontomys fulvescens*laceyi* J. A. Allen, 1896. Mean external measurements of three males are: total length, 169; tail length, 95.3; length hind foot, 19.67; ear length, 13.67. Selected mean cranial measurements of four males and four females from Montague County are respectively: greatest length skull, 20.52, 21.10; length rostrum, 7.13, 7.30; breadth rostrum, 3.5, 3.73; interorbital breadth, 3.93, 3.61; zygomatic breadth, 10.71, 10.70; cranial breadth, 10.21, 10.14.

**Specimens examined (10).—**

**Bexar Co.:** 14 541100E, 3284300N, 2; **Callahan Co.:** 14 447600E, 3562600N, 1; 14 460700E, 3572400N, 1; **Comal Co.:** 14 582400E, 3288200N, 1 (STSU). **Hays Co.:** 14 594600E, 3309800N, 1 (SWTU). **Kerr Co.:** 14 446800E, 3326300N, 1 (SWTU). **San Saba Co.:** 14 531300E, 3450800N, 1; **Travis Co.:** 14 618900E, 3341100N, 1 (SWTU); **Decker’s Lake, 1 (SWTU).**

**Additional records.—** **Kerr Co.:** 14 441600E, 3312500N (TCWC); 14 434200E, 3337400N (TCWC). **Val Verde Co.:** Unspecified Locality. (Hooper, 1952; Davis and Schmidly, 1994).
Reithrodontomys megalotis
Western Harvest Mouse

**Distribution.**—The western harvest mouse has an extensive distribution in North America. The species ranges from southern Mexico northward through portions of all the Great Plains states, eastward to Minnesota, Wisconsin, and Indiana. The western harvest mouse ranges westward throughout California, Oregon, and Washington, and northward into southern British Columbia, Alberta, and Saskatchewan, Canada.

The western harvest mouse appears to be only now expanding its range onto the Edwards Plateau from western Texas. This species has been recorded from Howard and Glasscock counties on the Edwards Plateau (Fig. 72), where populations may be expanding their ranges from the Llano Estacado region northwest of the Edwards Plateau.

*Reithrodontomys megalotis* is most easily confused with the fulvous harvest mouse (*R. fulvescens*) described in the previous account. The western harvest mouse differs in having a tail more nearly half the total length (*R. fulvescens* tail length is greater than the body length), and a more brownish pelage dorsally (*R. fulvescens* usually has golden-brown dorsal pelage and a buffy area laterally across the shoulders and lateral sides). Annulations are more readily distinguished on the tail of *R. fulvescens* than on the tail of *R. megalotis*, although neither species has a distinctly bicolored tail. The venter, feet, and underside of the tail are white in *R. megalotis*. The western harvest mouse and fulvous harvest mouse may be readily separated by characters of the third upper molars. *R. fulvescens* has a well-developed lingual fold, a distinct first labial fold, and the second labial fold is directed more horizontally across the occlusal surface of the tooth. *R. megalotis* has little or no lingual fold, a short first labial fold, and the second labial fold is directed more antero-posteriorly across the occlusal surface of M3.

The western harvest mouse favors grassy and weedy habitats such as lightly grazed pastures, meadows, fencerows, fallow fields, and edge habitats between agricultural and riparian areas (Webster and Jones, 1982). The western harvest mouse seems to tolerate higher percentages of brush in its habitat than does the plains harvest mouse (*R. montanus*).

*R. megalotis* is granivorous and consumes minor amounts of vegetable and animal matter (mostly arthropods). Seeds of various grasses, mustards, and legumes are included in the diet, as well as cultivated cereal grains, such as barley, wheat, and oats. Beetles, species of lepidopterans, and spiders have been reported from the stomach contents of *R. megalotis* (Jones et al., 1983). Harvest mice are strictly nocturnal in foraging and activity periods.

Western harvest mice live in nests constructed underneath brush, rocks, or sometimes arborally in shrubs and brush. The nests resemble those of birds, being constructed of plant fibers, and plant down obtained from species of thistles, milkweed, and other plants. An entrance hole close to the bottom of the globular-shaped nest leads to the inner nest chamber.

These small rodents are among the most tolerant of conspecifics of all murid rodents. Communal nesting is rather common in *R. megalotis*, and, under laboratory conditions, newcomers are even accepted into a nest containing females and young (Jones et al., 1983). Huddling together in the nest helps *R. megalotis* to conserve energy and reduce its metabolic rate by lowering overall surface area of the group exposed to the external environment. The western harvest mouse will enter torpor easily under low temperatures, but is readily revived from this state by warming from an external heat source. Torpor in *R. megalotis* is probably another mechanism to help reduce metabolic cost of maintaining a constant body temperature when at an unfavorable surface area to volume body ratio.

Females are polyestrous and may produce several litters per year, depending upon environmental conditions. Males are polygamous in breeding habit. One female in captivity produced 14 litters of young in 11 months (Jones et al., 1983). Gestation period is approximately 21 days, and a postpartum estrous is present in *R. megalotis*. Most reproduction occurs from early spring to late autumn months, with a reduction in reproductive activity in midsummer months (Webster and Jones, 1982). Litter size usually ranges from two to six young.

The subspecies occurring on the Edwards Plateau is *R. m. megalotis* (Baird, 1858). Mean external and cranial measurements of four adult males from Glasscock County are: total length, 141.75; tail length,
Figure 72. Distribution of Reithrodontomys megalotis on the Edwards Plateau.

71.75; length hind foot, 16.5; ear length, 14.5; greatest length skull, 21.04; length rostrum, 7.48; breadth rostrum, 3.39; zygomatic breadth, 10.61; least interorbital breadth, 3.14; cranial breadth, 10.04.


Reithrodontomys montanus
Plains Harvest Mouse

Distribution.—The plains harvest mouse ranges from northwestern Mexico, northward through southeastern Arizona, the southern and eastern portions of New Mexico, eastern Colorado, and north through portions of all of the Great Plains States of the United States. The plains harvest mouse ranges eastward to southwest ern Missouri, northwestern Arkansas, and southeastern Texas.

The plains harvest mouse’s range has been reported as including all except the southwestern portion of the Edwards Plateau (Wilkins, 1986). Records of the plains harvest mouse from the Edwards Plateau to verify this range are scarce. Records are available from Bexar, Coke, Kerr, Mason, McCulloch, Menard, Nolan, Schleicher, Tom Green, and Travis counties (Fig. 73).

Reithrodontomys montanus might be mistaken for a small Peromyscus, but its buffy dorsal pelage and smaller size usually serve to positively identify this species of harvest mouse. In addition, the upper incisors of Reithrodontomys have an anterior, lateral groove. The tail has a thin, distinct dark dorsal stripe down its length. Upperparts are buffy gray to gray with a distinct, dark,
mid-dorsal region. The venter, underside of the tail, and a small patch behind the ears are white in color. The plains harvest mouse is smaller than *R. fulvescens*, and has a much shorter and more heavily haired tail. The fulvous harvest mouse also has a greater amount of buffy pelage on the lateral sides than does *R. montanus*. The western harvest mouse has a tail nearly equal to, or longer than, its body length, and the tail is indistinctly bicollored, whereas the tail of *R. montanus* is shorter than its body length. The cusps of the first two upper molars are shorter and the principal enamel folds are broad and long in *R. montanus*, as opposed to longer cusps and shorter enamel folds in *R. megalotis* (Hooper, 1952). The plains harvest mouse and the western harvest mouse also may be separated by least breadth of the interorbital constriction. Least interorbital breadth averages 2.946 ± 0.124 in *R. montanus*, and 3.204 ± 0.119 in *R. megalotis* (Stangl et al., 1993).

These mice prefer grassy and weedy habitats throughout their range on the Edwards Plateau (McAllister and Earle, 1991; Goetze et al., 1993). Overgrown highway right-of-ways with mixed grasses and forbs, such as sunflowers, provide excellent habitats for these mice. Other suitable habitats include hayfields, moderately grazed pastures, sagebrush habitats, riparian habitats, and abandoned fields (Wilkins, 1986).

The plains harvest mouse is herbivorous and insectivorous (Wilkins, 1986). The diet of the plains harvest mouse consists mostly of grass seeds and some vegetation, but insects are consumed in minor amounts. Seeds are consumed from brome, grama, bluestem, foxtail, and other grasses. The seeds and flower heads of broomweeds, ironweed, and snow-on-the-mountain are known to be eaten by *R. montanus* (Wilkins, 1986).
This species is nocturnally active, like most other murid rodents.

Nests of grass are constructed in areas of dense vegetation, and are usually located a few centimeters off the ground (Wilkins, 1986). These aerial nests are globular in shape. Nests may also be constructed inside tin cans, bottles, and other objects near the ground, underneath discarded lumber, logs, and within burrows (Wilkins, 1986; Sealander and Heidt, 1990). The plains harvest mouse is active throughout the year, and does not hibernate within its nest.

Home ranges of *R. montanus* range from 0.23 ha to 0.84 ha in size in East Texas (Wilkins, 1986). Maximum distances moved within an area are small. Roadways may constitute effective barriers to dispersal of the plains harvest mouse (Wilkins, 1986). These mice are tolerant of conspecifics. Populations appear to be scattered over the Edwards Plateau and densities of this mouse at any single locality seem to be low. At any particular location, *R. montanus* is usually taken in the fewest numbers when compared to other rodents (Wilkins, 1986).

Males, females, and young may be caged together and no agonistic behavior is evident between individuals (Jones et al., 1983). Where the plains harvest mouse and the fulvous harvest mouse are sympatric, *R. montanus* occurs in areas of shorter or less dense vegetative cover (Wilkins, 1986). Where *R. montanus* is sympatric with the pygmy mouse and hispid cotton rat, the plains harvest mouse is subordinate to both of the aforementioned species; *R. montanus* exhibits avoidance behavior whenever it encounters cotton rats or pygmy mice (Putera and Grant, 1985). Odors and scents may enable the plains harvest mouse to avoid contact with other rodents in the wild (Putera and Grant, 1985).

The plains harvest mouse probably breeds throughout the year in Texas (Davis and Schmidly, 1994). Females are polyestrous, and may produce several litters per year, given favorable environmental conditions. Gestation period is approximately 21 days (Wilkins, 1986). Litter sizes range from two to five young (Schmidly, 1983). *R. montanus* may be able to produce young within 85 days of birth (Wilkins, 1986). Average external measurements of four specimens from the Edwards Plateau (three females and one male) are: total length, 114.75; tail length, 49.5; length hind foot, 15; ear length, 11.25. Selected mean cranial measurements for these same individuals are: greatest length skull, 18.90; zygomatic breadth, 10.02; least interorbital breadth, 3.04; length of rostrum, 6.51; cranial breadth, 9.30; length maxillary toothrow, 2.99.


**Peromyscus attwateri**

Texas Mouse

**Distribution.**— The Texas mouse ranges from the Edwards Plateau and Llano Uplift northward to the eastern escarpment of the Llano Estacado and onto the Rolling Plains of Texas. This mouse ranges through central and eastern Oklahoma, eastward into northwestern Arkansas and southwestern Missouri, as far north as southeastern Kansas.

The Texas mouse has a widespread distribution on the Edwards Plateau, but these mice are usually not taken in great numbers at any single locality. The Texas mouse ranges through all but the extreme southwestern and western counties of the Edwards Plateau. Records are available from Bandera, Callahan, Coke, Crockett, Edwards, Hays, Howard, Kendall, Kerr, Kimble, Llano, Mason, Menard, Nolan, Reagan, San Saba, Schleicher, Sutton, Taylor, Tom Green, Travis, and Uvalde counties (Fig. 74).

*Peromyscus attwateri* is a medium-sized mouse, with a tail longer than its body length and terminally tufted. The Texas mouse may sometimes be confused with the white-ankled mouse (*P. pectoralis*) on the
Edwards Plateau. Both *P. attwateri* and *P. pectoralis*, have buffy orange, lateral shoulder patches, and tails exceeding their body lengths. *P. attwateri* has larger hind feet (24-27) than *P. pectoralis* (21-23); the ankles of the Texas mouse are dusky or gray in color, whereas the ankles of *P. pectoralis* are white. The distal tip of the baculum of *P. attwateri* is rounded and blunt, whereas the bacalar tip of *P. pectoralis* is long and attenuated (Schmidly, 1974b).

The Texas mouse is most often found inhabiting juniper covered slopes on the Edwards Plateau. This mouse has a partially dendritic distribution throughout its range within Texas, and is saxicolous in its choice of habitat (Schmidly, 1974a). Level, grassy areas and meadows are generally avoided by *P. attwateri*. The Texas mouse and the white-ankled mouse often are ecologically separated in different habitats in many localities where they occur, but may be occasionally taken together in a single trapline.

Etheredge et al. (1989) discussed habitat selection between *P. attwateri* and *P. pectoralis* in Tom Green County. Where the two species were sympatric, *P. attwateri* utilized trees for refuge and escape cover more often than *P. pectoralis*.

Seeds and insects make up the bulk of this animal’s diet. *P. attwateri* readily feeds upon grasshoppers, crickets, and similar arthropods when these are available (Dalquest and Homer, 1984). Other diet items include juniper berries, green vegetation, acorns, and plant bulbs (Schmidly, 1974a). This mouse is highly arboreal and may forage for berries and nuts while in trees. The Texas mouse, like all species of *Peromyscus*, is nocturnal in foraging and activity period. The Texas mouse does not hibernate and is active throughout the year.
Nests are constructed of grasses, plant fibers, and dry leaves; the nest is globular in shape. *Peromyscus attwateri* constructs its nest underneath rocks, in rock crevices, or in other natural cavities (Sealander and Heidt, 1990).

Home ranges of the Texas mouse are small. Linear movements of males average 47.5 m, and linear movements of females average 27.4 m. Home ranges may nest together without agonistic behaviors when in or in other natural cavities (Sealander and Heidt, 1990). Constructs its nest underneath rocks, in rock crevices, dry leaves; the nest is globular in shape.

Ear movements of males average 47.5 m, and linear movements of females average 27.4 m. Home ranges may nest together without agonistic behaviors when in or in other natural cavities (Sealander and Heidt, 1990). Constructs its nest underneath rocks, in rock crevices, dry leaves; the nest is globular in shape.

There is little or no genetic interchange between populations on different ridges and mountaintops in Arkansas (Sealander and Heidt, 1990), indicating that *Peromyscus attwateri* is fairly habitat specific. Valley areas and other topographic features may act as barriers to dispersal, thereby isolating populations between ridges and other rocky areas. A similar situation may occur on the Edwards Plateau, as this species is rarely captured in or in other natural cavities (Sealander and Heidt, 1990). Constructs its nest underneath rocks, in rock crevices, dry leaves; the nest is globular in shape.

Little is known concerning reproduction in *Peromyscus attwateri*. The Texas mouse demonstrates seasonal variation in litter sizes with numbers of young ranging from three to six (Schmidly, 1974a). The gestation period is unknown. The Texas mouse is probably reproductively active throughout the year. Breeding peaks in the spring and autumn months, with a lull in the hot summer months (Sealander and Heidt, 1990). Mice may attain sexual maturity at approximately 21 days of age (Schmidly, 1974a).

*Peromyscus attwateri* (J. A. Allen, 1893) is a monotypic species. Only maxillary toothrow length is significantly different between sexes, all other mensural characters show no significant sexual variation (Schmidly, 1973). Average external measurements of 10 adults (five males and five females, combined) from the Edwards Plateau are: total length, 190.5; tail length, 98; length hind foot, 24; ear length, 19. Selected cranial measurements of six adults (two males and four females, combined) from the Edwards Plateau are: greatest length skull, 27.60 (four specimens); zygomatic breadth, 13.99; interorbital constriction, 4.65; length rostrum, 10.58 (four specimens); breadth rostrum, 4.63; cranial breadth, 13.13; length maxillary toothrow, 4.05.
Peromyscus eremicus
Cactus Mouse

Distribution.—The cactus mouse ranges from north central Mexico, north through Trans-Pecos, Texas, and southern New Mexico, and eastward through south central and northwestern Arizona. This species ranges northward as far as southern Utah and Nevada and westward to southern California, and Baja California. Several insular populations are found off the coast of Baja California.

The cactus mouse is known only from Val Verde County on the Edwards Plateau (Fig. 75). This rodent may occur along the eastern side of the Pecos River throughout much of the region, but specimens are not on hand to verify this range.

Peromyscus eremicus varies in color dorsally from huffy to almost slate gray. The tail is sparsely haired and only slightly bicolor. The length of the tail is approximately equal to body length in this species. The venter, feet, and underside of the tail are white in color. The soles of the hind feet are naked, as opposed to the haired heels and soles of other species of Peromyscus occurring on the Edwards Plateau. The phallus of P. eremicus has a vase-shaped glans, the baculum is broad or thick, and the dental pattern of the cactus mouse is simple with no or few accessory styles or lophs on the teeth.

The cactus mouse is taken mostly in desert shrub vegetation associations within its range in Texas. These mice occur in habitats varying from rocky areas with shallow soils to sandy substrates and riparian areas of relatively dense vegetative cover (Veal and Caire, 1979). The cactus mouse also inhabits stone walls, abandoned houses and huts, rock heaps, abandoned burrows of gophers and kangaroo rats, and burrows at the base of mesquite trees. P. eremicus is the most typical and widespread member of the genus Peromyscus found in arid and desert habitats (Baker, 1968).

The diet of P. eremicus consists primarily of the fruit and flowers of shrubs. Seeds, insects, and green vegetation are consumed, depending upon their abundance within a foraging area (Veal and Caire, 1979). Foraging and other activities away from sheltered areas are conducted nocturnally. The cactus mouse may forage both terrestrially and arborally in mesquite and other trees and shrubs in an area. Mesquite and hackberry fruits are included in the diet of this species.

Under laboratory conditions, P. eremicus constructs fluffy, globular nests from provided materials (Veal and Caire, 1979). The structure and composition of nests and burrows of the cactus mouse under natural conditions is not known. The cactus mouse sometimes inhabits portions of the nests of woodrats (Hoffmeister, 1986) and the abandoned burrows of other animals.

The cactus mouse has the ability to go into torpor when it is water-stressed. During torpor there is a marked reduction of body temperature and oxygen consumption. The basal metabolic rate is low. This factor helps in water conservation in the species. Other researchers have suggested that P. eremicus may aestivate during the hottest months of the year as a means of avoiding water deprivation and stress (Hoffmeister, 1986).

The social structure of P. eremicus is a loose monogamy with a higher tolerance of females toward males than is usually found within other members of the genus (Eisenberg, 1968). The home ranges of males show considerable overlap, whereas those of females are more exclusive. Other researchers have found individual P. eremicus to be mutually incompatible in the natural state (Veal and Caire, 1979).

Females of P. eremicus are polyestrous, and breed throughout the year in parts of their range, but reproduction is curtailed during the hottest months of the year. Mean age at first estrous in P. eremicus is 39 days, so maturation is rapid in this species (Millar, 1989). The number of young per litter varies from one to five; averaging about three (Schmidly, 1977).

The subspecies on the Edwards Plateau is P. e. eremicus (Baird, 1858). External measurements of two male specimens from Val Verde County are: total length, 155, 160; tail length, 80, 82; length hind foot, 18, 19; ear length, 16, 16. Selected mean cranial measurements of 20 individuals (Schmidly, 1977) are: greatest length...
skull, 25.48; length rostrum, 9.36; interorbital breadth, 4.05; mastoidal breadth, 11.14; skull depth, 9.10; length maxillary toothrow, 3.74.

Specimens examined (2).—Val Verde Co.: 14 289600E, 3299300N, 2 (MWSU).


**Peromyscus leucopus**
White-footed Mouse

**Distribution.** — The white-footed mouse ranges from southeastern Mexico, northward to Durango, Coahuila, and Chihuahua in central and northern Mexico, and into the conterminous United States. The white-footed mouse ranges from Arizona in the southwest, into New Mexico, southeastern Colorado, and throughout portions of all the Great Plains states, and into northeastern Wyoming and eastern Montana. This mouse is found throughout almost all of the eastern United States, excluding Florida, and reaches distributional limits in northern Vermont, New Hampshire, and Maine. The white-footed mouse ranges northward into southern Alberta, Saskatchewan, and Ontario provinces of Canada.

The white-footed mouse ranges throughout all of Texas except the northeastern coastal bend (Carleton, 1989). This species has a ubiquitous distribution on the Edwards Plateau, but is not collected as commonly as some other species of *Peromyscus*. Records are available from Blanco, Burnet, Callahan, Coke, Comal, Concho, Crane, Crockett, Ector, Edwards, Glasscock, Hays, Howard, Irion, Kendall, Kerr, Kimble, Llano, Mason, McCulloch, Menard, Nolan, Real, Runnels, San
Peromyscus leucopus is usually slate gray dorsally. The venter, inside of the legs, feet, chin, and underside of the tail are white. The white-footed mouse's tail is well-haired, but indistinctly bicolored. The tail length and head and body length are approximately equal. *P. leucopus* is most easily confused with the deer mouse (*P. maniculatus*) on the Edwards Plateau. *P. leucopus* has a longer, less bicolored tail, larger hind feet, and a longer rostrum than does *P. maniculatus*. The total length of *P. leucopus* is less than that of *P. attwateri* and *P. pectoralis*. The white-footed mouse also lacks an ochraceous lateral stripe that is found on *attwateri* and *pectoralis*, and the tail of *P. leucopus* does not have a terminal tuft, as does the tail of *attwateri* and *pectoralis*. *P. leucopus* is smaller in size, has a more heavily haired tail, and has a haired heel, as opposed to the larger size, sparsely haired tail, and naked heel of *P. eremicus*.

On the Edwards Plateau, the white-footed mouse is associated with level, brushy pasture lands. Where *P. leucopus* and *P. maniculatus* occur together, the white-footed mouse is more frequently trapped around brush and shrubs. *P. maniculatus* inhabits more open patches of habitat and grassy areas. The white-footed mouse usually is not trapped in rocky, broken terrain.

The white-footed mouse is primarily granivorous and herbivorous in diet. The diet includes seeds, plant leaves and stalks, acorns, pecan nuts, and fungi. Insects, snails, and other invertebrates are eaten occasionally (Schmidly, 1983). The white-footed mouse is a selective forager, and resident white-footed mice will choose a lower diversity diet than immigrants dispersing into an area (Kaufman and Kaufman, 1989).

*P. leucopus* forages for food items both upon the ground and in brush and trees (McShea and Franq, 1984). Seed-caching behavior occurs in *P. leucopus* and is most common in the autumn months (Kaufman and Kaufman, 1989). The white-footed mouse is nocturnally active throughout the year.

Nests are constructed in the abandoned burrows of other mammals, underneath rocks and brush piles, within the dens of woodrats, or in old logs, stumps, or other available cover (Wolff, 1989). Abandoned nests of tree squirrels are utilized sometimes, and nests may be constructed in the hollows of trees (Wolff, 1989). More than one nest may be utilized within an animal's home range. The nest is constructed from grasses, leaves, and the fibers of plants such as milkweed (Jones et al., 1983). Nests are usually occupied by a single individual, except for mother-young groups and communally nesting individuals in the winter months (Wolff, 1989).

Home range sizes may vary from 242 square meters to over 3000 square meters (Wolff, 1989). A vertical component is also present in the home range of *P. leucopus* in appropriate habitats (Wolff, 1988). Female *P. leucopus* have home ranges that are non-overlapping and are maintained by mutual avoidance when population densities are low. When population densities are high, females maintain home ranges by overt aggression (Wolff, 1989). Males have home ranges which overlap those of several females within an area. A resident male may cohabit with a female until the time of parturition, at which time the male is excluded from the nest (Wolff, 1989). Dispersal of young animals occurs shortly after weaning. Young born during the autumn months may remain within the maternal home range and nest communally throughout the winter months (Wolff, 1989). Individuals disperse from the communal nest in the spring and establish home ranges of their own (Wolff, 1989).

The white-footed mouse is probably reproductively active throughout the year. Factors known to influence the breeding season of *P. leucopus* include, temperature, precipitation, and food supply (Millar, 1989). Reproductive activity of *Peromyscus* is known to be extremely sensitive to food restrictions (Millar, 1989). The white-footed mouse is polyestrous. Males are promiscuous in mating habit (Wolff, 1989). The gestation period ranges from 23 to 37 days, depending upon the reproductive state of the female. Females that are still lactating from a previous brood have longer subsequent gestation periods (Millar, 1989). In Texas, three to six young are common litter sizes for *P. leucopus* (Dalquest and Horner, 1984). Multiple litters may be produced each year.

The subspecies of white-footed mouse on the Edwards Plateau is *P. l. texanus* (Woodhouse, 1853). Sexual dimorphism is not apparent in the white-footed mouse (Lowery, 1974). Average external measurements of five adults (four females and one male) from the...
Figure 76. Distribution of *Peromyscus leucopus* on the Edwards Plateau.

Edwards Plateau are: total length, 170.8; tail length, 74.4; length hind foot, 20.6; ear length, 16.6. Selected mean cranial measurements of four adults (three females and one male) from the region are: greatest length skull, 25.86; zygomatic breadth, 13.60; cranial breadth, 12.10; interorbital constriction, 4.24; length rostrum, 9.54; length maxillary toothrow, 3.61.

**Specimens examined** (133).—Burnet Co.: 14 562000E, 3383600N, 1 (SWTU). Callahan Co.: 14 447500E, 3562600N, 3; 14 447200E, 3558300N, 4. Coke Co.: 14 339700E, 3548800N, 1 (ASNHC); 14 355100E, 3548400N, 1 (ASNHC); 14 355600E, 3548100N, 1 (ASNHC); 14 339000E, 3522700N, 1 (ASNHC); 14 345800E, 3515200N, 4 (ASNHC); 14 347000E, 3512500N, 1 (ASNHC); 14 332000E, 3509800N, 1 (ASNHC); 14 334000E, 3509000N, 3 (ASNHC); 14 331300E, 3509200N, 2 (ASNHC). Comal Co.: 14 584600E, 3285500N, 1 (SWTU); 14 587600E, 3287500N, 1 (SWTU). Crane Co.: 13 743900E, 3491600N, 2 (ASNHC); 13 751400E, 3488400N, 1 (ASNHC); 13 753500E, 3470500N, 1. Crockett Co.: 14 240900E, 3423100N, 1. Ector Co.: 13 752400E, 351200N, 1. Glasscock Co.: 14 282800E, 3522800N, 3. Hays Co.: 14 588600E, 3321100N, 1 (SWTU); 14 606100E, 3309300N, 1 (SWTU). Howard Co.: 14 291400E, 356600N, 3 (ASNHC); 14 290400E, 3560500N, 1 (ASNHC); 14 282700E, 3555700N, 1 (ASNHC); 14 280700E, 3554800N, 1. Irion Co.: 14 296800E, 3477100N, 2 (ASNHC); 14 293500E, 3483100N, 1 (MWSU); 14 336800E, 3462800N, 1 (ASNHC). Kerr Co.: 14 448200E, 3326000N, 3 (SWTU). Kimble Co.: 14 4440400E, 3393800N (MWSU), 2; 14 353200E, 3386300N, 1; 14 425400E, 3372000N, 3. McCulloch Co.: 14 443000E, 3482400N, 1; 14 473500E,
3438000N, 2. Menard Co.: 14 451100E, 3415000N, 1. Nolan Co.: 14 368000E, 3592800N, 3 (MWSU). Real Co.: 14 426200E, 3288500N, 1; 14 428600E, 3278400N, 1 (SWTU). Runnels Co.: 14 406100E, 3506800N, 6. San Saba Co.: 14 508000E, 3427400N, 1 (MWSU). Schleicher Co.: 14 347400E, 3410600N, 1. Taylor Co.: 14 425600E, 3538800N, 1 (MWSU). Tom Green Co.: 14 333000E, 3504400N, 1 (ASNHC); 14 353200E, 3478000N, 2 (ASNHC); 14 352800E, 3487000N, 5 (ASNHC); 14 353800E, 3483800N, 3 (ASNHC); 14 357100E, 3446600N, 2 (ASNHC); 14 357800E, 3446000N, 1 (ASNHC); 14 357400E, 3444000N, 7 (ASNHC); 14 358400E, 3444000N, 1 (ASNHC). Travis Co.: Hwy. I35 and Stassney Rd., 1 (SWTU); 14 620300E, 3351600N, 1; 14 618400E, 3346800N, 1 (TNHC); 14 617000E, 3362900N, 1 (TNHC); 14 622000E, 3351400N, 1 (TNHC); 14 618400E, 3368000N, 2 (TNHC); 4 mi. E Gustin, 1 (TNHC); 14 622100E, 3330500N, 1 (TNHC). Upton Co.: 13 758200E, 3468600N, 7; 13 768400E, 3448400N, 3 (ASNHC); 14 423400E, 3273700N, 1 (SWTU); 14 430800E 3273600N, 15; 14 454500E, 3241800N, 3 (TNHC).


_Permyscus maniculatus_ is most easily confused with _P. leucopus_, which is described in the previous account. The deer mouse is smaller in size than _P. leucopus, _P. maniculatus_ has a shorter, more distinctly bicolored tail, and has smaller hind feet than _P. leucopus_, The rostrum of _P. maniculatus_ is shorter than _P. leucopus’_ rostrum (less than 9.40 mm in _P. maniculatus_ and greater than 9.40 mm in _P. leucopus_), and the anterior portion of the brain case has a more squarish appearance in the deer mouse, as opposed to a more rounded anterior braincase margin in _P. leucopus_. The zygomatic arches of the deer mouse are more nearly straight, as opposed to convex in _P. leucopus_. The deer mouse is much smaller in size than _P. eremicus_, and has a more heavily haired, shorter tail. _P. maniculatus_ is smaller than _P. attwateri_ and _P. pectoralis_, and lacks the terminal tail tuft and buffy lateral sides found on _P. attwateri_ and _P. pectoralis_.

_P. maniculatus_ is frequently trapped in lowland, grassy valleys and along grassy highway rights-of-way on the Edwards Plateau. This mouse may also be found inhabiting fields, abandoned buildings, and living commensally with humans in some areas (Jones et al., 1983). _P. maniculatus_ has probably benefited from human activities and habitat alterations since European settlement of the United States (Baker, 1968). The deer mouse rarely inhabits brushy areas whenever it is sympatric with _P. leucopus_, and _P. maniculatus_ is rarely captured in rocky, broken habitats. Habitats with dense leaf and plant litter also are avoided by _P. maniculatus_ (Clark and Kaufman, 1991).

The deer mouse feeds on vegetation, seeds, insects, and occasionally on other dead mice. There is some evidence that food is stored during the fall (Schmidly, 1983). These mice are nocturnally active. Activities are significantly curtailed during nights of higher moonlight illumination (Brillhart and Kaufman, 1991). Seeds upon the surface of the ground and seeds...
buried within the soil are located by olfaction (Kaufman and Kaufman, 1989). Deer mice do not hibernate, but may become torpid in cold weather conditions.

Deer mice den underneath rocks, stumps, brush piles, inside eroded root channels, and within soil cracks (Jones et al., 1983). *Peromyscus maniculatus* lives in burrows that either it constructs, or *P. maniculatus* utilizes burrows occupied after the previous resident has vacated. This mouse is sometimes captured near kangaroo rat burrows and woodrat nests (Hoffmeister, 1986). Burrow tunnels enter the ground at an inclination of approximately 30 degrees. The main tunnel branches and leads to a nest chamber (Flury, 1948). Nests are constructed of grasses and are lined with plant down (Jones et al., 1983). Food may also be stored within the burrow, especially in winter (Jones et al., 1983). Multiple burrows may be utilized within an individuals' home range (Wolff, 1989).

The deer mouse is rather territorial in social habit, with females becoming more territorial during the breeding season. Size of territories and spacing effects are not strictly density dependent. Apparently, a minimum area is occupied regardless of population density (Wolff, 1989). Age structure of the population, habitat characteristics, and sex ratios also may affect home range sizes. Home range size may vary from 5 to 25 ha (Stickel, 1968). The home ranges of individuals of similar sex do not overlap, but the home ranges of males may overlap the home ranges of several females (Wolff, 1989). Nightly movements vary, however, adult females usually move the shortest distances and dispersing juveniles the longest distances (Jones et al., 1983).
Females are polyestrous and are promiscuous breeders. Males are polygamous in mating habit. More than one litter of young may be produced per year. Most young of *P. maniculatus* are born in spring and summer months. Pregnant females have been collected on the Edwards Plateau in the months of March, May, and June. The gestation period ranges from 22 to 27 days (Sealander and Heidt, 1990). Three to six young usually constitute a litter, with larger numbers possible (Dalquest and Horner, 1984).

Two subspecies of *P. maniculatus* occur on the Edwards Plateau. *P. m. pallescens* J. A. Allen, 1896 throughout most of the region, and *P. m. blandus* Osgood, 1904 on the far western Edwards Plateau (Hollander et al., 1987). The two subspecies of *P. maniculatus* are not sexually dimorphic (Cooper et al., 1993). Average external measurements of three females and seven males (combined) from the Edwards Plateau are: total length, 135; tail length, 55; length hind foot, 18; ear length, 14. Selected mean cranial measurements of seven individuals from the region (two females and five males, combined) are: greatest length skull, 23.26; zygomatic breadth, 11.98; interorbital constriction, 3.72; length rostrum, 8.74; breadth cranium, 10.82; length maxillary toothrow, 3.30.

*T. W. Sealander* and *J. A. Allen*.


**Peromyscus pectoralis**

White-ankled Mouse

**Distribution.—** The white-ankled mouse ranges from central Mexico northward into the conterminous United States in Texas. This species ranges from central Texas westward throughout most of Trans-Pecos, Texas, and into southeastern New Mexico. The white-ankled mouse occurs on the Rolling Plains of Texas, northward into south-central Oklahoma.

The white-ankled mouse occurs throughout all except the extreme northwestern Edwards Plateau. Records exist from Bandera, Bexar, Blanco, Burnet, Callahan, Coke, Comal, Concho, Crane, Crockett, Edwards, Hays, Irion, Kendall, Kerr, Kimble, Kinney, Llano, Mason, McCulloch, Menard, Nolan, Real, San Saba, Sutton, Taylor, Tom Green, Travis, Upton, Uvalde, and Val Verde counties (Fig. 78).

*Peromyscus pectoralis* is similar in appearance to *P. attwateri*, and may occasionally be confused with that species. The tail of the white-ankled mouse is less heavily haired and more distinctly bicolored than the tail of the Texas mouse. Annulations are rather conspicuous on the tail of *P. pectoralis*. Length of the molar toothrow is usually less than 4.1 in *pectoralis*, and greater than 4.1 in *attwateri*. For additional comparisons of morphological characters of the two species, see the account of *P. attwateri*.

The white-ankled mouse is a saxicolous species. *P. pectoralis* is an inhabitant of steep slopes and rocky ledges on the Edwards Plateau. The white-ankled mouse is often found along massive limestone outcrops characteristic of stream canyons (Schmidly, 1974b), and in persimmon-shin oak and juniper-oak associations. Where *P. pectoralis* and *P. attwateri* occur together, *pec-
*P. pectoralis* seems to outcompete and displace *attwateri* from rocky habitats and escape cover (Etheredge et al., 1989). In areas where it resides, the white-ankled mouse may be taken in reasonable numbers. Both *pectoralis* and *attwateri* are absent from areas lacking rocky cover, and both are rarely found in grassy, valley areas.

Diets of *pectoralis* and *attwateri* appear to be similar; seeds, lichens, and other fungi make up most of the food items (Dalquest and Horner, 1984). Juniper berries, hackberries, acorns, other fruits, and insects are included in the diet. These mice are active nocturnally and do not hibernate through the winter months.

Where *pectoralis* and *attwateri* are sympatric, the white-ankled mouse makes more extensive use of rocky ledges and rock piles as escape cover. The Texas mouse utilizes trees more frequently as escape cover and refuge sites (Etheredge et al., 1989). The white-ankled mouse is a more tentative climber, and does not appear to be as well adapted to arboreal foraging as the Texas mouse (Etheredge et al., 1989). Nests are located underneath rocks, in crevices, and in brushpiles. The nests are constructed of grass and other vegetation, and are globular in shape.

Little is known regarding the reproductive behavior and mating habits of *P. pectoralis*. Multiple litters are probably produced each year; young of this species may be born throughout the year. Pregnant females have been captured in the months of January, February, March, July, August, September, October, November, and December on the Edwards Plateau. Gestation period is approximately 23 days (Schmidly, 1974b). Embryo records indicate from two to six young born per litter (Dalquest and Horner, 1984).

Figure 78. Distribution of *Peromyscus pectoralis* on the Edwards Plateau.
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The subspecies of white-ankled mouse residing
Sexual dimorphism is more pronounced in pectoralis
than in other species of Peromyscus, but the degree of
sexual dimorphism varies geographically across the
range of P. pectoralis (Schmidly, 1972). Average ex­
ternal measurements of 10 adults (five males and five
females,combined) from the Edwards Plateau are: to­
tal length, 189.5; tail length, 100.5; length hind foot,
21.5; ear length, 17. Selected mean cranial measure­
ments of these same individuals are: greatest length
skull,27 .20; zygomatic breadth,13.31; interorbital con­
striction,4.27; length rostrum,10.42; breadth rostrum,
4.73; cranial breadth,12.53; length maxillary toothrow,
3.77.
Specimens examined (830).- Bandera Co.: 14
443300E, 3302700N, 7; 14 487100E, 3290300N, 2;
14 504800E, 3284800N, 1 (SWTU); 15.6 mi. W Hwy.
Bexar Co.: 14 552900E, 3288700N, 1 (TNHC); 14
548900E, 32891 00N, 1 (TNHC); 14 548900E,
3284300N, 2 (TNHC); 14 540300E, 3281700N, 10;
14 526700E, 3270500N, 4 (SWTU); 14 530500E,
3277300N, 7 (TNHC). Blanco Co.: 14 541900E,
3350900N, 6; 14 577300E, 3340000N, 7 (SWTU).
Burnet Co.: 14 566600E, 3393700N, 4 (SWTU).
Callahan Co.: 14 447500E,3562600N,1. Coke Co.:
14 355600E, 3548500N, 1 (ASNHC); 14 333900E,
3529700N, 3 (ASNHC); 14 347000E, 3521700N, 1
(ASNHC); 14 348000E, 3521300N, 2 (ASNHC); 14
337200E, 3512800N, 3 (ASNHC); 14 363100E,
3510400N, 4; 14 332500E, 3508700N, 1 (ASNHC);
14 359300E, 3508200N,6 (ASNHC). Comal Co.: 14
584100E,3286400N,2 (SWTU);Loop 337 and Landa
Drive, 1 (SWTU). Concho Co.: 14 436900E,
3481800N, 2 (ASNHC); 14 437300E, 3481700N, 2
(ASNHC). Crane Co.: 13 751800E, 3474800N, 1;
13 755000E, 3470200N,5. Crockett Co.: 14 229000E,
3423000N,2; 14 240800E,3423000N,1; 14 225800E,
3420300N, 1. Edwards Co.: 14 411200E, 3349200N,
41; 14 425400E, 3337900N,1 (TNHC); 14 393400E,
3331800N, 1 (TNHC); 14 342100E,3340600N,1;14
342100E, 3339000, 1; 14 385500E, 3325300N, 1.
Hays Co.: 14 581800E, 3349800, 1 (SWTU); 14
581800E, 3348300N, 1 (SWTU); 14 583JO0E,
3345900N, 1 (SWTU); 14 581800E, 3316800N, 1
(SWTU); 14 601200E, 3321900N, 11 (SWTU); 14
587400E, 3318600N, 1 (SWTU); 14 581200E,
3314000N, 2 (SWTU); 14 587400E, 3311000N, 1

(SWTU); 14 601200E, 3313800N, 7 (SWTU); 14
590500E, 3312800N, 1 (SWTU); 14 597000E,
3311200N, 1(SWTU);14 596800E, 3308200N, 3; 14
584100E, 3306500N, 1 (SWTU); 14 585700E,
3306500N, 3 (SWTU); 14588900£, 3306500N, 1
(SWTU); 14 590500E, 3306500N, 4 (SWTU); 14
593700E, 3306500N, 7 (SWTU). Irion Co.: 14
336700E, 3456000N, 1 (ASNHC). Kendall Co.: 14
522600E, 3317700N, 1 (SWTU); 14 524000E,
3319200N,3. Kerr Co.: 14 446500E, 3325900N, 10
(SWTU); 14 483200E, 3324700N, 1 (TNHC); 14
481800E, 3313800N, 4 (MWSU); 14 451500E,
3318400N, 1; 14 486100£, 3315500N, 1 (MWSU);
14 486100E, 3314700N,8 (TNHC). Kimble Co.: 14
443400E, 3390200N, 3; 14 442200£, 3388000N, 3
(MWSU); 14 442900E, 3386300N, 1; 14 442100E,
3386300N, 3; 14 443000£, 3385600N, 6; 14 443000E,
3384700N, 1; 14 426000£, 3380300N,2; 14 419700E,
3383300N,1; 14 431400E,3379500N,1; 14 425500E,
3373600N, 12; 14 425500E, 3372800N, 9 (1 TIU, 5
MWSU, 3 TCWC); 14 425400E, 3372000N, 28; 14
420900E, 3373300N, 1; 14 423600E, 3372800N, 2;
14 427000£, 3372000N, 1; 14 430000£, 3372800N,
1; 14 431600£, 3372800N,1 (MWSU); 14 434800E,
3372800N, 5 (MWSU); 14 436400E, 3372800N, 7
(MWSU); 14 438000E, 3372800N, 10 (MWSU); 14
441200E, 3372800N, 22 (MWSU); 14 444400E,
3372800N, 2 (MWSU); 14 460700£, 3366600N, 2
(ASNHC); 14 425500E, 3372100N, 1; 14 426200E,
3372100N, 7; 14 424400E, 3371500N, 2; 14 426500E,
3371600N, 1 (MWSU); 14 425500E, 3370900N, 1;
14 425500E, 3371300N, 8; 14 424400£, 3371600N,
1; 14 426500£, 3371600N, 7; 14 425800E, 3371200N,
1; 14 420700E, 3370500N, 2; 14 425500E, 3369700N,
3; 14 423600£, 3370300N, 1; Walter Buck Wildlife
Management Area, 1; Seismograph Hill, 14; 14
427800E, 3370000N, 5 (MWSU); 14 426900E,
3368200N, 1; 14 440100E, 3363400N, 2; 14 425300E,
3365000N, 2 (TCWC); 14 436200E, 3353100N, 2
(TCWC); 14 427000E, 3362000N, 2; 14 424500E,
3360700N,1; 14 416200£, 3362600N, 2; 14 425500E,
3359200N, 1. Llano Co.: 14 527400E, 3401900N, 1
(TNHC); 14 504000E,3396300N,5. Mason Co.: 14
474500E, 3382100N, 3; 14 490500E, 3390700N, 42
(TNHC); 14 457500E, 3386800N, 2 (ASNHC).
McCulloch Co.: 14 443100E, 3458400N, 1; 14
456500E, 3436300N, 2 (MWSU). Menard Co.: 14
424800E, 3416900N, 3; 14 417700E, 3397900N, 1;
14 430300E, 3404200N,3. Nolan Co.: 14 343300E,


3551000N, 1 (MWSU). Real Co.: 14 411000E, 3288800N, 4. San Saba Co.: 14 508000E, 3427400N, 8(MWSU). Sutton Co.: 14 328800E, 3388600N, 2; 14 342100E, 3382700N, 2; 14 362200E, 3356600N, 6; 14 332900E, 3354100N, 1 (MWSU). Taylor Co.: 14 428400E, 3566000N, 2 (MWSU); 14 408700E, 3570200N, 4. Tom Green Co.: 14 342100E, 3459700N, 1 (MWSU); 14 357500E, 3444000N, 89 (88 ASNHC, 1 MWSU); 14 358300E, 3444000N, 26 (ASNHC). Travis Co.: 14 588200E, 3366400N, 1 (SWTU); 14 611600E, 3354200N, 1 (TNHC); Town Lake, Austin, 1 (MWSU); 14 616700E, 3351700N, 5 (TNHC); 1.2 mi. N Mt. Bonnell, 5 (TNHC).

Upton Co.: 13 772900E, 3454400N, 9; 13 772600E, 3448000N, 1.

Uvalde Co.: 14 396100E, 3274400N, 1 (TNHC); 14 427100E, 3276100N, 1 (SWTU); 14 43 0600£, 3273400N, 4 (SWTU); 14 432100E, 3265200N, 7; 14 454400£, 3248000N, 5 (TNHC). Val Verde Co.: 14 254600E, 3342500N, 2 (TNHC); 14 294400E, 3323600N, 1; 14 306600E, 3315400N, 4; 14 307500E, 3303400N, 2; 14 328700E, 3310800N, 15; 14 289600E, 3315800N, 1 (TNHC); 14 327200E, 3303000N, 1; 14 289600E, 3299200N, 5 (MWSU); 14 313000E, 3258200N (TCWC); 14 313000E, 3281500N (TCWC); 14 304000E, 3254100N (TCWC); Amistad Reservoir, Long Point (TCWC); 14 303000E, 3262800N (TCWC); Amistad NRA, Governor's Landing (TCWC); Amistad Reservoir, Diablo East (TCWC); Amistad Reservoir, Amistad NWR (TCWC); 14 298400E, 3270200N (TCWC); 14 270400E, 3287600N (TCWC). (Davis and Schmidly, 1994).

**Baiomys taylori**

Northern Pygmy Mouse

**Distribution.**—The northern pygmy mouse is distributed from central Mexico northward along the eastern and western coasts of Mexico into the eastern two-thirds of Texas and extreme southern Oklahoma. This species ranges eastward and northward into southwestern New Mexico and southeastern Arizona.

The northern pygmy mouse presently ranges throughout most of the Edwards Plateau region. The species is actively expanding its range within this and adjacent areas within Texas. Records are available from Bexar, Callahan, Coke, Comal, Concho, Glasscock, Hays, Howard, Kendall, Mason, McCulloch, Menard, Reagan, Runnels, San Saba, Schleicher, Sterling, Tom Green, Travis, Upton, and Val Verde counties (Fig. 79).

**Baiomys taylori** is the smallest murid rodent in North America. Dorsal pelage varies in color from gray to brown. The venter is buffy, gray, or white in color. The tail is relatively short and covered by short hairs. The tail is darker above and lighter in color on the ventral side. Ears are short and rounded, but are conspicuous in the northern pygmy mouse. The upper incisors of *B. taylori* are ungrooved, as opposed to the grooved upper incisors of *Reithrodontomys*.

The northern pygmy mouse has a strong preference for weedy and overgrown habitats on the Edwards Plateau. Fallow fields, unmowed highway rights-of-way, railroad rights-of-way, valley areas, riparian areas, and other locations with dense ground cover are favored by the northern pygmy mouse. Dense ground cover is an important component of optimal habitat for *B. taylori*, and disturbances that reduce ground cover may reduce population densities of this species within an area (Eshelman and Cameron, 1987).

The diet of *B. taylori* is mostly herbivorous and granivorous, but animal matter is also readily consumed if available. Stems and fruits of prickly pear, seeds and leaves of grasses, mesquite beans, insects, terrestrial snails, and small reptiles are included in the diet.
Figure 79. Distribution of *Baiomys taylori* on the Edwards Plateau.

(Eshelman and Cameron, 1987). Northern pygmy mice are crepuscular to nocturnal in activity period (Packard, 1960).

Runways are often constructed within an area. These travel routes resemble those made by cotton rats and voles, but are smaller in size. Home ranges are small for *B. taylori* in favorable habitats, but vary from 45 to 729 square meters (Eshelman and Cameron, 1987). There is a great deal of overlap among and between home ranges of individuals within an area, suggesting a low level of territoriality. Habitat segregation and competition is evinced between pygmy mice and cotton rats, if the two rodent species are sympatric, with *B. taylori* occupying less favorable habitats as a result.

Small nests are constructed mostly of grasses and other plant materials. Secondary refuge nests are not uncommon (Packard, 1960). Nests are found in burrows, under logs, cactus plants, and other vegetation, as well as underneath rocks. Multiple entrances are constructed and several runways usually lead from the nest. Family groups of male, female, and young may occupy a nest. Communal nesting of *B. taylori* has been observed on one occasion in north-central Texas (Stangl and Kasper, 1987), but this habit may occur more frequently at the northern extremes of this species’ range.

Reproduction in *B. taylori* occurs throughout the year. The gestation period is 22 to 23 days in the pygmy mouse and a postpartum estrous is frequent (Hudson, 1974). Reproductive peaks occur in the late fall and early spring months (Eshelman and Cameron, 1987). Litters range in size from one to five young. In captivity, both male and female pygmy mice care for the offspring (Packard, 1960).
The subspecies on the Edwards Plateau is *B. t. taylori* (Thomas, 1897). Sexual dimorphism has not been reported for this species. Average external measurements of 10 females from within the region are: total length, 103.9; tail length, 40.3; length hind foot, 13.95; ear length, 9.45. Selected mean cranial measurements from 22 adults from Coahuila, Mexico (Packard, 1960), are: occipitonasal length, 18.0; zygomatic breadth, 9.6; least interorbital breadth, 3.6; breadth brain case, 8.8; length maxillary toothrow, 3.1.

Specimens examined (78).—**Bexar Co.:** 14 540300E, 3281700N, 7. **Callahan Co.:** 14 447600E, 3562600N, 1; 14 447300E, 3555900N, 1; 14 444400E, 3556000N, 5. **Coke Co.:** 14 338500E, 3523200N, 1 (ASNHC); 14 332700E, 3509100N, 2 (ASNHC); 14 376000E, 3512400N, 1 (ASNHC). **Comal Co.:** 14 585100E, 3286400N, 3 (SWTU). **Concho Co.:** 14 412200E, 3447400N, 1. **Glasscock Co.:** 14 255200E, 3541300N, 1; 14 282800E, 3522800N, 1. **Hays Co.:** 14 602000E, 3314000N, 1 (SWTU); 14 596300E, 3307100N, 2; 14 602100E, 3304900N, 3 (SWTU); 14 596300E, 3308000N, 1 (SWTU). **Kendall Co.:** 14 259600E, 3564800N, 3; 14 273100E, 3555100N, 2. **Menard Co.:** 14 4477900E, 3392300N, 1. **Mcculloch Co.:** 14 467900E, 3392300N, 1. **Reagan Co.:** 14 259700E, 3453900N, 2. **Runnels Co.:** 14 406000E, 3507400N, 7. **San Saba Co.:** 14 531600E, 3450800N, 2. **Schleicher Co.:** 14 347300E, 3410500N, 5; 14 344400E, 3410500N, 2; 14 336800E, 3409000N, 6. **Sterling Co.:** 14 288300E, 3518400N, 1. **Tom Green Co.:** 14 362900E, 3503000N, 4 (ASNHC); 14 353300E, 3455800N, 1; 14 357800E, 3444400N, 2 (ASNHC); 14 357100E, 3444000N, 1 (ASNHC). **Travis Co.:** 14 345200E, 3352000N, 1 (SWTU); 14 621900E, 3351500N, 1 (TNHC). **Upton Co.:** 13 758200E, 3468800N, 1. **Val Verde Co.:** 14 294400E, 3323600N, 1.


**Onychomys arenicola**

Mearn's Grasshopper Mouse

**Distribution.**—Mearn's grasshopper mouse ranges from central Mexico northward through Trans-Pecos, Texas, and areas immediately to the west. This species' range extends through southern New Mexico, Arizona, and California, and extends northward to include southern Nevada and the extreme southwestern corner of Utah.

On the Edwards Plateau, the species has been collected only from Crockett County (Fig. 80).

**Onychomys arenicola** is very similar in appearance to the northern grasshopper mouse (*O. leucogaster*). Mearn's grasshopper mouse is a short-tailed, stocky mouse with bicolor pelage. The dorsum is pale brown to grayish, or pinkish cinnamon. The venter is white. The tail is bicolor and the tip is often white in color. Mearn's grasshopper mouse may be distinguished from *O. leucogaster* by the following characteristics: Tail length usually greater than half of body length in *O. arenicola*; tail less than half body length in *O. leucogaster*. Maxillary toothrow short (3.3 to 4.0) in *O. arenicola*; maxillary toothrow long (3.8 to 4.8) in *O. leucogaster*. Length of mandible usually less than 14 mm in *O. arenicola*; mandible length usually greater than 14 mm in *O. leucogaster*. Grasshopper mice may be mistaken for peromyscine rodents; however, *Onychomys* are stockier, have short, clubeke tails, larger front feet, and more hypsodont molars than members of the genus *Peromyscus*. Grasshopper mice also have a distinctive odor that *Peromyscus* lacks.

Mearn's grasshopper mouse is usually found in desert shrub habitats. These mice are often found in association with mesquite and various cacti, and require soil that is suitable for burrowing without collapse (Hoffmeister, 1986). Ground cover is usually scanty in areas where these mice are trapped.

The diet of grasshopper mice is unique among North American rodents. Diet items include mostly insects and mammalian prey. Prey items of *O. arenicola* include scorpions, beetles, grasshoppers, spiders, mites, ants, pocket mice, and harvest mice. *O. arenicola* has been found to need no additional water in the diet when provided a diet of fresh arthropods or other animal tissues. Water balance problems may be encountered by this species during winter months when such material is in shorter supply (McCarty, 1975).

Mearn's grasshopper mouse is nocturnal in foraging and activity period. The grasshopper mice are vocal, and often emit high-pitched chirps or "howls"
when foraging in an area. *O. arenicola* is highly territorial and these vocalizations may help to identify specific territories and reduce antagonistic encounters with conspecifics.

Adults utilize burrows for habitation, with the burrow usually occupied by a male-female pair and offspring (McCarty, 1975). Burrows are simple and consist of an entrance shaft that is nearly vertical, with an adjoining horizontal burrow. Males are excluded from the nest and burrow for a period of about four days following the birth of young. Afterward, the male is allowed to take an active role in care of the offspring (McCarty, 1975).

Female *O. arenicola* are polyestrous and may produce multiple litters per year. Breeding senility is rapid in this species. Laboratory animals seldom remained reproductively active after their second year (McCarty, 1975). Gestation period of *O. arenicola* has been reported to range between 27 and 30 days. Mearn's grasshopper mouse demonstrates a postpartum estrous. Litter sizes usually range from one to five in Mearn's grasshopper mouse. Courtship rituals before mating include bouts of boxing, wrestling, and naso-nasal and naso-anal contacts between males and females (McCarty, 1975).

The subspecies which resides on the Edwards Plateau is *O. a. arenicola* Mearns, 1896. Selected external and cranial measurements of a female from Coahuila, Mexico (Baker, 1956), are: total length, 152; tail length, 54; length hind foot, 21; ear length, 22; greatest length skull, 26.9; basilar length, 20.9; zygomatic breadth, 13.0; breadth braincase, 11.6; least interorbital breadth, 4.6; nasal length, 10.7; length palatine slits, 5.2; length maxillary tooththrow, 3.8.
Specimens examined (0).

Additional records.—Crockett Co.: 14 241400E, 3395600N; Unidentified locality. (Bailey, 1905; Riddle and Honeycutt, 1990).

**Onychomys leucogaster**
Northern Grasshopper Mouse

Distribution.—The northern grasshopper mouse ranges from Tamaulipas, Mexico, north through the Great Plains and Rocky Mountain regions of the United States. The northern grasshopper mouse occurs as far north as the Canadian provinces of Alberta, Saskatchewan, and Manitoba.

The northern grasshopper mouse may range throughout the entire Edwards Plateau, but records of occurrence are scarce (Fig. 81). Records are available from Concho, Crane, Crockett, Howard, and Val Verde counties.

**Onychomys leucogaster** is most easily confused with species of *Peromyscus*. The tail length of the northern grasshopper mouse is much shorter than that of most species of *Peromyscus* which occur on the Edwards Plateau. The tip of the tail often is white in color. Underparts are white, whereas, the dorsum is either a slate-gray or cinnamon color. Grasshopper mice are rather blocky and short in overall appearance, with relatively large front feet. Soles of the hind feet are densely furred from the heel to the plantar tubercles. The molars of *O. leucogaster* are more hypsodont than those of *Peromyscus*, and the coronoid process is longer and more pointed. Grasshopper mice have a distinct musky odor, which is lacking in *Peromyscus*.

Northern grasshopper mice favor areas with loose, sandy, or loamy soils. Vegetation associations that these mice have been trapped in range from short grass prairies to shrubby areas, with little or no understory vegetation. The northern grasshopper mouse may be restricted to habitats with edaphic conditions that are suitable for frequent dustbathing (McCarty, 1978).

Grasshopper mice are unique among North American rodents in diet. The majority of the diet is made up of animal matter of various kinds. Very little vegetable material is consumed under ordinary circumstances. The diet of *O. leucogaster* may contain as much as 89 percent animal material (McCarty, 1978). Diet items include grasshoppers, crickets, scorpions, moths, praying mantis, and some species of flies. Mammals that *O. leucogaster* is known to prey upon include *P. maniculatus*, *Perognathus parvus*, and *Microtus montanus* (McCarty, 1978). Grasshopper mice are known to kill kangaroo rats, hispid pocket mice, harvest mice, and cotton rats when placed together in captivity.

Grasshopper mice are solitary except when forming mating pairs and family groups. If two individuals are placed together, the subordinate animal is killed within a few days (Hoffmeister, 1986). Four types of burrows are constructed and include nest, retreat, cache, and miscellaneous burrows. Seeds are often stored in the cache burrows; perhaps to provide a supply of food in winter months when insect numbers are low (McCarty, 1978). Burrows of other animals only are used temporarily while the grasshopper mouse constructs its own living quarters in an area. This species seems to display territorial behavior, and utilizes a series of mark-burrows and calls to advertise and delineate a territory within a community.

The northern grasshopper mouse has a rather complex courtship ritual. Breeding may occur throughout most of the year in some parts of *O. leucogaster*’s range within Texas. The breeding season extends at least from May through October (Davis and Schmidly, 1994). One animal from Crane County carried six embryos in January. Two specimens captured in April and March were juveniles, indicating an extended breeding season in this species. Three to six litters of young may be produced annually. Litter size varies from two to six (McCarty, 1978; Davis and Schmidly, 1994).

Two subspecies occur on the Edwards Plateau. *O. l. arcticeps* Rhoads, 1898, in Crane, Crockett, and Howard counties of the northern and western Edwards Plateau, and *O. l. longipes* Merriam, 1899, in Tom Green, Val Verde, and other counties farther south and east on the Edwards Plateau. External measurements of a male specimen from Crane County are: total length, 155; tail length, 39; length hind foot, 23; ear length, 15. Ranges for the species given in McCarty (1978) are: total length, 119-190; tail length, 29-62; length hind foot, 17-25; ear length, 12.4-16.9.

Specimens examined (3).—Crane Co.: 13 752600E, 3506500N, 1 (MWSU); 13 751300E,
Figure 81. Distribution of *Onychomys leucogaster* on the Edwards Plateau.

3490000N, 1 (ASNHC); 13 752200E, 3488600N, 1 (ASNHC).


**Sigmodon hispidus**
Hispid Cotton Rat

*Distribution.* — Hispid cotton rats range from northern South America, northward through all but extreme western and northwestern Mexico, and into the conterminous United States. Within the United States, hispid cotton rats range from southern California, eastward to southern Arizona and southern New Mexico, and throughout all of Texas except the northwestern Panhandle region. The hispid cotton rat ranges northward through most of Oklahoma, southeastern Colorado, central and eastern Kansas, and into southern Nebraska. The range of *S. hispidus* extends eastward through the southern half of Missouri, southern Iowa, Tennessee, and Virginia, and southward throughout Florida.

The hispid cotton rat has a ubiquitous distribution on the Edwards Plateau. This species is one of the most common mammals taken on the region. Records are available from Bandera, Bexar, Blanco, Burnet, Callahan, Coke, Comal, Concho, Crane, Crockett, Edwards, Glasscock, Hays, Howard, Kendall, Kerr, Kimble, Kinney, Llano, Mason, McCulloch, Medina, Menard, Midland, Real, Runnels, Schleicher, Taylor, Tom Green, Travis, Upton, Uvalde, and Val Verde counties (Fig. 82).
Figure 82. Distribution of *Sigmodon hispidus* on the Edwards Plateau.

*Sigmodon hispidus* is a rather large rat (total length of adults greater than 200 mm), with grizzled, brown pelage dorsally, and a grayish colored venter. The tail is of moderate length, sparsely haired, and dark in color. The ears are nearly concealed by the long hairs of the head. The feet are blackish in color. The enamel folds of the molar teeth form a distinctive S-shaped pattern, unlike that of any other murid rodent on the Edwards Plateau.

The hispid cotton rat favors habitats with dense grasses and almost complete ground cover (Cameron and Spencer, 1981). *S. hispidus* may be found residing adjacent to rivers and streams, in grassy and weedy valleys, overgrown highway rights-of-way, and around fieldcrop areas on the Edwards Plateau.

The hispid cotton rat is herbivorous. Various grasses, forbs, and seeds are consumed, as are insects and bird eggs (Meyer and Meyer, 1944; Cameron and Spencer, 1981; Jones et al., 1983; Dalquest and Horner, 1984). Cotton rats are selective foragers and tend to choose a combination of food items that provide an adequate, balanced diet (Cameron and Spencer, 1981). Insects are consumed during seasons of greatest availability (Cameron and Spencer, 1981). Cotton rats clip sizable quantities of vegetation during the autumn and winter months which they pile along runways, however, very little of this material is consumed (Jones et al., 1983). Runways through rank vegetation are utilized for traveling and foraging. *S. hispidus* is mostly crepuscular and nocturnal but, depending upon food availability and other environmental conditions, may also be diurnally active. *S. hispidus* is active throughout the year.
Hispid cotton rats nest in hollows beneath logs, rocks, or debris. These rats may also den in shallow burrows of ground squirrels or other rodents, abandoned dens of small carnivores, or may excavate their own burrows (Jones et al., 1983). Hispid cotton rats also occupy buildings and other man-made structures. Nests are utilized and are constructed of woven grasses. Nests may be cup-shaped or may be hollow balls with a single entrance (Cameron and Spencer, 1981).

Home ranges are usually less than 1 ha in size for both males and females. Males have larger home ranges than females; home ranges of female cotton rats are exclusive (Cameron and Spencer, 1981). Seasonal differences in movement patterns within an area are influenced by the reproductive stage of individuals or availability of cover. Daily movements of males average 17 m and daily movements of females average 6.6 m (Cameron et al., 1979). Cotton rats have the ability to climb and travel along vines and branches within a habitat. Dispersal of *S. hispidus* is positively correlated with population density (Spencer and Cameron, 1981).

Cotton rats may undergo population explosions, where they become extremely abundant in an area, and then undergo a rapid population decline (Bailey, 1905; Chipman, 1965; Dalquest and Horner, 1984). *S. hispidus* has the potential to occasionally cause considerable damage to cultivated crops and other agricultural enterprises as a result of this type of population cycle.

Cotton rats do not seem to be territorial, although there is a definite dominance hierarchy and, probably, avoidance behaviors to reduce agonistic encounters between conspecifics within an area (Cameron and Spencer, 1981). Males are dominant over females within a cotton rat population. *S. hispidus* seems to be a solitary species, however, pair bonds may be formed between individuals maintained in laboratory settings (Cameron and Spencer, 1981). *S. hispidus* demonstrates interference competition when in sympathy with *R. fulvescens*, and cotton rats probably displace *B. taylori* into marginal habitats whenever the two species are sympatric (Cameron and Spencer, 1981).

Cotton rats are reproducively active throughout the year in Texas (Cameron and Spencer, 1981). Females are polyestrous and give birth to multiple litters each year. Males are probably polygamous in mating habit. The gestation period is approximately 27 days in length. Litter sizes range from one to 15 young (Cameron and Spencer, 1981). The offspring mature rapidly and are capable of surviving without their mother at five days of age (Meyer and Meyer, 1944). Population turnover is rapid and most individuals live less than one year in the wild (Cameron and Spencer, 1981).

Two subspecies of hispid cotton rat occur on the Edwards Plateau. *S. h. texianus* (Audubon and Bachman, 1853) on the eastern Edwards Plateau to around Midland and Val Verde counties, and *S. h. berlandieri* Baird, 1855 in the remainder of the region to the west. Sexual dimorphism has not been reported for this species. Average external measurements of 10 adult *S. h. berlandieri* (five females and five males) from Crockett, Midland, Upton, and Val Verde counties are: total length, 282; tail length, 118.1; length hind foot, 31.6; ear length, 19.2. Average external measurements of 10 adult *S. h. texianus* (two females and eight males) from Callahan, Kimble, McCulloch, and Schleicher counties are: total length, 278; tail length, 111.2; length hind foot, 32.4; ear length, 19.2. Selected mean cranial measurements of 10 adults from Kimble County (five females and five males) are: greatest length skull, 33.82; zygomatic breadth, 19.33; length rostrum, 12.83; interorbital constriction, 4.99; mastoid breadth, 13.85; length maxillary toothrow, 6.07.

*Specimens examined (247).— Bandera Co.: 14 504800E, 3284800N, 1 (SWTU). Bexar Co.: 14 540300E, 3281700N, 7. Burnet Co.: 14 598300E, 3409900N, 2 (MWSU). Callahan Co.: 14 447500E, 3562600N, 4; 14 447400E, 3558200N, 5; 14 444200E, 3555800N, 1. Coke Co.: 14 335600E, 3548800N, 1 (ASNHC); 14 339800E, 3548700N, 5 (ASNHC); 14 339700E, 3534200N, 2 (ASNHC); 14 334000E, 3529700N, 3 (ASNHC); 14 345800E, 3515200N, 6 (ASNHC); 14 347600E, 3512300N, 1 (ASNHC); 14 331600E, 3508900N, 1 (ASNHC); 14 331200E, 3508400N, 1 (ASNHC). Comal Co.: 14 587000E, 3286900N, 1 (SWTU); 14 578600E, 3304100N, 1 (SWTU); 14 584100E, 3286400N, 1 (SWTU); 14 567200E, 329200N, 2. Concho Co.: 14 436900E, 3481800N, 1 (ASNHC); 14 412300E, 3447400N, 1. Crane Co.: 14 753000E, 3470600N, 1; 13 754100E, 3470600N, 10; 13 755000E, 3470200N, 4. Crockett Co.: 14 226600E, 3423000N, 3; 14 242200E, 3395000N, 2. Edwards Co.: 14 345200E, 3282000N, 4. Glasscock Co.: 14 248800E, 3550900N, 1. Hays

Neotoma albigula
White-throated Woodrat

Distribution.—The white-throated woodrat ranges from central Mexico northward to southern California, southeastern Utah, southern Colorado, and most of New Mexico. Eastern limits of distribution are on the western Oklahoma panhandle, and the Rolling Plains and Edwards Plateau regions of Texas.

The white-throated woodrat ranges throughout the Edwards Plateau in suitable habitats (Macêdo and Mares, 1988). However, specimens from within the study area are not numerous. Records are available from Coke, Concho, Edwards, Howard, Kerr, Kimble, Llano, Mason, Nolan, Taylor, Tom Green, Uvalde, and Val Verde counties. Bailey (1905) included Crockett, Ector, Menard, Midland, Reagan, and Schleicher counties within the range of the white-throated woodrat on the Edwards Plateau (Fig. 83).

The white-throated woodrat has brownish fur dorsally, interspersed (especially laterally) with buffy pelage. The underside, feet, and throat are white; and the tail is long and heavily furred. Ears are rather long, hairless, and rounded. The southern plains woodrat (N. micropus) by contrast is slate-gray colored dorsally and laterally; no brown pelage is present. The underside and feet are white in both species of woodrat, but the bases of the throat hairs are dark in color in N. micropus. The tail of N. micropus is also heavily furred, with a distinct dark, dorsal stripe. The white-throated woodrat has a maxillovomerine notch interrupting the nasal septum; N. micropus lacks a maxillovomerine notch.

The white-throated woodrat occurs in a variety of habitats throughout its range (Finley, 1958; Macêdo and Mares, 1988). N. albigula is an inhabitant of slopes and other rocky areas on the Edwards Plateau. This species is often associated with juniper, sagebrush, and other arid-land vegetation (Macêdo and Mares, 1988).
The white-throated woodrat is primarily herbivorous in diet. Cacti, juniper needles, yucca blades, juniper berries, and some grasses are included in the diet. Cacti likely serve as a source of water for the white-throated woodrat in arid habitats. The mean daily consumption of cactus, in certain habitats, is approximately 60 percent of the woodrat's body mass (Macedo and Mares, 1988). *N. albigula* is nocturnal in foraging and other activity and is active throughout the year. Behavioral adaptations enable the white-throated woodrat to survive in arid habitats. Succulent foods are selected in the diet and dens are occupied during diurnal hours. Foraging and other activities are conducted during the cooler evening and early morning hours. White-throated woodrats have no better ability to concentrate their urine than many rodents occurring in mesic habitats (Macedo and Mares, 1988). However, the white-throated woodrat is able to safely ingest oxalic acid found in cacti without harm, and, thus, obtains a ready supply of water. Water consumption is inversely related to its availability within a habitat (Macedo and Mares, 1988).

Dens are usually constructed at the bases of boulders or around clefts in a rock face. Cacti, sticks, and other materials may be added to the outside of these natural retreats (Finley, 1958). Mound-like houses may also be constructed of these same materials and other items such as bones, cow and horse manure, bottle caps, rifle shells, and aluminum cans. Mound dens have multiple entrances leading into a large central chamber (Finley, 1958). A nest of grasses is found within this chamber. Feces are not deposited within the den or house; fecal material is usually deposited in a single area, or midden, in the vicinity of the den.

Figure 83. Distribution of *Neotoma albigula* on the Edwards Plateau.
The white-throated woodrat is solitary in habit, except during the mating season and mother-young groups. Home ranges are rather small in size; ranging from approximately 161 m to 468 m (Macêdo and Mares, 1988). Home ranges of individuals overlap within an area and only the dens are defended. Males and females do not show significant differences in movement patterns within a habitat. Males deposit secretions from midventral glands at specific locations. Scent is used in social functions involving sexual and agonistic interactions, hierarchic organization, and territoriality (Macedo and Mares, 1988).

Woodrats are probably polygamous in mating habit. The breeding season may extend throughout the year, at least on the southern Edwards Plateau. Juvenile animals have been captured on the Edwards Plateau in May and June, and males with scrotal testes were obtained in October. Gestation period is approximately 30 days in length (Macedo and Mares, 1988). Two young are most common per litter, but occasionally three are born (Bleich and Schwartz, 1975; Dalquest and Homer, 1984). Females may produce more than one litter each year (Findley, 1958).

The subspecies of white-throated woodrat on the Edwards Plateau is *N. a. albigula* Hartley, 1894. Males are consistently larger than females. Average external measurements of 27 *N. albigula* from Arizona (Hoffmeister, 1986) are: total length, 320.20; tail length, 140.80; length hind foot, 33.30; ear length, 28.60. Selected mean cranial measurements of these same individuals are: greatest length skull, 43.56; zygomatic breadth, 22.01; interorbital breadth, 5.63; nasal length, 16.29; mastoidal breadth, 17.62; length maxillary toothrow, 8.52.

*Neotoma floridana* Eastern Woodrat

*Distribution.*— The range of the eastern woodrat extends from eastern Texas, north to Colorado, and thence, eastward to New York and south to Florida. An isolated population of this species also is resident in northern Nebraska.

The range of this species in Texas (as mapped in Schmidly, 1983) extends along the Balcones Fault zone from Travis County to Bexar County in the south. The species is then mapped as extending westward on the Edwards Plateau in an ever-narrowing fashion to end in Edwards County. There is a paucity, however, of actual specimens of *N. floridana* from within this area (Fig. 84).

The eastern woodrat is often difficult to distinguish from *N. micropus* within this area of sympatry on the Edwards Plateau, and there is some evidence that the two species may hybridize with each other in this area (Birney, 1973). *N. floridana* is reddish brown to blackish in color dorsally, and the venter is white or buffy in color. The tail is distinctly bi-colored and is blackish dorsally and grayish white below. Overall, *N. floridana* is a large rat, with rather prominent, almost naked ears. The feet are white and comparatively small. Cranial characters useful in separating *N. floridana* from *N. micropus* are (1) a V-shaped anterior palatal spine in *N. floridana*; spine more rounded in *N. micropus*; (2) a sharp re-entrant angle on the lingual side of M1 of *N. floridana*; re-entrant angle less acute in *N. micropus*; (3) no, or weakly developed spine on posterior palate in...
N. floridana; usually a well-developed spine in N. micropus; (4) small sphenopalatine vacuity openings in N. floridana; larger openings in N. micropus.

Although the eastern woodrat occupies a variety of different habitats in East Texas, the species is probably limited to mesic, upland habitats and riparian areas on the Edwards Plateau. Lowery (1974) stated that, in Louisiana, the eastern woodrat was rare or absent in dry, wooded upland areas. These rats build conspicuous nests, usually of sticks and other material, at the bases of trees or under rock outcrops. In Louisiana (Lowery, 1974), N. floridana sometimes constructs an arboreal nest in tangles of vines or in willow trees. Other species of mammals, such as Peromyscus leucopus and Sylvilagus floridanus, sometimes use the houses of the eastern woodrat as shelters (Wiley, 1980).

The diet of this species consists of varied plants, fruits, and seeds; seeming, in part, to depend upon local availability of the food sources. Gnawed bones have been found associated with the nests of N. floridana. It is believed that the woodrats carry bones back to their nests in order to gnaw to sharpen their teeth and to obtain mineral nutrients (Wiley, 1980).

The breeding season extends from at least March through September in Texas. Females usually give birth to two young. Immature eastern woodrats have been collected in Texas in the months of June and July (Davis and Schmidly, 1994).

The subspecies occurring on the Edwards Plateau is N. f. attwateri Mearns, 1897. Assignment of this species to the Edwards Plateau is based upon examination of two specimens. One has been previously reported in the literature as N. f. attwateri (Birney, 1973).
A third specimen (SWTSU) from 2 mi. W Oakalla, Burnet County, although similar in pelage to a *N. f. attwateri* from Williamson County, proved to be closer to *N. micropus* based upon the above-listed cranial characters. Adult males average slightly larger than females and average external measurements for males from Kansas (Wiley, 1980) are as follows: total length, 374; tail length, 160; length hind foot, 40; ear length, 26. External measurements of a specimen from Travis county are respectively; 348, 144, 39, 29. Skulls were not available for specimens from the Edwards Plateau examined by me. Birney (1973) presented selected cranial measurements for *N. f. attwateri*. Selected cranial measurements (Birney, 1973) for females and males are, respectively: greatest length of skull, 49.4, 50.7; condylobasilar length, 48.1, 49.6; zygomatic breadth, 26.9, 27.7; least interobital constriction, 6.5, 6.7; mastoid breadth, 19.2, 19.9; length of rostrum, 19.2, 19.7; length maxillary toothrow, 9.4, 9.6.

Specimens examined (2).— Kerr Co.: 14 475400E, 3317300N, 1 (TNHC). Travis Co.: 14 611600E, 3354200N, 1 (SWTSU).

Additional records.— Kerr Co.: 14 475400E, 3317300N, 10 (5 AMNH, 5 USNM) (Birney, 1973). Travis Co.: 14 621900E, 3351400N, 1 (USNM) (Schmidly, 1983).

**Neotoma micropus**

Southern Plains Woodrat

**Distribution.**— The southern plains woodrat ranges from northeastern Mexico northward through the western half of Texas and Oklahoma, and into south-central Kansas. This species ranges westward into the southeastern corner of Colorado, and over all but the northwestern region of New Mexico, south into northern Chihuahua.

The southern plains woodrat occurs throughout most of the Edwards Plateau region. Specimens are lacking from some central and eastern counties, but this is probably due to collecting bias, as suitable habitat is present throughout the region. Records are available from Bexar, Callahan, Coke, Coleman, Concho, Crane, Crockett, Ector, Glasscock, Hays, Howard, Irion, Kerr, Kimble, Kinney, McCulloch, Midland, Nolan, Reagan, Runnels, San Saba, Taylor, Tom Green, Upton, Uvalde, and Val Verde counties (Fig. 85).

**Neotoma micropus** has been compared to *N. albigula* in the preceding account. The most distinctive difference is *N. micropus'* steel gray dorsal pelage color as opposed to the browner color of *N. albigula*. The southern plains woodrat is easily confused with *N. floridana* on the eastern Edwards Plateau. Pelage color is slightly grayer in *N. micropus* in this area of sympathy, but specimens are more readily separated by cranial characters. The lingual re-entrant angle of M1 is shallow, the anterior palatal spine is less V-shaped, and the sphenopalatine vacuities are large in the southern plains woodrat. This is opposed to a deep re-entrant angle, rounded anterior palatal spine, and small sphenopalatine vacuities in *N. floridana*.

The southern plains woodrat is found primarily in valley pastures and around watercourses on the Edwards Plateau. Where *albigula* and *micropus* are sympatric, *albigula* is most often found in rocky, slope habitats, whereas *micropus* resides in the valleys. The Florida woodrat is more often found in riparian vegetation, whereas the southern plains woodrat inhabits upland, grassy habitats in areas of sympathy (Braun and Mares, 1989). *N. micropus* is frequently found associated with grassland, mesquite, catclaw, and yucca vegetation.

The southern plains woodrat is herbivorous. Diet items include cactus stems and fruits, mesquite beans, acorns, and yucca seeds and capsules (Braun and Mares, 1989). Cacti and other food items are stored in chambers within the woodrat's nest. Cacti are an important moisture supplement in many habitats where free water is limited (Braun and Mares, 1989). Water is utilized readily if it is available within the habitat, but the southern plains woodrat can survive in areas with little or no available water. *N. micropus* is most active from dusk until midnight. Foraging begins at twilight, or earlier if the sky is overcast (Braun and Mares, 1989).

Large, domed nests are usually constructed at the bases of trees and shrubs. Nest building materials usually are branches (such as mesquite), cactus pads, and, if present, liberal amounts of dried cow and horse manure. Several exits and runways serve as routes of travel to and from the nest; a midden away from the nest is usually present. Nests are occupied singly, an exception being females with young.

Territories are established and maintained by resident adults within an area. Young animals may either
disperse from the immediate area, occupy abandoned dens, or displace a tenured resident (Braun and Mares, 1989). Home ranges of individuals are relatively small, and most home ranges overlap within an area. The southern plains woodrat only defends areas around its den. Males and females mark territories and houses with urine, feces, and ventral gland secretions (August, 1978; Braun and Mares, 1989). Home ranges are centered around cactus patches and other food sources, and range in size from 232 m to over 1000 m. Scent plays an important identification role during the mating season. During this time both male and female woodrats travel through an area seeking mates by olfactory clues (August, 1978).

Breeding seasons vary geographically and may be correlated to some degree with phenological changes in vegetation (Braun and Mares, 1989). Breeding peaks occur in early spring and late fall months, with a low point in late summer (Braun and Mares, 1989). Woodrats are polygamous. One or two litters may be produced annually. Gestation period ranges from 30 to 39 days. Litter size usually is two to three young (Warren, 1925; Braun and Mares, 1989).

Two subspecies of southern plains woodrat occur on the Edwards Plateau; *N. m. micropus* Baird, 1855, on the eastern Edwards Plateau to about Howard and Val Verde counties, and *N. m. canescens* J. A. Allen, 1891, on the remainder of the Edwards Plateau to the northwest. Males of *N. micropus* are larger than females. External measurements of an adult male and female, respectively, from the Edwards Plateau are: total length, 382, 300; tail length, 146, 110; length hind foot, 37, 36; ear length, 29, 28. Selected cranial measurements of the same two specimens (male and female,
that specimens from opposite ends of the cline were quite
micropus
3542200N, 3 (ASNHC).

darker coloration to the south and east, was found in
ciated (Birney, 1973). Birney (1973) stated, however,
5.31, 6.40; length of rostrum, 19.78, 19.11; mastoid
breath, 19.76, 19.70; cranial breath, 20.24, 20.34;
length maxillary toothrow, 8.81, 7.81.

Birney (1973) treated the systematics of
micropus
in his monograph on woodrats in central North
America. As a result of this research, he assigned all
in Texas to
m. canescens.
A northwest to southeast cline, with decreasing size and
darker coloration from the north to the south, was found in
micropus.
No sharp subspecific boundaries were elu-
cinated (Birney, 1973). Birney (1973) stated, however,
that specimens from opposite ends of the cline were quite
different in size and coloration.

Specimens examined (80).— Callahan Co.: 14
447200E, 3573000N, 1. Coke Co.: 14 356200E,
3542200N, 3 (ASNHC). Coleman Co.: 14 438600E,
3493400N, 1. Concho Co.: 14 4158000E, 3486100N,
1 (ASNHC). Crane Co.: 13 755800E, 3491400N, 5
(ASNHC); 13 752000E, 3499900N, 3 (ASNHC); 13
749700E, 3488700N, 8 (ASNHC); 13 752200E,
3488400N, 1 (ASNHC); 13 754200E, 3470300N, 1;
13 755000E, 3470200N, 2. Crockett Co.: 14 240800E,
3423000N; 14 230600E, 3415600N. Ector Co.: 13
751900E, 3513000N, 2. Glasscock Co.: 14
246700E, 3540600N, 1 (ASNHC); 14 249400E,
3528400N, 1 (MWSU); 14 247400E, 3524700N, 1.
Hays Co.: 14 601200E, 3313800N, 1 (SWTU).
Howard Co.: 14 287300E, 3557800N, 1 (ASNHC).
Irion Co.: 14 293800E, 3477000N, 1 (ASNHC); 14
297400E, 3477000N, 3 (ASNHC). Kerr Co.: 14
446500E, 3325900N, 1 (SWTU). Kinney Co.: 14
725400E, 3382700N, 1; 14 431500E, 3378600N, 3;
14 425400E, 3372800N, 2; 14 430000E, 3372800N,
1. McCulloch Co.: 14 443800E, 3482200N, 1; 14
467500E, 3424300N, 2 (MWSU); 14 478000E,
3422000N, 2. Midland Co.: 13 760100E, 3513200N,
6. Nolan Co.: 14 265700E, 3464700N, 1; 14 367800E,
3582300N, 1. Reagan Co.: 14 266200E, 3480600N,
1 (ASNHC); 14 243100E, 3453500N, 1 (ASNHC); 14
250500E, 3453500N, 1 (ASNHC); 14 53400E,
3453500N, 1 (ASNHC); 14 250200E, 3457000N, 1
(SM). Runnels Co.: 14 059000E, 3507500N, 1; Road-
side Park S Ballinger, 1 (WTAM). San Saba Co.: 14
500200E, 3454000N, 2 (MWSU). Taylor Co.: 14
415100E, 3578600N, 1 (MWSU); 14 429600E,
3555600N, 1 (SWTU). Tom Green Co.: 14 353800E,
3483600N, 1 (ASNHC); 14 357800E, 3445800N, 1
(ASNHC); 14 357800E, 3444200N, 2 (ASNHC); 14
358300E, 3444000N, 1 (ASNHC). Upton Co.: 13
757700E, 3468600N, 2; 13 768200E, 3448400N, 1.
Uvalde Co.: 14 454400E, 3248000N, 1 (TNHC).

Additional records.— Bexar Co.: Common in
Bexar County (Unspecified Locality); 14 538300E,
3264900N (TCWC). Crockett Co.: 14 223100E,
3441800N. Kinney Co.: Unspecified Locality. Uvalde
Co.: Unspecified Locality. Val Verde Co.: 14 302800E,
3260100N (TCWC). (Allen, 1896; Chapman and Spence,

Microtus pinetorum
Woodland Vole

Distribution.— The woodland vole ranges from
eastern Texas, Oklahoma, and Kansas northward
through parts of Nebraska and Iowa to Illinois. The
northern range extends eastward to Maine and thence
southward to northern Florida, and west again to Texas.

The woodland vole is known from the Edwards
Plateau from only a few specimens collected in Kerr
and Gillespie counties (Fig. 86). The most recent speci-
mens were taken in 1941 in Kerr County. The Edwards
Plateau populations were probably isolated from more
eastern vole populations at the close of the Pleistocene,
when the species had a wider range within the region
(Graham, 1987). The species may now be extirpated
on the Edwards Plateau.

Microtus pinetorum
is adapted for a fossorial
existence. The torso is cylindrical in shape, append-
gages are short, and the tail is rather bicolored and less
than twice the length of the hind foot. The dorso is a
chestnut brown color, while the venter is often ochraceous.
Only the tips of the hairs are brown in
color, the remainder of the hair stalk is gray. Ears are
short, rounded, and barely extend past the ends of the
cranial pelage; eyes are small. The front feet have well-
developed claws. The head is blunt and broad in pro-
file. The skull of
M. pinetorum
may be indentified by
the distinct, prismatic, molars and small size (as op-
posed to the muskrat).

Grassy areas and old brush piles are favored by
M. pinetorum
on the Edwards Plateau (Bryant, 1941).
Associated vegetation may include Spanish oak, red-
bud, and sumac. Woodland voles utilize subsurface
runways within an area, and require soil types favorable to the construction of runways and burrows. If dense vegetation and ground cover is present, *M. pinetorum* will construct surface runways through grassy areas and in accumulated leaf litter (Smolen, 1981). Well drained soils, with a thick ground cover of either leaf litter or other vegetation, are common parameters in habitats of the woodland vole (Smolen, 1981).

The diet of *M. pinetorum* is comprised mostly of plant roots and tubers. Various grasses, clover sprouts, stalks of dock, acorns, and other items are also a part of the woodland vole's diet (Smolen, 1981). Woodland voles may damage tuber crops in areas where they occur in large numbers, and some young fruit trees in orchards may be girdled during *M. pinetorum*’s foraging activities. The woodland vole conducts most of its foraging during nocturnal hours, but occasionally is active diurnally.

Woodland voles burrow by using the front feet and incisors to loosen the soil, which is then pushed laterally and backward behind the vole. When enough loose soil has accumulated, the vole turns and pushes the soil out of the burrow with its head. Most burrows occur five to 10 cm from the soil surface and extend 15 to 31 cm (Smolen, 1981). Surface runways are constructed in order to connect entrances of subsurface burrows and runways. Nests of grass are constructed in the burrow systems, and are usually globular in shape (Lowery, 1974).

Voles are sedentary in nature and travel only short distances from burrows. This habit contributes to high numbers of voles in one area, while there is an absence

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**Figure 86.** Distribution of *Microtus pinetorum* on the Edwards Plateau.
of the species in an adjacent habitat. A sedentary habit makes this species subject to local extirpation within an area if habitat is altered or a stochastic environmental event occurs. Territoriality is lacking in this species. Several individuals may even utilize a single nest within one burrow (Smolen, 1981). Homing behavior has been observed in the woodland vole.

Breeding may occur throughout the year in Texas. Females may bear from one to four litters per year (Smolen, 1981). Glands located in the hip region of males may be responsible for inducing female receptivity to mating. Females are the aggressors in mating behavior in *M. pinetorum* (Smolen, 1981). Gestation period is approximately 25 days in length. Litter size ranges from two to four young. Larger litters are occasionally produced, but as female woodland voles have only four mammae, only three or four offspring usually survive (Smolen, 1981).

The subspecies occurring on the Edwards Plateau is *M. p. auricularis* Bailey, 1898. A latitudinal cline with an increase in body size to the north is noted for this species (Smolen, 1981). Average external measurements (Schmidly, 1983) are: total length, 128; tail length, 21; length hind foot, 17; ear length, 11. Selected cranial measurements for a sample of woodland voles from Louisiana (Lowery, 1974) are: greatest length, 25.2; cranial breadth, 12.9; zygomatic breadth, 15.2; interorbital breadth, 4.4; nasal length, 7.1; palatilar length, 11.6.

*Specimens examined* (0).

*Additional records.*—Gillespie Co.: 14 514600E, 3347300N. Kerr Co.: 14 486200E, 3320200N. (Bailey, 1905; Bryant, 1941).

**Ondatra zibethicus**

*Common Muskrat*

*Distribution.*—The muskrat is distributed from northern Mexico, throughout the conterminous United States, excepting Florida, and northward throughout most of Canada and Alaska. Populations have been introduced into some areas for commercial purposes.

Muskrats are limited in extent on the Edwards Plateau to the Pecos River and its immediate tributaries, and along the Rio Grande and its tributaries. Bailey (1905) opined that the species probably occurred along the entire length of the Pecos River. (Not mapped).

*Ondatra zibethicus* is the largest microtene rodent which occurs on the Edwards Plateau. Its partially-webbed hind feet and laterally compressed, long tail make the muskrat difficult to confuse with other mammals in the region. Pelage color is chestnut brown to black, but is subject to local variation. Underparts are lighter in color than the dorsum; the feet and tail are almost black in color. Ears are short and barely extend past the fur. The lips are valvular and may be closed behind the incisors. The tail and feet are sparsely haired or naked. The eyes are small, and the ankles are modified to enable lateral motions with the feet. Tail length is only slightly less than body length in *O. zibethicus*. Air is trapped in the underfur of the muskrat, making the pelage waterproof under normal conditions.

Habitats are restricted to rivers, streams, ponds, irrigation ditches, and other aquatic areas on the western Edwards Plateau. Marshy areas and habitats with a preponderance of cattails, sedges, and other aquatic plants are favored by muskrats.

Muskrats feed on a variety of aquatic plants, utilizing stems, leaves, and underground roots and tubers of the plants. Muskrats may gnaw underwater because of the valvular lips and other adaptations that allow for extended dives. Cattails, sedges, and other emergent vegetation are consumed. A significant amount of animal matter occasionally may be consumed. Animal foods include crayfish, mussels, fish, and turtles (Willner et al., 1980). Diets vary between populations, depending upon the availability of edible plants and animals at a particular location. Muskrats are usually nocturnal in foraging habit, but may occasionally be observed during daytime hours (Lowery, 1974).

Muskrats may construct houses of grasses, twigs, and other materials in a marsh habitat. Houses are constructed above water-level and exits from the dens lead to the water. Houses are relatively clean, as *O. zibethicus* usually defecates in the water. One or more nest chambers lined with fresh plant material are found within the main dwelling of *O. zibethicus*. Feeding platforms and shelters are also constructed within a muskrat’s territory. The locations of dens and feeding shelters and platforms is not random within an area; most are placed within short distances of the living quar-
ters of the muskrat. Muskrats also utilize burrows along the banks of rivers, streams, irrigation ditches, and around the margins of lakes.

Muskrats are territorial in nature and are usually found in small family groups within an area. Females are more tolerant of each other than are males, however, many encounters between two conspecifics result in the death of one of the animals. Females may even attack and kill males when defending their breeding territories (Willner et al., 1980). Dominance hierarchies are established by fighting during mating season. Low ranking muskrats will retreat from breeding areas at this time (Willner et al., 1980). Muskrats actively disperse to establish new breeding territories and to exploit new habitats in an area. Territories are scent marked on sign posts, houses, feeding shelters, and in other places within an area. Home ranges are relatively small for this species. Most foraging activity often occurs within a five to 10 m radius of a lodge or a feeding shelter or platform. Lodges and feeding shelters are utilized to help maintain a constant body temperature while foraging in colder waters in the winter months, so home ranges of _O. zibethicus_ would be expected to be somewhat restricted in radius.

Muskrats probably breed throughout the year in Texas. Females are polyestrous and produce multiple litters each year under favorable conditions. Reproductive activity reaches its lowest point during the winter and mid-summer months. Highest reproductive activity occurs in November and March (Schmidly, 1984b). The gestation period of _O. zibethicus_ varies from 26 to 28 days; the young muskrats mature rapidly after birth. A postpartum estrous is demonstrated in this species. Average litter size varies from four to eight per litter, depending upon latitude and other environmental factors (Willner et al., 1980).

The subspecies of muskrat on the Edwards Plateau is _O. z. ripensis_ (Bailey, 1902). No sexual dimorphism has been observed in this mammal. Geographic variation has been studied in _O. zibethicus_, and a significant body size-seasonality of habitat effect has been described (Boyce, 1978). Average external measurements given in the description of the type specimen from Carlsbad, New Mexico (Bailey, 1902) are: total length, 470; tail length, 202; length hind foot, 67. Cranial measurements from the same source are: basal length, 55; nasal length, 18; zygomatic breadth, 35; mastoid breadth, 25; length maxillary toothrow, 15.

Specimens examined (0).

Additional records.—Pecos and Rio Grande rivers and their immediate tributaries. (Davis and Schmidly, 1994).

**Family Erethizontidae—**
**New World Porcupines**

_Erethizon dorsatum_

_Porcupine_

**Distribution.**—The porcupine ranges from northern Mexico, north throughout the western half of Texas, and northeast through parts of Oklahoma, Kansas, Iowa, Illinois, Tennessee, North Carolina, and Virginia. Its range covers all of the western states to the Pacific Ocean and all of the states north of the aforementioned boundary to the Atlantic Ocean. Also, the porcupine's range extends north through all of the provinces of Canada, and throughout most of Alaska.

The porcupine ranges through the western half of the Edwards Plateau. Records are available from Coke, Concho, Crockett, Irion, Kerr, Kimble, Mason, Nolan, Reagan, Schleicher, Sterling, Sutton, Taylor, Tom Green, and Val Verde counties (Fig. 87).

_Erethizon dorsatum_ is a rather large rodent with a distinctive body covering of quills, and yellowish brown coloration. The face and feet are black in color, and the toes have well developed claws. The incisors are deeply pigmented a dull yellow to deep orange color. The hystricognathous angular process, prominent postcondyloid process, and open pterygoid fossa aid in identifying the skull of this species.

Porcupines prefer habitats of mixed hardwood and softwood trees throughout their range. In open areas the porcupine is most often found inhabiting riparian areas, draws, and brushy stream bottoms (Woods, 1973). I have most often observed porcupines along streams and rivers in the eastern parts of their range on the Edwards Plateau. On the western borders of the Edwards Plateau, I have seen the species along the Pecos River, and in brushy, upland juniper habitats.

Porcupines are herbivorous in diet. Diet items vary according to location and season throughout the
range of the porcupine. During the fall and winter months, *E. dorsatum* consumes the bark, pith, and cadmium of trees. In spring and summer months, the porcupine feeds upon leaves, buds, berries, seeds, flowers, and the bark of plants (Jones et al., 1983). Porcupines are nocturnal in their foraging and activity periods. *E. dorsatum* does not hibernate and is active throughout the year, except for extremely cold days when the animal stays within a den (Woods, 1973).

Porcupines are not territorial in habit, although they will defend feeding trees within an area (Woods, 1973). *E. dorsatum* is solitary throughout most of the year. The porcupine is an able climber and will often utilize trees as retreats and refuges in an area. Dens are usually located in caves, logs, or hollow trees. The den is not defended and several animals may utilize it on a rotating basis (Woods, 1973). A bedding area or nest is not constructed within the den. Dens may be located by searching for piles of feces around them (Jones et al., 1983).

Breeding takes place in late summer and early fall; the peak breeding period is in September and October (Davis and Schmidly, 1994). Gestation lasts from 205 to 217 days (Woods, 1973). A single young is usually produced, and, rarely, twins (Woods, 1973). Parturition usually occurs in April and May. The newborn porcupine is precocial and fully quilled. Females are not sexually mature until two years of age (Davis and Schmidly, 1994).

A single subspecies of *E. dorsatum* in Texas is *E. d. epixanthum* Brandt, 1835. No significant sexual dimorphism has been noted in southern populations of the porcupine (Stangl et al. 1991). External measurements
of an adult female and male from the Llano Estacado (Choate, 1991) respectively are: total length, 730, 686; tail length, 200, 162; length hind foot, 105, 90; ear length, 40, 22.


ORDER CARNIVORA—CARNIVORES

KEY TO FAMILIES OF CARNIVORA

1 Molars 1/1, upper molar much reduced; premolars 2/2 or 3/2; claws retractile ................................................................. Felidae
1' Molars 1/2 or more, upper molar (or first upper molar if more than one molar present) a large tooth; premolars never 2/2 or 3/2; claws nonretractile ........................................................................................................ 2

2 Molars 1/2; last upper molar dumbell-shaped (at least in some members); mandibular fossa of squamosal curving well around articular process of lower jaw forming an almost locked joint; well-developed anal scent glands ...................................................................................... Mustelidae
2' Molars 2/2 or 2/3; last upper molar not dumbell-shaped; mandibular fossa not curving far around articular process of lower jaw; anal glands not especially modified for scent production and discharge .................................................. 3

3 Molars 2/3; tail not ringed with black stripes ................................................................. Canidae
3' Molars 2/2; tail ringed with conspicuous black stripes .................................................. Procyonidae

KEY TO CANIDAE

1 Greatest length of skull 190 mm or greater; prominent sagittal crest present; total length 1000 mm or greater ................................................................. Canis latrans
1' Greatest length of skull less than 190 mm; sagittal crest weakly developed or absent; total length less than 1000 mm.................................................. 2
Temporal ridges distinctly U-shaped; truncated indentation on lower margin of dentary anterior to angular process; dorsal color a salt and pepper gray ................................................................. *Urocyon cinereoargenteus*

Temporal ridges V-shaped; lower margin of dentary smooth; dorsal color reddish or tan ................................................................................................................................. 3

Greatest length of skull 132 mm or larger; length maxillary toothrow 58 mm or larger; reddish dorsal pelage; back of ears and legs black; tip of tail white ............................................................................................................ *Vulpes vulpes*

Greatest length of skull less than 132 mm; length maxillary toothrow less than 58 mm; dorsal pelage tan; back of ears and legs tan; tip of tail black ......................... *Vulpes velox*

**Family Canidae—Canids**

*Canis latrans*

**Coyote**

*Distribution.*—The coyote ranges from Costa Rica northward throughout all of Mexico and the contiguous United States. The coyote has apparently been transplanted into Florida and Georgia (Bekoff, 1977). The coyote is found throughout most of Canada and Alaska northward to the Arctic Circle.

The coyote ranges throughout the Edwards Plateau region (Schmidly, 1984b). Museum specimens of coyotes are not common, but querying of residents within the region, night driving, and listening for vocalizations of coyotes at appropriate times help to confirm the presence of this species throughout the Edwards Plateau. Records are available from Bandera, Bexar, Blanco, Burnet, Coke, Crane, Crockett, Glasscock, Howard, Irion, Kerr, Kimble, Llano, Midland, Nolan, Reagan, Runnels, San Saba, Schleicher, Sterling, Tom Green, and Val Verde counties (Fig. 88).

*Canis latrans* is the largest non-introduced canid extant on the Edwards Plateau. It is difficult to confuse with other canids (except for feral dogs) because of its size. The ears are large, upright, and pointed; the tail is long and bushy. Pelage is usually long and thick, with the dorsal color varying from pale tan to almost black. The venter is lighter in color than the dorsum. Claws are moderate in size and are non-retractile. The rostrum is moderately long and pointed, and the nose pad is black in color. Ratio of palatal width to length of upper molariform toothrow helps to separate *C. latrans* from feral dogs. If the toothrow is 3.1 times the palatal width, the specimen of concern is a coyote (Howard, 1949).

The coyote occupies all major terrestrial habitats on the Edwards Plateau. Coyotes occupy wooded uplands, riparian areas, juniper scrub areas, rocky slope habitats, cropland habitats, savannah, and prairie habitats on the Edwards Plateau. The coyote is even found in urban areas, living in garbage dumps, abandoned buildings, and other structures near humans (Bekoff, 1977, 1982). This canid even lives in areas more than a day’s travel from any sources of water (Bailey, 1905).

Coyotes are omnivorous and consume a great deal of vegetable matter and carrion (Bekoff, 1977). Percentages of animal and vegetable matter in their diets vary according to season and availability within an area (Bekoff, 1982). Diet items include rabbits, cotton rats, mice and other rodents, birds, poultry, eggs, deer (mostly as carrion), sheep, goats, other domestic livestock, vegetable crops, watermelons, prickly pear fruits, and insects (Hilton, 1978; Bekoff, 1982). Coyotes occasionally hunt in pairs and have been observed running down jackrabbits in relays. Coyotes are primarily nocturnal in foraging and activity period, but are seen frequently in early morning and late afternoon hours. Young animals are more active during daylight hours, and coyotes become more diurnal in activity during the winter months (Bekoff, 1982; Jones et al., 1983).

The size of prey items available in any particular habitat determines, to some extent, the social structure of resident coyotes (Bekoff, 1982). If larger prey such as deer are abundant, coyotes tend to form groups. Cooperative group defense appears to be the major selective force for increased sociality, not necessarily the ability to subdue larger prey. Most large animals, such as deer and cattle, are fed upon as carrion (Bekoff, 1982). The coyote shows no tolerance for foxes and...
avoids wolves, if *C. latrans* is sympatric with these species (Bekoff, 1982).

Natal dens are constructed by females, often beneath fallen trees, rocks, cutbanks, or in brushy areas. New dens may be dug, or abandoned dens may be remodeled by the coyote (Jones et al., 1983). Dens are approximately 15 inches in diameter and may extend 15 to 20 feet in length (Jones et al., 1983). Two or more entrances are common. Communal denning of females is rare. If a natal den is disturbed, the pups may be moved to another den within the home range.

Home range size is influenced by social organization. Coyotes living in packs and feeding upon carrion in the winter have smaller home ranges than solitary coyotes or male-female pairs (Bekoff, 1982). Home ranges may vary from 14.3 km to 30.1 km (Bekoff, 1982).

Females are monestrous and mate once a year, usually in late winter or early spring (Bekoff, 1977). Some males may be polygamous in mating behavior, as suggested by communal den sharing by females (Jones et al., 1983). Courtship behavior may last three months or more before a male and female mate (Bekoff, 1982). The gestation period lasts approximately 63 days. Litter size varies depending upon habitat, population density, prey availability, and age of the female (Bekoff, 1977). Average litter size is six (Jones et al., 1983). Young coyotes do not emerge from the den until about three weeks of age. The male provisions the female until the pups can be left unattended at the burrow. The parents feed the pups by regurgitation of stomach con-
Two subspecies of coyote occur on the Edwards Plateau; *C. l. texensis* Bailey, 1905, on the western Edwards Plateau to San Saba County, and *C. l. frustror* Woodhouse, 1851 on the remainder of the region to the east. However, because of a possible hybrid swarm effect mentioned by Nowak (1979), subspecies designations of coyotes on the Edwards Plateau may have little validity. Adult male coyotes are usually larger and heavier than adult females (Bekoff, 1978). Average external measurements of five coyotes from Louisiana (Lowery, 1974) are: total length, 1194; tail length, 355; length hind foot, 199; ear length, 108. Selected mean cranial measurements of 25 coyotes from Louisiana (Lowery, 1974) are: greatest length skull, 204.0; condylobasal length, 191.7; zygomatic breadth, 103.6. Selected measurements of the holotype of *C. l. texensis* Bailey, 1905 (an adult male from Corpus Christi, Texas) are: total length, 1143; tail length, 355; length hind foot (dry), 180; condylobasal length, 169; greatest length nasals, 67; zygomatic breadth, 94; mastoid breadth, 61; interorbital breadth, 30; length upper carnassial crown, 19.8.


**Canis lupus**

Gray Wolf

Distribution.— The gray wolf historically ranged from central Mexico, northward throughout most of the United States, excepting Arkansas, and Louisiana, and most of Florida. This species ranged throughout Canada and all of Alaska and northward and eastward to Greenland and is still common in some of these areas.

The gray wolf once ranged throughout the Edwards Plateau region, but has been extirpated from the region. Records exist from Crockett, Edwards, Kimble, Llano, Reagan, and Upton counties (Fig. 89).

*Canis lupus* was the largest native canid species to reside on the Edwards Plateau. Gray wolves are much larger in size than either the coyote or the red wolf (*C. rufus*). The gray wolf also may be distinguished from the coyote by its heavier and much broader skull profile. The color of the pelage varies from almost white to black dorsally, but is usually grayish in color. The venter, underside of the tail, and legs are lighter in color than the dorsum. The fur is rather long and course, with a distinct mane of longer guard hairs over the neck and shoulders. Five toes are present on the front feet (including a short fifth toe with a dew claw); the hind feet have four toes each. A group of stiff hairs is present over the precaudal gland at the dorsal base of the tail. Ears are furred, upright, and pointed terminally, and the tail is relatively short and bushy.

Gray wolves originally occupied most major habitats in the northern hemisphere (Mech, 1974). This species was found in all habitats of the Edwards Plateau from the xeric habitats of the western portion to mesic woodland habitats to the east.

The gray wolf is almost exclusively carnivorous. Large prey such as deer, pronghorn, peccaries, or (historically) bison are preferred, but beaver, rabbits, and
many other prey items are taken if available (Young, 1944; Mech, 1974). Most foraging is conducted nocturnally, but the gray wolf also may be active during daylight hours. Wolves usually hunt in pairs or larger numbers if large prey is available. Wolves are reported for indiscriminately killing livestock in greater numbers than they can consume (Young, 1944). However, when a gray wolf makes a kill, it will feed until gorged and remain in the vicinity of the kill after the feeding event (Young, 1944).

Gray wolves utilize dens only during the mating season. A den may be located in a rocky crevice, a hole dug into the ground, a hollow log, overturned stump, or other places of shelter (Mech, 1974). Wolves utilize resting areas throughout the remainder of the year within their territories. Dens are simple in construction and contain no litter or other material. Feces of the young are consumed by the female until they are weaned and do not accumulate within the den. If a den is excavated by the parents, it is sufficiently deep and extends laterally far enough to shelter the pups from the external elements (Young, 1944).

Gray wolves range over large areas and maintain large hunting territories (Young, 1944; Mech, 1974). Home ranges are large and vary in size from 50 to 5000 square miles. Wolves may occur singly, in pairs, or in packs. Packs are usually composed of family groups of related individuals (Mech, 1974) and usually are headed by an alpha male. If several adult males and females are members of a pack, a linear hierarchy is established first between males, then females, then offspring of each family (Mech, 1974). The family groups or packs exclude strange wolves from within the pack’s home range. Scent-mark stations are utilized at various spots along
runways within and around the home range (Young, 1944).

Wolves are believed to form pair bonds that last for the life of the animals. Courtship may extend for only a few days to months in duration for *C. lupus*. Breeding season begins in December and lasts until at least February, but varies according to latitude (Mech, 1974; Davis and Schmidly, 1994). Young are born in late winter or early spring months, after a gestation period of approximately 63 days (Mech, 1974). The number of young per litter ranges from four to six. The male provides food for both mother and young until the pups are old enough to be weaned. Food is offered to young pups and the female by disgorging of the male's stomach contents after returning to the den (Young, 1944). After pups are weaned, they are led to kills made by the parents and allowed to feed.

The subspecies which occurred on the Edwards Plateau was *C. l. monstrabilis* Goldman, 1937. Selected measurements from the type specimen (an adult male) from Upton County, Texas (Goldman, 1937) are: total length, 1620; tail length, 423; length hind foot, 230; greatest length skull, 261; condylobal length, 237; zygomatic breadth, 138; squamosal constriction, 81.2; width rostrum, 43.4; interorbital breadth, 45.9; postorbital constriction, 39.6; lengthmaxillary toothrow, 103.2.

Specimens examined (0).


*Canis rufus*

Red Wolf

Distribution.— This wolf originally ranged throughout the southeastern United States from Virginia and Florida, westward to Texas, Oklahoma, and Missouri. The red wolf originally ranged as far north as southern Indiana.

The red wolf ranged throughout at least the eastern half of the Edwards Plateau, perhaps as far west as Tom Green County (Nowak, 1979). This author, in his monograph of North American *Canis*, assigned all previous specimens of *C. rufus* from the region to hybrids of *C. latrans* and *C. rufus*. However, he opined that the "hybrid swarming event" was probably of short duration. In that regard, red wolves no doubt inhabited the area before their eventual decline and extinction from the region. Localities of specimens indicated in Figure 90 are taken from Nowak's (1979) list of specimens from Central Texas.

*Canis rufus* was a moderately large canid, and was intermediate in size between the smaller coyote and the larger gray wolf. The dorsal pelage was usually a cinnamon to tawny color, washed more heavily with black along the center of the dorsum and down the length of the tail. A melanistic phase, wherein the pelage was almost all black in color, excepting small white patches around the chin, throat, and inguinal area, occurred in some individuals of *C. rufus*. The rhinarium and feet are broader and larger than in *C. latrans*, and the legs of *C. rufus* are rather long and slender. External appearance, otherwise, closely resembles that of the coyote and wolf.

The preferred habitats of *C. rufus* likely were warm, moist, and densely vegetated areas on the Edwards Plateau (Paradiso and Nowak, 1972). The red wolf occurs in pine forest, bottomland hardwood forests, coastal prairies, and marshes of the southeast. Because of the long legs of *C. rufus*, it has been hypothesized that the red wolf was well-adapted to open, prairie habitats and long distance pursuit of prey (Paradiso and Nowak, 1972).

Little is known concerning the diet of these wolves upon the Edwards Plateau. Lowery (1974) stated that the species preyed upon wild hogs, deer, and, occasionally, cattle in Louisiana. Other researchers have indicated that *C. rufus* did not prey upon larger ungulates to the extent of the gray wolf; rabbits, rodents, and other small game may have been mainstays in the diet of *C. rufus* (Paradiso and Nowak, 1972). Most foraging and other activities were conducted during nocturnal hours.

The red wolf was similar to the gray wolf in denning behavior. Dens were utilized during the breeding season only. Suitable denning sites (along the gulf coastal area of Texas) included hollow logs, stumps, road culverts, sand knolls, and the banks of canals,
ditches, and reservoirs (Paradiso and Nowak, 1972). During other periods of the year, *C. rufus* probably utilized grassy areas and areas of dense cover as resting places within its hunting range.

Red wolves maintained a hunting territory, and were usually found in small, family groups. This species of wolf does not seem to have associated in large packs as was noted in the gray wolf. The animals were usually encountered in pairs of mated animals, sometimes with an extra male animal present (Paradiso and Nowak, 1972). The hunting range was probably extensive, as in the gray wolf, and was marked along regularly used runways by urine and feces deposited in specific areas and upon urine posts. Scratching around these areas also served to designate a group's territory. Red wolves were believed to form pair bonds for life. The only courtship behavior noted was holding the tail high above the back when males and females initially met (Paradiso and Nowak, 1972).

The mating season probably began in late December and early January and lasted until late February to early March. The gestation period was probably similar to that of the gray wolf, and lasted from 60 to 62 days (Paradiso and Nowak, 1972; Lowery, 1974). Based upon trapping data and museum records, Paradiso and Nowak (1972) estimated that litter sizes ranged from two to ten in *C. rufus*. Litter sizes from the gulf coastal area of Texas averaged seven young, but most died before six months of age. Populations in this area seemed to be highly susceptible to hookworms and heartworms.

The subspecies which occurred on the Edwards Plateau was *C. r. rufus* Audubon and Bachman, 1851.
Based upon measurements reported in the literature, sexual dimorphism existed in red wolves, with males being larger than females. External measurements given by Goldman (1944) for two adult males from Oklahoma are: total length, 1403, 1454; tail length, 381, 420; length hind foot, 210, 221. Selected cranial measurements of two males from Llano County, Texas are: greatest length skull, 225, 226.9; condylobasal length, 207.8, 209; zygomatic breadth, 117.5, 112.3; squamosal constriction, 68.7, 66; width rostrum, 34.6, 33.3; interorbital breadth, 39.7, 35; postorbital constriction, 36, 34.8; length maxillary toothrow, 98.2, 94.6.

**Specimens examined (0).**

*Additional records.— Bexar Co.: Near San Antonio. Blanco Co.: 14 555500E, 3330000N; 14 563000E, 3366600N. Burnet Co.: 14 569600E, 3374900N. Coleman Co.: 14 459100E, 3545200N. Concho Co.: (Unspecified Locality). Edwards Co.: 14 363800E, 3306300N; 14 424900E, 3420000N. Gillespie Co.: 14 4486100E, 3324700N; Unspecified Locality. Llano Co.: Baby Head; 22 mi. S Bird Range; 14 504100E, 3396400N; Click; 14 531000E, 3402100N; 14 523000E, 3409000N; 14 553500E, 3400400N; 14 531000E, 3374200N; 14 517400E, 3413800N; Unspecified Locality. Kerr Co.: 14 363800E, 3443800N; 14 451500E, 3433500N; 14 449400E, 3468900N. Medina Co.: Callan; 14 394200E, 3410800N; 14 424900E, 3420000N. San Saba Co.: 14 531400E, 3411600N; 14 527900E, 3427400N. Sutton Co.: 14 312200E, 3382500N; 14 342200E, 3382500N. (Nowak, 1979).*

**Vulpes velox**
Swift or Kit Fox

**Distribution.**—Consequent to the synonymizing of *V. macrotus* with *V. velox*, the distribution of this species extends from north-central Mexico and Baja California, northward throughout all of the Great Plains states, and westward to California and southern Oregon. This species ranges through portions of all the Rocky Mountain states, and occurs as far north as Alberta, Saskatchewan, and Manitoba, Canada.

This small fox ranges through approximately the western half of the Edwards Plateau. Records are at hand from Crane, Crockett, Glasscock, Howard, Menard, Reagan, and Val Verde counties (Fig. 91).

*Vulpes velox* is a relatively small fox. This species may be distinguished by its large ears, rather long, bushy, and black-tipped tail, and orange-tan venter, throat, and legs. The dorsum is buffy gray, with tan sides. Legs are slender and long, and the snout has a blackish to brown spot on each side. This fox lacks the prominent, black mane found on the dorsum of the gray fox (*Urocyon cinereoargenteus*). The skull of *V. velox* lacks a strongly developed sagittal crest, which is present in *V. vulpes* and *U. cinereoargenteus*. The foot pads are almost completely concealed by fur in *V. velox*.

These small foxes inhabit both grassland and desert-shrub habitats throughout their range (Egoscue, 1979; McGrew, 1979). Short and midgrass habitats are preferred in the northern part of the range and xeric, creosote shrub habitats are occupied in the southwestern portion of this species’ range. This fox sometimes is found in cropland and urban habitats, but these associations should be considered marginal at best (McGrew, 1979). Predator control is believed to have reduced populations within many areas of the species’ original range (Jones et al., 1983). Overgrazing, and other disturbances within many areas may have resulted in a decline in the numbers of this species (Egoscue, 1979).

Diet of *V. velox* consists in large part of rodents and other small mammals. Prey items apparently are selected according to availability within a particular area, and there is little evidence to support prey-switching behaviors when prey is in short supply (McGrew, 1979). Known diet items include kangaroo rats, cotton rats, hispid pocket mice, black-tailed jackrabbits, cottontail rabbits, quail, small reptiles and amphibians, carrion, and grass (Cutter, 1958b). Foraging is conducted nocturnally, but *V. velox* occasionally may be seen sunning adjacent to its den during warm morning or early evening hours (Jones et al., 1983).

This fox is the most den-dependent canid in North America. In arid, hot areas, *V. velox* spends most of the daylight hours within a den. Denning may also provide protection from predators, such as coyotes. Dens are constructed from abandoned prairie dog burrows, other vacant burrows, or may be dug by the occupant (Cutter, 1958a; Egoscue, 1979). The den usually has more than one entrance, some of which may be plugged in older dens. Cutter (1958a), from his examination of *V. velox* dens in Texas, indicated that a central chamber is present, with perhaps one or two side chambers. Depth
varies within the den but may be at least 32 inches below the surface in the central chamber. The nest chamber is often bare, but may contain grass and other plant litter (Jones et al., 1983). These foxes commonly utilize more than one den in an area, perhaps in response to heavy ectoparasite infestations. In addition to fleas and other ectoparasites, dens may be co-occupied by spiders, centipedes, and amphibians. Abandoned dens are often used by skunks, burrowing owls, small rodents, and snakes (Egoscue, 1979).

This species of fox forms a pair bond between males and females that lasts for at least one year. However, there is disagreement as to whether or not the pair bond lasts for the lifetime of the partners (McGrew, 1979). The male fox helps to care for offspring by foraging and bringing food to the den. The female rarely leaves the natal den when pups are very young. Both parents lose weight as a result of provisioning activities while raising a litter of pups. Prey items are brought to the den intact; no regurgitation of food has been observed in V. velox. Family groups break up in the fall months, and the pups disperse to new areas. Home ranges of foxes overlap within an area, and there is little evidence that a specific hunting territory is maintained or defended by an individual (McGrew, 1979). Young foxes mate during their first year of life.

Breeding occurs from December to February; pups are born in March or April (Schmidly, 1984b). Female foxes are monestrous. Litters range in size from three to six (Egoscue, 1979). The gestation period is approximately seven weeks in length.

Dragoo et al. (1990) studied systematic relationships between V. velox and V. macrois. On the basis of
congruent morphological and electrophoretic data, these authors placed *macrothis* as a subspecies under *V. velox*. *V. v. macrothis* Merriam, 1888 occurs in the extreme western Edwards Plateau and ranges as far east as Glasscock and Reagan counties. *V. v. velox* (Say, 1823) occurs in the remainder of the region and ranges northward onto the Llano Estacado of Texas. There is no evidence of significant sexual dimorphism in *V. velox*. Males, however, are usually heavier than females. Average external measurements (Schmidly, 1977) are: total length, 823; tail length, 301; length hind foot, 123; ear length, 82. Selected cranial measurements of a male and female from Menard County (Hollander et al., 1987) are respectively: condylobasal length, 106.4, 104.7; zygomatic breadth, 63.9, 60.5; least interorbital constriction, 22.9, 21.3; breadth braincase, 44.6, 42.8; length maxillary toothrow, 51.1, 49.3.

**Specimens examined (18).— Crockett Co.: 14 230900E, 3411300N, 1 (ASNHC). Glasscock Co.: 14 277400E, 3519100N, 1 (ASNHC), 14 274200E, 3527900N, 1 (ASNHC). Howard Co.: 14 283000E, 3568000N, 2 (ASNHC). Menard Co.: 14 415400E, 3410800N, 2. Reagan Co.: 14 283000E, 3473900N, 3 (ASNHC); 14 258700E, 3465200N, 2 (ASNHC); 14 250300E, 3460000N, 1 (ASNHC); 14 250500E, 3453800N, 2 (ASNHC); 14 253800E, 3453800N, 1 (ASNHC); North Concho Research Area, 1 (ASNHC).**


**Vulpes vulpes**  
Red Fox

**Distribution.**— The red fox ranges throughout the Eastern United States, northwest to western Washington, Oregon, and California, and throughout Canada, and Alaska to the Arctic Circle. The red fox is excluded from parts of the Rocky Mountains within the conterminous United States, and has not been recorded from the driest regions of the southwest, parts of the arid High Plains, and South Texas.

The range of the red fox has been documented to include all of the Edwards Plateau, except the extreme western counties, most of Val Verde County, Kinney County, and most of Uvalde County (Schmidly, 1984b). Records exist for Burnet, Coke, Crockett, Glasscock, Howard, Kerr, Kimble, Reagan, Runnels, Schleicher, Sterling, Tom Green, and Travis counties (Fig. 92).

**Vulpes vulpes** is easily recognized by its small size and red colored fur on its dorsum. The nose pad is black, as are the lower legs, feet, and ears. The tail is long, bushy, and white-tipped, and the ventral side, throat, and chin sometimes are white. The only canid *V. vulpes* may be confused with is the gray fox (*Urocyon cinereoargenteus*); however, *U. cinereoargenteus* has a different color of pelage. The skull of the red fox has V-shaped temporal ridges, whereas the temporal ridges of *U. cinereoargenteus* are U-shaped.

The red fox may be found in oak-juniper upland habitats, edge habitats around field borders, intermixed cropland-woods habitats, rolling farmland habitats, brushy habitats, and pasturelands on the Edwards Plateau. Edge habitats are heavily utilized by *V. vulpes* (Samuel and Nelson, 1982). Numbers of these foxes were introduced in the Cross-Timbers region of Texas around 1891 (Bailey, 1905), and subsequently expanded their range in East Texas and on the Edwards Plateau.

The red fox also inhabits urban areas, and areas around farmsteads. The most important factors in red fox habitats are availability of cover, den sites, and water, as well as a suitable prey base (Samuel and Nelson, 1982).

The red fox is an opportunistic omnivore in its foraging habits. Major food items are rodents, rabbits, wild fruits and berries, and insects (Schmidly, 1983). Carrion of various animals is consumed; one instance of cannibalism is known (Samuel and Nelson, 1982). Other diet items include poultry, quail, eggs, turtles, cats, young opossums, passerine birds, shrews, and moles (Samuel and Nelson, 1982). Prey switching occurs seasonally. The red fox may rely heavily upon deer carrion and cottontail rabbits in the winter months, rodents in the spring and fall, and insects and fruits in summer months (Samuel and Nelson, 1982). *V. vulpes* is most active at night, and often travels down trails. This canid may occasionally be observed during dawn and dusk hours in an area.

Red foxes cache food at different locations within their territories. Red foxes will continue to hunt even when satiated and, conversely, may cache food items
when still hungry (Samuel and Nelson, 1982). Unlike some canids, *V. vulpes* must feed on a regular basis, so food caching is an adaptive behavior (Samuel and Nelson, 1982).

Red foxes may dig their own dens, but frequently utilize the dens of other animals as winter shelters and natal dens. The same den may be used for many generations, with burrows being added each year (Samuel and Nelson, 1982). Dens are often located on the sides of embankments, in wooded areas, or along wooded rivers and streams (Sealander and Heidt, 1990). Burrows may be 20 to 30 feet in length and are usually a little more than three feet in depth (Sealander and Heidt, 1990). Occasionally, dens are occupied by more than one pair of foxes (Samuel and Nelson, 1982).

The red fox centers its home range around a natal den. Home ranges tend to be about twice as long as they are wide, but extent and shape are determined by habitat features (Samuel and Nelson, 1982). In less diverse habitats, home ranges tend to be larger in size; a maximum home range of 5.12 km has been reported (Samuel and Nelson, 1982). The male of the mated pair patrols the boundary of the territory and scent marks localities with urine and feces.

Females are monestrous and monogamous. Mating occurs from December into February (Sealander and Heidt, 1990). The gestation period is approximately 52 days in length. Litter size varies from one to eleven, with five being the usual number of pups per litter (Samuel and Nelson, 1982). The male provides food for the female while the pups are too small to be left
alone; both parents hunt when the pups may be left unattended at the den. The family group, including the adult male, remains together until the young are old enough to disperse. Dispersal of young foxes usually occurs in the fall.

The subspecies of red fox on the Edwards Plateau is *V. v. fulva* (Desmarest, 1820). Males are somewhat heavier than females (Lowery, 1974). Average external measurements of seven specimens from the southeastern United States (Lowery, 1974) are: total length, 97.5; tail length, 31.0; length hind foot, 15.1; ear length, 8.5. Selected mean cranial measurements of eight individuals from the same source are: greatest length skull, 140.0; condylobasal length, 125.3; cranial breadth, 46.8; zygomatic breadth, 70.8; interorbital breadth, 23.4; rostral breadth, 20.1; length maxillary toothrow, 61.7.

**Specimens examined (53).—** Burnet Co.: 14 571900E, 3382200N, 1 (STU). Coke Co.: 14 338400E, 3514300N, 2 (ASNHC); 14 330100E, 3514000N, 1 (ASNHC). Crockett Co.: 14 311200E, 3382800N, 2 (ASNHC). Glasscock Co.: 14 4265300E, 3534600N, 1 (ASNHC); 14 256100E, 3535700N, 2 (ASNHC); 14 265000E, 3534000N, 1 (ASNHC); 14 267900E, 3528100N, 2 (ASNHC); 14 277400E, 3537000N, 1 (ASNHC). Howard Co.: 14 282800E, 3568000N, 1 (ASNHC). Reagan Co.: 14 266300E, 3479400N, 2 (ASNHC); 14 280500E, 3476200N, 6 (ASNHC); 14 257300E, 3464200N, 1 (ASNHC); 14 250300E, 3460000N, 1 (ASNHC); 14 249300E, 3453700N, 1 (ASNHC). Runnels Co.: 14 1412500E, 3513400N, 5 (ASNHC); NE of Ballinger, 7 (ASNHC). Sterling Co.: Foster Ranch, 3 (ASNHC); Unspecified Locality, 4 (ASNHC). Tom Green Co.: 14 336900E, 3497300N, 1 (ASNHC); 14 342800E, 3482400N, 1 (ASNHC).

**Additional records.—** Kimble Co.: 14 425500E, 3372900N (Raymond Trimble: Personal Communication, 1994). Kerr Co.: Unspecified Locality. Travis Co.: 14 622000E, 3541500N.

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**Urocyon cinereoargenteus**

**Common Gray Fox**

**Distribution.**—The common gray fox ranges from northern Venezuela and Colombia, northward throughout most of Central America, and all of Mexico. The gray fox is found throughout most of the conterminous United States, except for portions of the mountainous northwest and Great Plains. This species' range extends northward to southern Manitoba, Ontario, and Quebec, Canada.

The gray fox reputedly ranges throughout the Edwards Plateau region (Schmidly, 1984b). Records are available from Bandera, Bexar, Burnet, Coke, Comal, Crockett, Hays, Irion, Kerr, Kimble, Llano, Mason, McCulloch, Midland, Reagan, Runnels, Sterling, Tom Green, Travis, Uvalde, and Val Verde counties (Fig. 93).

**Urocyon cinereoargenteus** is slightly smaller than the red fox. The dorsal fur of *U. cinereoargenteus* is gray and black, giving the animal a distinctive salt and pepper appearance. The throat is white, and the ears, neck, legs, and ventral side of the tail are reddish colored. The skull of *U. cinereoargenteus* has lyre-shaped temporal ridges; the temporal ridges of *V. vulpes* are more V-shaped. The ventral border of the mandible of the gray fox is notched, whereas it is smooth in the red fox. Both foxes are much smaller than the coyote.

Gray foxes are animals of forest, woodland, or rocky and brush-covered country (Jones et al., 1983). *U. cinereoargenteus* is closely associated with deciduous forests and woodlands throughout North America (Hall, 1981; Samuel and Nelson, 1982). They are found more commonly in the vicinity of rocky slopes and mesquite pastures on the Edwards Plateau; these foxes may be found also in woodland-farmland edge habitats on the Edwards Plateau.

The gray fox is omnivorous. Diet items include birds, rabbits, rodents, insects, fruits and berries, deer carrion, and some cereal grains (Jones et al., 1983). Important plant fruits include mesquite beans and juniper berries (Samuel and Nelson, 1982). Specific foods consumed vary according to location and season (Fritzel and Haroldson, 1982). Gray foxes are primarily nocturnal or crepuscular in foraging and activity periods.
Figure 93. Distribution of *Urocyon cinereoargenteus* on the Edwards Plateau.

*U. cinereoargenteus* is somewhat arboreal and may take refuge in trees to escape predators and to hunt birds (Jones et al., 1983).

Dens are utilized by *U. cinereoargenteus* as shelter for pups and refuge during periods of inclement weather. Dens are usually located in brushy or wooded habitats (Fritzell and Haroldson, 1982). Suitable den sites include hollow logs or trees, rock outcrops, underground burrows, cavities underneath rocks, abandoned buildings, and piles of wood and brush (Fritzell and Haroldson, 1982). Most underground burrows are probably abandoned dens of other animals.

Social behavior centers around family groups, at least during the whelping period (Fritzell and Haroldson, 1982). Home range size varies according to sex and locality (Fuller, 1978; Fritzell and Haroldson, 1982). Males maintain larger home ranges than females (Fritzell and Haroldson, 1982). Home range size increases during late fall and winter months. The home range of females decreases after pups are born in the spring (Samuel and Nelson, 1982). The home range size of males increases during this period of time, perhaps indicating increased foraging ranges for males while provisioning both the female and pups (Samuel and Nelson, 1982).

Female gray foxes are monestrous; most breeding occurs from December to March, or later. Males and females establish pair bonds in October and November. The gray fox is monogamous for a single breeding season, but mated pairs are not necessarily the same from year to year (Schmidly, 1984b). One to seven fetuses have been reported (Fritzell and Haroldson, 1982), but because of intrauterine mortality and other factors, litter size averages four young (Samuel and...
Nelson, 1982). Gestation period may range from 53 to 63 days (Fritzell and Haroldson, 1982), and pups are born in March or April (Schmidly, 1984b).

The subspecies of gray fox on the Edwards Plateau is *U. c. scottii* Mearns, 1891. Males are slightly heavier than females (Fritzell and Haroldson, 1982). Average external measurements (Schmidly, 1977) are: total length, 1028; tail length, 441; length hind foot, 141; ear length, 68. Selected cranial measurements of two adults (sex unknown) from the Edwards Plateau are: greatest length skull, 117.70, 119.45; zygomatic breadth, 66.62, 65.33; interorbital breadth, 22.38, 22.28; cranial breadth, 45.67, —; breadth postorbital processes, 42.10, 37.76; length maxillary toothrow, 49.93, 49.97; width across molars, 34.05, 35.05.

Specimens examined (112).—Bandera Co.: 14 443900E, 3202700N, 1. Bexar Co.: 14 568200E, 3265400N, 1 (TNHC). Burnet Co.: 14 561300E, 3403000N, 1 (ASNHC). Coke Co.: 14 339600E, 3516300N, 1 (ASNHC). Comal Co.: 14 577800E, 3309700N, 1 (SWTU). Crockett Co.: 14 230900E, 3409700N, 1 (ASNHC). Hays Co.: 14 588000E, 3338400N, 1 (TNHC); 14 601600E, 3309700N, 1 (SWTU). Irion Co.: 14 293300E, 3483600N, 1 (MWSU); 14 305900E, 3477400N, 2 (ASNHC). Hemphill Ranch, 3 (ASNHC). Kimble Co.: 14 425400E, 3372000N, 1; 14 429800E, 3372800N, 2 (MWSU); 14 434600E, 3372800N, 2 (MWSU); 14 436200E, 3372800N, 6 (MWSU); 14 437800E, 3372800N, 1 (MWSU); 14 441000E, 3372800N, 8 (MWSU); 14 444200E, 3372800N, 5 (MWSU); 14 412900E, 3354600N, 1 (TCWC). Llano Co.: 14 556000E, 3375000N, 1 (MWSU); Mc Culloch Co.: 14 466100E, 3456500N, 1 (MWSU); 14 468100E, 3451400N, 1 (MWSU); 14 468100E, 3441100N, 16 (ASNHC). Midland Co.: Hyw. 349 (Unspecified Locality), 1. Reagan Co.: 14 266800E, 3495800N, 1 (ASNHC); 14 266800E, 3491000N, 1 (MWSU); 14 266800E, 3480600N, 15 (ASNHC); Rocker B Ranch, 6 (ASNHC); 14 266800E, 3479000N, 4 (ASNHC); 14 266800E, 3475800N, 1 (ASNHC); 14 269700E, 3471400N, 1 (ASNHC); 14 271800E, 3470900N, 3 (ASNHC); 14 266800E, 3456000N, 1 (ASNHC); 14 239500E, 3454700N, 1 (ASNHC); 14 243100E, 3453500N, 2 (ASNHC); 14 250500E, 3453500N, 1 (ASNHC); 14 245700E, 3457000N, 1 (ASNHC); 14 250200E, 3451600N, 1 (ASNHC). Runnels Co.: 14 394500E, 3548700N, 1. Sterling Co.: 14 298000E, 3538000N, 1 (ASNHC); 14 312100E, 3519000N, 1 (ASNHC). Tom Green Co.: 14 349300E, 3447700N, 1 (ASNHC); 14 357700E, 3451800N, 1 (ASNHC); 14 357700E, 3444200N, 2 (ASNHC). Uvalde Co.: Animal Damage Control (Unspecified Locality), 1 (SWTU).

Additional records.—Bexar Co.: North of San Antonio. Comal Co.: 14 586600E, 3299700N (TCWC). Kerr Co.: 14 443400E, 3324200N (TCWC); 14 446300E, 3336800N (TCWC); West of Turtle Creek; 14 452000E, 3115700N (TCWC); 14 443700E, 3309000N (TCWC). Mason Co.: 14 477900E, 3382800N (TCWC); 14 477900E, 3379600N (TCWC). Travis Co.: Unspecified Locality. ValVerde Co.: Unspecified Locality. (Allen, 1896; Davis and Schmidly, 1994).

Family Ursidae—Bears

*Ursus americanus*  
Black Bear

Distribution.—The historical distribution of the black bear extended from northern Alaska, southward through all of Canada, and the conterminous United States, terminating in central Mexico. The current distribution includes much of Alaska and Canada, the Rocky Mountain, Pacific Coast, Great Lakes and most Atlantic coast states of the conterminous United States, and parts of northern Mexico. Small numbers are also found in Missouri, Arkansas, Louisiana, and the Trans-Pecos of Texas.

Although once widespread on the Edwards Plateau of Texas, black bear populations have been extirpated from the region since European settlement. Records of specimens examined reported herein are from caves, and represent subfossil remains of black bears. Specimens exist from Edwards, Kendall, and Medina counties. Literature records are available from Comal, Gillespie, and Kerr counties. In addition, a personal communication with J. Barnes indicated a wandering bear in Crockett County (Fig. 94).

The black bear is the largest carnivore that occurred on the Edwards Plateau. Its black pelage, inconspicuous tail, and rather large, clawed feet are distinct. The facial profile is rather blunt, the eyes are small, and the nose pad is broad. White patches are...
sometimes present on the lower throat and chest. Each foot has five toes and locomotion of bears is plantigrade.

A prime black bear habitat is characterized by relatively inaccessible terrain, thick understory vegetation, and abundant sources of food in the form of shrub or tree-borne soft or hard mast (Pelton, 1982). Rough, broken areas, and canyon areas on the Edwards Plateau meet most ideal habitat requirements and probably supported limited populations of bears (Doughty, 1983).

Bears are omnivorous in diet. Diet items include grasses and forbs, juniper berries, acorns, insects, grapes, and carrion. Hoffmeister (1986) reported that black bears will occasionally feed upon prickly pear fruits. The bear reported from Crockett County by John Barnes was implicated in killing sheep and was subsequently dispatched by a local rancher. Foraging ranges increase in the late summer and early fall months as black bears searching for abundant food sources to help provide them with fat.

Bears utilize bed sites during periods of inactivity, usually in brushy tangles and other inaccessible areas. Bed sites usually consist of a simple shallow depression in the forest leaf litter. Black bears are adept at climbing, and will utilize hollow trees, caves, or simply nests on the ground as winter denning sites, depending upon the specific habitat and portion of the geographic range (Pelton, 1982). *U. americanus* is crepuscular, but will alter its activity period in relation to available food supplies. Black bears may become diurnal if foraging along roads or may become nocturnally active if consuming garbage items around campgrounds.
Black bears exhibit a period of winter dormancy even in the extreme southern portions of their range. Winter dormancy probably helps *U. americanus* to circumvent severe food shortages during the winter months. Although heart rate decreases and body temperature lowers during dormancy, *U. americanus* may be easily aroused during this period. Hoffmeister (1986) reported that black bears were sometimes active during winter months in Arizona. The young of *U. americanus* are born in the winter, and easy arousal during dormancy may be an aid to the female in caring for her offspring.

Black bears are solitary, except during the mating season. Exceptions to this are family groups of mother and young, and feeding congregations of bears at a particular resource (Pelton, 1982). Black bears breed in the summer. A period of delayed implantation occurs, and young are born during the winter. The gestation period, overall, is about seven months (Hoffmeister, 1986). Two young is the usual number per litter, but the range may be one to four young per litter. The young are altricial when born, but, when the mother is ready to leave the winter den, offspring are strong enough to follow her. Cubs remain with their mother until two years of age, at which time they disperse. Normally females mate once every two years (Davis and Schmidly, 1994).

The subspecies that occurred on the Edwards Plateau was *U. a. americanus* Pallus, 1780. Ranges of external measurements for males and females (Jones et al. 1985) are: total length, 1270-1780; tail length, 80-125; length of hind foot, 190-280; ear length, 110-125. Weight may range as high as 226.80 kg.

**KEY TO PROCYONIDAE**

1. Bony palate terminating just posterior to last upper molar; upper molars transversely elongated, much broader than long; greatest length skull averaging 80 mm; tail about as long as head and body; no black facial mask present ............................................................... *Bassariscus astutus*

1'. Bony palate terminating far posterior to last upper molar; upper molars not transversely elongated, about as broad as long; greatest length of skull averaging greater than 80 mm; tail much shorter than head and body length; conspicuous black facial mask present .............................................. *Procyon lotor*

**Family Procyonidae—Procyonids**

*Bassariscus astutus*  
Ringtail

*Distribution.*—The range of the ringtail extends from southern Mexico, northward through parts of Louisiana and Arkansas at the eastern limits of its range within the conterminous United States. Ringtails occur throughout most of Texas, Oklahoma, and northward to Kansas. This species ranges westward through parts of Colorado, Wyoming, Utah, Nevada, Oregon, and California on the Pacific coast. The ringtail also is found throughout Baja, California.

The ringtail’s range has been mapped as extending throughout the Edwards Plateau (Hall, 1981; Schmidly, 1984b). Records are available from Bandera, Bexar, Blanco, Burnet, Coke, Comal, Crockett, Edwards, Hays, Howard, Kerr, Kimble, Llano, Mason, McCulloch, Menard, Nolan, Reagan, Runnels, San Saba, Sutton, Tom Green, Travis, Uvalde, and Val Verde counties (Fig. 95).

*Bassariscus astutus* is about the size of a domestic cat when fully grown. The tail is ringed with about 16 black and white stripes, black tipped, and is about as long as the body. The fur on the dorsum is fulvous...
colored and heavily frosted with black, whereas the venter is white or pale buff. Ringtails have white circles around the eyes. The muzzle is elongate, grizzled, and pointed. The nose pad is black. Appendages are short, and the rear appendages are longer than the front appendages. Ringtails are plantigrade and have semi-retractile claws on the feet.

The ringtail inhabits rocky, slope habitats throughout the Edwards Plateau. \textit{B. astutus} also inhabits oak woodlands, juniper woodlands, riparian areas, and other habitats within the region, provided there are rocky outcrops present (Poglayen-Neuwall and Toweill, 1988). Ringtails prefer habitats with open water, but may maintain water balance through a high protein or high fruit diet (Poglayen-Neuwall and Toweill, 1988).

Ringtails are omnivorous in diet. Plant materials make up about 74 percent of this animal’s diet on the Edwards Plateau (Toweill and Teer, 1977). Berries and fruit of Ashe juniper, hackberry, Texas persimmon, and mistletoe are common plant items in the diet. Similar food items are found in ringtail feces at Sonora, Texas (Chavez-Ramirez and Slack, 1993). Insects are taken when available and contribute a major proportion to the diet. Birds, rodents, and other small mammals make up about 14 percent of the diet.

The ringtail is primarily nocturnal in its foraging activity. Almost all activity is conducted during crepuscular or nocturnal hours. Vibrissae and elongated hairs on the forearms help provide tactile information to \textit{B. astutus} during nocturnal activities. The night vision of \textit{B. astutus} is acute (Poglayen-Neuwall and Toweill, 1988). Young ringtails develop an aversion to
light at an early age (Poglayen-Neuwall and Toweill, 1988). When foraging, instead of jumping from rock to rock as many other mammals do, the ringtail proceeds by climbing around the rocks.

The ringtail utilizes crevices, hollow trees, rock piles, and buildings for resting and nesting sites. Ringtails also utilize the burrows of other species as dens, and sometimes share dens with hog-nosed skunks and armadillos (Poglayen-Neuwall and Toweill, 1988). Burrow dens are not constructed or otherwise improved, but a nest of grass and other vegetation may be constructed for the young (Poglayen-Neuwall and Toweill, 1988).

Ringtails are solitary in habit. There is little or no intrasexual overlap in home ranges, but the home ranges of males and females may overlap. The size of home ranges varies with season and specific habitat. *B. astutus* may shift home ranges within an area on a seasonal basis (Poglayen-Neuwall and Toweill, 1988). Social structure and territory acquisition is based on a land-tenure system, with individuals denning separately (Poglayen-Neuwall and Toweill, 1988).

In central Texas, female ringtails come into heat in early April (Davis and Schmidly, 1994). Females are monestrous; litter size ranges from one to four young (Poglayen-Neuwall and Toweill, 1988). The gestation period is from 51 to 54 days in length. The young are altricial when born and attain their full size at about 30 weeks of age. Postpartum estrus is rare in the ringtail (Poglayen-Neuwall and Toweill, 1988). Males have no real tendency toward monogamy (Poglayen-Neuwall and Toweill, 1988), but may assist the female in caring for the young about three weeks after their birth. Prior to this time, the female excludes the male parent from the young (Poglayen-Neuwall and Toweill, 1988).

The subspecies of ringtail on the Edwards Plateau is *B. a. flavus* Rhoads, 1894. Males are slightly larger than females in most body measurements (Lowery, 1974). Average external measurements of three males and three females from the Edwards Plateau, respectively, are: total length, 777, 757; tail length, 365, 375; length hind foot, 70, 63; ear length, 50, 50. Selected mean cranial measurements of the same males and females, respectively, are: greatest length skull, 82.42, 79.63; zygomatic breadth, 52.34, 48.66; least interorbital constriction, 16.85, 16.26; breadth supraorbital processes, 26.42, 27.97; postorbital constriction, 16.00; 17.74; breadth mastoid process, 36.80; 35.40; length maxillary toothrow, 31.35, 30.09; width across molars, 25.78, 24.25.

**Specimens examined (107).**—Bandera Co.: 14 451400E, 3307100N, 1 (TNHC). Burnet Co.: 14 560800E, 3430900N, 1. Coke Co.: 14 347400E, 3297600N, 1 (SM); 14 580600E, 3304900N, 1 (SWTU). Edwards Co.: 14 383200E, 3343400N, 1. Hays Co.: 14 586300E, 3319100N, 4 (SWTU); 14 582000E, 3550400N, 1 (SWTU); 14 576200E, 3346200N, 1 (SWTU); 14 601300E, 3306600N, 1 (SWTU). Howard Co.: 14 277200E, 3560100N, 1 (MWSU). Kerr Co.: 14 446600E, 3326100N, 1 (MWSU). Kimble Co.: 14 418000E, 3372800N, 1; 14 433000E, 3372800N, 1 (MWSU); 14 434600E, 3372800N, 2 (MWSU); 14 436200E, 3372800N, 17 (MWSU); 14 437800E, 3372800N, 14 (MWSU); 14 441000E, 3372800N, 22 (MWSU); 14 444200E, 3372800N, 8 (MWSU); 14 421200E, 3370400N, 3. McCulloch Co.: 14 446400E, 3344000N, 1 (MWSU); 14 476100E, 3435500N, 1 (TNHC). Menard Co.: 14 413000E, 3426100N, 1; 14 404000E, 3416700N, 1; 14 453000E, 3420000N, 1; 14 455000E, 3420000N, 1 (MWSU). Nolan Co.: 14 383700E, 3570900N, 1. Reagan Co.: 14 257300E, 3453700N, 1 (ASNHC); 14 551600E, 3434200N, 1 (ASNHC); 14 552300E, 3431500N, 1 (TNHC); 14 520400E, 3427000N, 1 (TNHC). Sutton Co.: 14 341200E, 3375500N, 1; 14 392800E, 3382600N, 2. Tom Green Co.: 14 346400E, 3500700N, 1; 14 357700E, 3448200N, 1 (ASNHC); 14 357700E, 3447300N, 1 (ASNHC); 14 357700E, 3444100N, 1 (ASNHC). Travis Co.: 14 614600E, 3351300N, 1 (TNHC); 14 602400E, 3378400N, 2; 14 608700E, 3344800N, 1 (TNHC). Val Verde Co.: 14 289200E, 3303200N, 1 (MWSU); 14 315100E, 3314400N, 1; Mayfield Ranch on Pecos River, 14 259900E, 3315600N, 1 (ASNHC). Additional records.—Bexar Co.: Rough Country North and West of San Antonio. Blanco Co.: 14 553300E, 3352600N. Crockett Co.: 14 289300E, 3405300N (TCWC). Kerr Co.: 14 434000E, 3324200N (TCWC); 14 456300E, 3324500N (TCWC); 14 446300E, 3336800N (TCWC); 14 486100E, 3324800N (TCWC); 14 486100E, 3315500N (TCWC); 14 457100E, 3325900N (TCWC). Llano Co.: 14 531800E, 3413500N.
**Procyon lotor**

**Common Raccoon**

**Distribution.**—The raccoon ranges from Panama northward throughout the conterminous United States. The raccoon’s range extends north to include all of the southern Canadian provinces.

The raccoon has a ubiquitous distribution on the Edwards Plateau (Schmidly, 1984b). Records are available from Bexar, Blanco, Burnet, Coke, Coleman, Concho, Crockett, Edwards, Hays, Irion, Kerr, Kimble, Llano, Mason, Menard, Nolan, Reagan, San Saba, Schleicher, Sterling, Sutton, Tom Green, Travis, and Val Verde counties (Fig. 96).

**Procyon lotor** is easily recognized by its black, facial mask around the eyes, short, black-tipped tail, and short legs. The pelage is long, coarse, and ranges from gray to almost black in color. The venter is lighter in color than the dorsum. The tail usually is ringed by five to seven black bands. Raccoons are pentadactyl and plantigrade; front feet have well developed, curved, and laterally compressed claws.

Raccoons are found throughout the state of Texas, so are adaptable in their habitat choices to an extent. However, *P. lotor* is seldom found far from water, which has an important influence on its distribution (Schmidly, 1984b). The most favored habitats on the Edwards Plateau would be riparian areas, mesic upland wooded areas, cultivated and abandoned farmlands, and, in many cases, areas around human habitations.

Raccoons are omnivorous and opportunistic in diet, consuming crayfish, snails, small fishes, cereal grains, acorns, plums, and other vegetable matter, frogs, birds, small mammals, and insects (Lowery, 1974; Kaufmann, 1982). Plant foods may constitute more than 50 percent of a raccoon’s diet, with insects next in importance, followed by mammals, invertebrates other than insects, cold-blooded vertebrates, and birds (Wood, 1954). Diets vary according to season of the year (Kaufmann, 1982), and no animal matter may be consumed in the diet, depending upon locality and prey availability (Chavez-Ramirez and Slack, 1993). Most foraging activities are conducted nocturnally.

Raccoons use a variety of shelters. Hollow trees and rock ledges are utilized as denning sites, and raccoons also will use vacant buildings and other structures as dens. Abandoned badger, fox, and skunk dens also may be used as shelters (Kaufmann, 1982). Daytime sleeping sites include all of the aforementioned sites, areas of dense ground cover, brush piles, bare tree limbs, inside clumps of Spanish moss, and smashed down squirrel nests (Kaufmann, 1982). Dens of all kinds are located near a source of water. Raccoons may shift their sleeping sites daily during the year, but some sites are utilized more than others (Kaufmann, 1982). Usually no nest is prepared within a den site.

Raccoons are most commonly solitary in habit, but occasionally small groups of two or more individuals are observed (Schmidly, 1984b). Whenever population density of raccoons is high within an area, *P. lotor* is evenly distributed throughout the area (Lotze and Anderson, 1979). Size of home range varies according to habitat, and, although long range movements are known, movements are usually limited within a habitat (Lotze and Anderson, 1979; Kaufmann, 1982). Males typically have larger home ranges than females, and males may expand their home ranges to visit several females during the mating season (Kaufmann, 1982). Dominant individuals mark areas within their home ranges by neck-rubbing, and anal rubbing against objects (Ough, 1982).

Male raccoons typically mate with several females within an area, but some evidence exists for the establishment of pair bonds between individual males and females in some instances, (Kaufmann, 1982). Females bond with familiar males in an area about one month before the mating season, but will mate with other males during the peak of estrous. The mating season begins in February and continues through August. Females are monestrous. The gestation period is approximately 63 days in length (Lotze and Anderson, 1979). The number of young born per litter varies from two to four (Schmidly, 1984b). Only the female is involved in care of the young raccoons until their dispersal at about nine months of age or in the following spring (Lotze and Anderson, 1979).
The subspecies of raccoon found on the Edwards Plateau is *P. l. fuscipes* Mearns, 1914. Males are significantly larger than females for most characters (Kennedy and Lindsay, 1984). Average external measurements (Schmidly, 1983) are: total length, 728; tail length, 217; length hind foot, 111; ear length, 60. Selected cranial measurements of two adult females from the Edwards Plateau, respectively, are: greatest length skull, 112.21, 115.25; zygomatic breadth, 70.48, 73.82; cranial breadth, 47.49, 50.49; mastoid breadth, 58.13, 60.35; width postorbital process, 27.48, 28.75; length maxillary toothrow, 42.75, 43.52; width across molars, 39.48, 40.50; length auditory bullae, 17.70, 18.67; width auditory bullae, 18.63, 18.20.

Specimens examined (90).—Blanco Co.: 14 571800E, 3351200N, 1. Coke Co.: 14 364100E, 3513600N, 1 (ASNHC); 14 362300E, 3509000N, 1 (ASNHC). Coleman Co.: 14 4592000E, 3530200N, 1. Comal Co.: 14 579600E, 3302900N, 1 (SWTU). Concho Co.: 14 4204000E, 3490800N, 1 (ASNHC). Crockett Co.: 14 3112000E, 3382800N, 1 (ASNHC); 14 2309000E, 3409700N, 1. Edwards Co.: 14 4248000E, 3327600N, 1 (WTAM). Hays Co.: Ranch Rd. 12, next to San Marcos Academy, 1 (SWTU); 14 6013000E, 3306600N, 2 (SWTU). Irion Co.: Hemphill Ranch (Unspecified Locality), 1 (ASNHC); 14 2933000E, 3475600N, 1 (ASNHC); 14 3270000E, 3480600N, 1 (ASNHC). Kimble Co.: 14 3989000E, 3382200N, 1 (ASNHC); 14 4199000E, 3378800N, 1; 14 3955000E, 3372800N, 1; 14 4254000E, 3372000N, 1; 14 4362000E, 3372800N, 1 (MWSU); 14 4378000E, 3372800N, 2 (MWSU); 14 4410000E, 3372800N, 14 (MWSU); 14 4442000E, 3372800N, 2 (MWSU); 14 4254000E, 3371200N, 1; 14 4254000E, 3369600N, 3; 14 4219000E, 3370100N, 1; 14 3955000E, 3396800N, 1; 14 4131000E,
Nasua narica is about the size of a raccoon, but has a long, hairy tail with indistinct light bands. The snout of the white-nosed coati is long, slender, and quite mobile; the muzzle, chin, and throat are whitish. Thin white streaks extend from the muzzle between, and over the eyes. The ears are relatively short and white-tipped with yellow to white postauricular patches. The overall color is pale brown to reddish, often overlaid with yellow in the neck and shoulders. The feet are blackish and the venter is yellowish in color.

The coati is often found in wooded and rocky habitats, and only seems to venture out into grasslands and other open areas when dispersing between woods (Kaufmann et al., 1976). Across its range, it is found from desert to rainforest habitats. At the northern extreme of its range, the coati is often found in rocky, wooded canyons, with oak and pine trees (Hoffmeister, 1986). N. narica is usually found close to streams, creeks, or other sources of water.

White-nosed coatis are opportunistic omnivores. Diet items include acorns, various types of fruits, soil inhabiting invertebrates, tarantulas, scorpions, lizards, snakes, rodents, and carrion. Coatis have also been reported to feed upon garden crops, and fruit from orchards. They feed upon what is available in an area and, it has been postulated, they leave the area when the food supply is depleted (Kaufmann et al., 1976).

Coatis forage through an area by poking their long snouts into and under vegetation and debris and searching for food items. In forests in Central and South America, N. narica often forages in trees, and is quite adept at climbing and moving from one tree to another in a heavy forest (Ingles, 1957). The long tail is rather prehensile, and is used for balance and for support when in trees.

Coatis are often found in groups of as few as two to as many as 30 or more. The groups are matriarchal in nature, and are comprised of females and young ani-
mals. Adult males are usually solitary in habit (Kaufmann et al., 1976).

In forested areas, *N. narica* frequently utilizes trees for denning sites. The white-nosed coati utilizes rocky crevices, cavities among tree roots, caves, and old mines for dens in the northern part of its range (Hoffmeister, 1986).

Mating in the white-nosed coati is thought to occur in April; young are born in June. Coatis are believed to be polygamous in mating habit. Davis (1974) reported one litter that was thought to number four young.

The subspecies occurring in Texas is *N. n. molaris* Merriam, 1902. Average external measurements (Schmidly, 1977) are: total length, 1130; tail length, 500; length hind foot, 91; ear length, 30. Selected cranial measurements of four males from New Mexico (Hoffmeister, 1986) are as follows: condylobasal length, 125.70; zygomatic breadth, 70.70; interorbital breadth, 27.88; length maxillary toothrow, 48.21; breadth braincase, 47.38; bullar length, 14.33.

Specimens examined (0).

Additional records.— Real Co.: 14 428600E, 3278400N. (Hall, 1981).
KEY TO MUSTELIDAE

1 Premolars 4/3; infraorbital foramen large, roughly oblong, greatest diameter more than 8 mm; last upper premolar and first molar roughly rectangular in shape; tail long, heavy, and flat on the ventral side; toes of each foot fully webbed ................................................................. Lutra canadensis

1' Premolars 2/3 or 3/3; infraorbital foramen less than 8 mm, ovoid, triangular, or oblong; last upper premolar and first molar not rectangular in shape; tail not especially long and heavy, and tail not flat on the ventral side; toes of feet unwebbed, or toes of hind feet only partially webbed ................................................................. 2

2 Greatest length of skull 90 mm or more; skull roughly triangular in outline; body thickset and heavy; single, narrow white stripe extending from the nose to the neck or beyond; ears white on the inside ................................................................. Taxidea taxus

2' Greatest length of skull less than 90 mm; skull not triangular in outline; body not especially thickset and heavy; no white dorsal stripe, bifurcated white stripe, or a single, broad white dorsal stripe extending from the pate to the shoulders or farther; ears not white on the inside ................................................................. 3

3 Upper molar noticeably dumbell-shaped; dorsal color tan to chocolate brown; no pronounced white stripes or spots on the dorsum; tail not especially bushy ................................................................. 4

3' Upper molar rather square in shape; dorsum black with conspicuous white spots and/or stripes; tail rather bushy ................................................................. 5

4 Greatest length skull less than 55 mm; auditory bulla longer than upper cheektooth row; total length less than 500 mm; dorsum tan colored, venter buffy or yellow-white; tail tipped with black; toes of hind feet not partially webbed ..................................................................................... Mustela frenata

4' Greatest length of skull more than 55 mm; auditory bulla about as long as upper cheektooth row; total length more than 500 mm; dorsum a uniform dark brown in color; venter similar in color to dorsum; tail uniform dark brown; toes of hind feet partially webbed ......................................................... Mustela vison

5 Premolars 2/3; mastoid breadth 36 mm or greater; single, broad white stripe extending from the pate to the tip of the tail................................................................. Conepatus mesoleucus

5' Premolars 3/3; mastoid breadth less than 36 mm; dorsal stripe bifurcated down the dorsum, or dorsum spotted with white patches ................................................................. 6

6 Greatest length of skull less than 65 mm; total length averaging about 400 mm; hind foot less than 60 mm; dorsum black with numerous white patches and spots ......................................................................................... Spilogale gracilis

6' Greatest length of skull more than 65 mm; total length more than 400 mm; hind foot length more than 60 mm; dorsum usually a uniform black, with a bifurcated white stripe from behind the pate to the shoulders or beyond ......................................................................................... Mephitis mephitis
Family Mustelidae—Mustelids

*Mustela frenata*
Long-tailed Weasel

**Distribution.**—The long-tailed weasel is distributed throughout the conterminous United States. The range of this species extends northward into British Columbia, and southward throughout Mexico.

The range of *Mustela frenata*, as mapped by Hall (1981), covers the entire Edwards Plateau. Jones and Jones (1992) stated that this weasel is probably found throughout most of Texas. Schmidly (1984b), however, maps the range of *M. frenata* as extending north and west only as far as San Saba, southern Schleicher, and southern Crane counties. Although this species may be widespread on the Edwards Plateau, museum records are scarce. Specimens are at hand only from Bexar, Gillespie, and Kerr counties on the Edwards Plateau, with one specimen from Val Verde county, at a locality approximately 10 mi. S of the Edwards Plateau (Fig. 98).

The long-tailed weasel is easily recognized by its long, tubular torso, short legs, long neck, and black facial mask. The pelage is brown dorsally and huffy in color on the venter. The chin is white in color and white markings are present behind the eyes. The distal tip of the tail is black in color, and ear pinnae are short and rounded.

Long-tailed weasels occupy a variety of habitats within Texas (Schmidly, 1984b), but may be more common in riparian areas in association with water, and in upland and wooded habitats on the Edwards Plateau. These small carnivores reside in dens in an area, usurping them from former residents or occupying vacant dens (King, 1989). Long-tailed weasels sometimes occupy sheds and other out-buildings in association with humans (Schmidly, 1984b).

Weasels have rather definite home ranges in areas where there are established populations, and they are often territorial in behavior, depending upon local conditions (King, 1989). Young animals, especially males, may disperse long distances when the family groups dissolve. Weasels scent mark their territories with musk secretions from anal glands, by rubbing cheek glands against objects, urinating upon objects, and by depositing scats at a location within the territory (King, 1989).

Weasels are not known to hibernate or aestivate; they are active year-around. The diet is made up of rodents, ground nesting birds, bird’s eggs, rabbits, shrews, moles, and other animal matter (Jones et al., 1983). Long-tailed weasels have a very high basal metabolism, and may be active day or night. Body fat is low in these small predators, so they must hunt often to secure sufficient supplies of food. Food is often stored in caches within a weasel’s territory (King, 1989). Weasels do not readily consume the hair of their prey, thus, leaving distinctive carcass remains consisting of inverted skin and hair at feeding localities.

Weasels are polygamous and breed in July and August in Texas (Schmidly, 1984b). Implantation of the fertilized eggs is delayed for several months, so young are not born until April or May of the following year. A litter of from five to seven young usually is produced. Females are sexually mature at around three months of age and males reach sexual maturity at approximately one year of age (King, 1989).

Hall (1981) maps the range of three subspecies upon the Edwards Plateau. Based upon this work and upon specimens examined by me, two subspecies of long-tailed weasel may occur on the Edwards Plateau. Hall (1981) lists as a marginal record a specimen of *M. f. frenata* Lichtenstein, 1831, from San Antonio, and I have examined specimens of *M. f. texensis* Hall, 1936, from Kerr and Gillespie counties on the Edwards Plateau, and Val Verde County immediately south of the Edwards Plateau. As far as I know, no specimens are available to verify the occurrence of the third subspecies, *M. f. neomexicana* (Barber and Cockerell, 1898), on the Edwards Plateau. The nearest records of this subspecies are a record from Lozier, Terrell County, approximately 80 miles west of the Edwards Plateau (Hall, 1981), and specimens from Hockley County, approximately 110 miles north of the Edwards Plateau. Average external measurements (Schmidly, 1984b) for *M. frenata* are: total length, 430; tail length, 225; length hind foot, 42; and ear length, 21. Sexual dimorphism occurs in this species with males averaging larger than females. Selected cranial measurements of the specimen from Val Verde County were taken from Davis (1961) and are as follows: basilar length, 45.5; interorbital breadth, 11.7; mastoidal breadth, 25.4; zygomatic breadth, 29.5; length of tympanic bullae, 15.8; width of tympanic bullae, 8.7; length maxillary toothrow, 17.2. These same measurements taken from a speci-
Figure 98. Distribution of Mustela frenata on the Edwards Plateau.

men of unknown sex from Gillespie County, are respec­
tively; 52.43; 10.98; 24.13; 29.87; 15.18; 8.39; 14.87.

Specimens examined (3).— Gillespie Co.: 14
512300E, 3349500N, 1 (TCWC). Kerr Co.: 14
433600E, 3313100N, 1 (TCWC). Val Verde Co.: 14
315900E, 3249200N, 1 (TCWC).

Additional records.— Bexar Co.: 14 550200E,
3255000N (Hall, 1981).

Mustela nigripes
Black-footed Ferret

Distribution.— The historic range of the black­
footed ferret extended from west-central Texas north­
ward through the great plains states, and into Alberta,
and Saskatchewan, Canada. The eastern limits of the
range extended to Nebraska, and the western limits to
Montana, and Arizona.

Bailey (1905) stated that the black-footed ferret
had been reported from a number of localities east and
south of the Staked Plains. This species has been closely
associated with prairie dogs throughout its range. If,
indeed, the black-footed ferret occurred along with prai­
rice dogs on the Edwards Plateau, it may have extended
over the western portion of the area as far east as Ma­
son County and south to Crockett County (not mapped).
This area is coincident with the original range of C.
ludovicianus within the Edwards Plateau as mapped
by Bailey (1905). The species has been extirpated from
Texas. The last reported record was of an individual
from Dallam County in 1993 (Cahalane, 1954), but
Jones (1993) was of the opinion that this species was
extirpated from Texas at least a decade earlier, and doubted the authenticity of the unverified record.

*Mustela nigripes* is a rather large ferret, with black legs and a distinctive, black facial mask. Ears are prominent and rounded, and the dorsum is rather yellowish in color. There is no sharp demarcation between the dorsal and ventral pelage, as in other weasels. The venter is buffy or cream colored. The tail is rather long and is tipped with black. Appendages are short, and the torso is rather tubular in shape, as in other species of weasels.

Ideal habitats for this ferret were grassland areas, in association with prairie dogs. Hillman and Linder (1979) stated that, in South Dakota, the black-footed ferret was observed away from prairie dog towns by local residents, but these authors could not verify any of these sightings.

The black-footed ferret is carnivorous in diet. *M. nigripes* preys heavily upon prairie dogs. Alternate prey items included thirteen-lined ground squirrels, cotton-tail rabbits, deer mice, and birds (Hillman and Clark, 1980). The predator-prey relationship between *M. nigripes* and *Cynomys* apparently has existed since the Pleistocene, as prairie dog and ferret remains have been found associated in several Pleistocene-age fossil faunas. This stenophagous diet may be a factor in the extirpation of the black-footed ferret throughout most of its range. Extensive eradication programs have been carried out in the present century (Cahalane, 1954), and populations of *Cynomys* are much reduced throughout the former range of the species. Foraging and other activities are conducted nocturnally, but young *M. nigripes* also may be active during early morning hours. The black-footed ferret is believed to kill only enough to eat at any single foraging event (Hillman and Linder, 1979). Ferrets may occupy a prairie dog town for extended periods of time, but do not greatly reduce the number of *Cynomys* resident there (Hillman and Linder, 1979).

The black-footed ferret reputedly makes its home in the burrows of prairie dogs (Hillman and Clark, 1980). The species is secretive and rarely observed in nature. Because of its subterranean habitat, information on much of the life history of the black-footed ferret is lacking. Black-footed ferrets probably are solitary in habit until the breeding season.

In a study involving captive animals, females entered breeding condition in late February to early March. Copulation occurred in March and early April, and the gestation period of one female was 42 and 45 days over two breeding seasons (Hillman and Clark, 1980). Litter size of wild *M. nigripes* ranged from one to five young. The young remain with their mother until they disperse from the area of the natal den in September or early October.

*Mustela nigripes* (Audubon and Bachman, 1851) is a monotypic species. Females average approximately ten percent smaller than males in linear measurements. Range of external measurements for males (Hillman and Clark, 1980) are: total length, 500-533; tail length, 114-127; length hind foot, 60-73; ear length, 29-31.

Specimens examined (0).

Literature records (0).

*Mustela vison*

*Mink*

Distribution.—The mink ranges throughout all of the conterminous United States, except Arizona. This species occurs throughout all provinces of Canada, with the exception of Anticosti Island and the Queen Charlotte Islands, and westward throughout all except extreme northern Alaska.

The mink has been reported from the eastern half of Texas, and extends westward on the Edwards Plateau as far as Kimble, Mason, and Taylor counties (Fig. 99). In Texas, museum records are scarce for this species.

*Mustela vison* may be recognized by its weasel-like shape, and overall dark brown pelage. The head is rather triangular in shape, and the face lacks the white markings around the eyes that are present in *M. frenata*. The feet are well-haired and the toes are partially webbed in *M. vison*. White patches of pelage may be present on the chin and throat. The tail of *M. vison* is bushy, and the ears are short and rounded.

Mink are distinctly aquatic in their habitat preference, and this fact probably is a factor limiting their distribution on the Edwards Plateau. Preferred areas are major watercourses, ponds, and lakes. Mink will disperse along streams and tributaries of major rivers during times of flooding.
Figure 99. Distribution of *Mustela vison* on the Edwards Plateau.

Mink almost are exclusively carnivorous in diet, with plant material being ingested only incidentally while feeding (Linscombe et al., 1982). Prey items consumed vary seasonally, as does foraging activity. *M. vison* has been reported to adjust its activity period according to the availability of prey within its range (Linscombe et al., 1982). Diet items include fish, frogs, snakes, birds, eggs, rodents, crayfish, and insects. Seemingly, *M. vison* will feed upon any animal that it can capture and kill.

Digestion is rapid in minks, with some items being passed within an hour of consumption. Hard, indigestible items are passed through the digestive system quickly, whereas softer materials are retained for a longer period of time.

Both sexes of mink have definite home ranges within an area. The male has a much larger range than does the female of the species (Sealander and Heidt, 1990). Juveniles, however, may range over greater distances whenever dispersing after the breakup of family groups. Dens are utilized as shelter within a home range. Males typically occupy multiple dens, seeming to utilize whatever den site is most convenient at any particular time (Linscombe et al., 1982). Females may also utilize more than one den within their area, but usually utilize fewer dens than do males.

The breeding season of *M. vison* extends from January through March (Sealander and Heidt, 1990). Males are polygamous, but often stay with the last female mated to help raise the young (Schmidly, 1984b). The mink demonstrates delayed implantation of the fertilized eggs. Young are usually born in late spring and
early summer months. Females that are mated later in
the breeding season undergo pregnancies of shorter du­
ration (Linscombe et al., 1982). Litter sizes normally
range from five to seven.

The subspecies of mink on the Edwards Plateau
is *M. v. mink* Peale and Palisot de Beauvois, 1796.
Sexual dimorphism occurs in *M. vison*, with males av­
eraging as much as ten percent larger than females.
External measurements of a male specimen from Hays
County are as follows: total length, 497, tail length,
156; length hind foot, 57; ear length, 22. Selected cra­
nial measurements of this same individual are: nasal
length, 10.10; zygomatic breadth, 34.45; postorbital
breath, 16.16; length maxillary toothrow, 19.34; width
maxillary toothrow, 21.92; least breadth braincase,
28.13; mastoid breath, 32.07; condylobasal length,
61.97; bullar length, 16.20; bullar breadth, 8.30.

*Specimens examined* (1).— *Hays Co.*: 14
603600E, 3303900N, 1 (TNHC).

*Additional records.*— *Kimble Co.*: (Personal
14 477900E, 3401100N. *Taylor Co.*: unknown local­
ity. *Travis Co.*: 14 621900E, 3351400N. (Bailey, 1905;
Taylor, 1944; Davis and Schmidly, 1994).

*Taxidea taxus*  
American Badger

*Distribution.*— The American badger ranges from
central Mexico northward to all Canadian provinces,
except Quebec. Badgers range from the Pacific coast
eastward through Ohio, Missouri, western Arkansas,
and all of Texas, except the extreme eastern portion.

The badger’s range reputedly covers the entire
Edwards Plateau, but specimens are relatively few and
from scattered localities within the region. Records are
available from Coke, Crane, Glasscock, Kerr, Mason,
Reagan, Sterling, Sutton, Tom Green, and Val Verde
counties (Fig. 100).

The American badger may be recognized by its
short, stocky, shape and wedge-shaped head, with black
and white “badges” beside the eyes. A single, narrow
white stripe extends from the tip of the nose usually to
the base of the tail. Pelage is long and course. The
dorsum varies in color from yellowish brown to silvery
gray, and the venter is a light cream to buffy color. The
feet are black with long, sharp claws on the front pair
and shovel-like claws on the rear feet. The tail is short
and the ears are short and oriented rather laterally on
the skull. The small eyes have a nictitating membrane.
Anal glands are present, as in other mustelids.

*Taxidea taxus* is usually found in open habitats
and grassland situations. Heavily wooded areas and
areas with shallow, stony soils are usually avoided. An
apparent exception to this occurs in young animals dur­ing
periods of dispersal. While dispersing young bad­
gers frequently traverse areas that would seem to be
quite unfavorable for habitation (Lindzey, 1982). Num­ers of these mustelids may now be reduced on the
Edwards Plateau as a result of the eradication of prairie
dog towns in the area and other habitat alterations.
Bailey (1905) reported badgers commonly associated
with prairie dog towns throughout most of central Texas.

Badgers are primarily active at night, but may
occasionally forage during diurnal hours. The badger’s
diet is almost exclusively animal material, and varies
depending upon season of the year, prey availability in
an area, and other factors (Long, 1973; Lindzey, 1982).
Preferred food items include ground squirrels and pocket
gophers. Badgers often use their sense of olfaction to
detect a particular prey item in a subterranean burrow,
and then employ a variety of stratagems to capture the
prey.

Badgers utilize dens they have constructed for
shelter and protection. Although *T. taxus* is not known
to hibernate, it is known to have occupied dens for up to
38 days (Lindzey, 1982). While in dens during cold
periods, badgers undergo bradycardia and diurnal hy­
pothemia (Lindzey, 1982). Badgers are territorial and
the ranges of males show no overlap. Scent marking
around dens and other areas within an individual’s home
range is utilized to delineate territories (Lindzey, 1982).

Badgers are mostly solitary, except for family
groups of mother and young. Siblings have been ob­served in association for a short time after dispersing
from their mother (Lindzey, 1982). Badgers will occa­sionally fight, but the absence of scars on most indi­
viduals indicates that fighting is rare.

Badgers are polygamous in breeding habits. Bad­
gers, like other mustelids, exhibit delayed implantation
of embryos. The mating season occurs throughout the
months of July and August, with young being born the
following spring (Davis and Schmidly, 1994). The number of young born per litter is usually two to five. As many as seven embryos have been reported (Long, 1973).

The subspecies of badger occurring on the Edwards Plateau is *T. t. berlandieri*, Baird 1858. Average external measurements (from Schmidly, 1984b) are: total length, 660.5; tail length, 120; length hind foot, 110; ear length, 47. Cranial measurements of two males (previous holotypes of different subspecies) are from Long (1972). Selected average cranial measurements are: greatest length skull, 116.95; length palate, 61.2; zygomatic breadth, 74.6; postorbital breadth, 36; cranial depth, 39; length maxillary toothrow, 39.25; carnassial length, 11.3.


Figure 100. Distribution of *Taxidea taxus* on the Edwards Plateau.
*Spilogale gracilis*
Western Spotted Skunk

**Distribution.**—The western spotted skunk ranges from central Mexico, northward through most of the western conterminous United States from the western half of Texas north to South Dakota, thence westward through most of Wyoming and Idaho. The species ranges through southern and western Washington to British Columbia. The western spotted skunk ranges south through most of California and throughout Baja California.

Schmidly (1984b) mapped the range of the western spotted skunk as extending throughout all but the extreme northern counties of the Edwards Plateau. However, specimens to verify this extensive range are scarce. Records exist from Bexar, Gillespie, Howard, Irion, Kendall, Kerr, Mason, Menard, Tom Green, and Val Verde counties on the Edwards Plateau (Fig. 101).

*Spilogale gracilis* is similar in size and appearance to the eastern spotted skunk (*S. putorius*). Mead (1968) based his separation of the two species primarily upon reproductive isolation between eastern and western spotted skunk populations, even in regions of sympatry. The eastern spotted skunk has not been collected on the Edwards Plateau, but occurs close to the eastern margin of the region. The western spotted skunk has more white in its color pattern than does *S. putorius*. The dorsal black and white stripes are nearly equal in width in *S. gracilis*. The tip of the tail is extensively white and the underside of the tail is white for almost half of its length. Spotted skunks have from four to six white stripes, whereas other species of skunks have only one or two. The western spotted skunk also has a broad, triangular, white nose patch that is lacking in other skunks. Spotted skunks are the smallest skunks on the Edwards Plateau, being about the size of small house cats. All four feet are pentadactyl, and the forefeet have well-developed claws. Ears are relatively small and rounded, and, as in all skunks, anal glands are present and well-developed.

Spotted skunks are often found in rocky areas, but may also occur in the vicinity of farmsteads, in old fields, upland woods, and canyon drainages (Howard and Marsh, 1982; Hoffmeister, 1986). Broad habitat tolerances are found in this species of skunk, and these animals are believed to be rather nomadic in nature. The home range of males has been reported to be larger than that of females, especially during the mating season.

The western spotted skunk is omnivorous in diet. Items consumed include beetles, grasshoppers, crickets, rodents, rabbits, carrion, some species of birds, eggs, fruits, and cereal grains. Food hoarding is not known to occur in spotted skunks (Howard and Marsh, 1982). Jones et al. (1983) report that spotted skunks are good "mousers," but Howard and Marsh (1982) report that there is no evidence that these skunks can effectively reduce rodent populations within an area. Percentages of insects, mammals, fruits, and grains in the diet of the western spotted skunk vary with availability and season.

The western spotted skunk is nocturnal in its foraging activity. This species is described as a quick and active predator with weasel-like habits (Jones et al., 1983). Moonless nights and other nights of intense darkness are favored for activity and foraging. Spotted skunks are good climbers, and may forage in trees and raid bird nests for both the avian occupants and eggs.

Spotted skunks den in a variety of different locations and utilize woodpiles, outbuildings, barns, abandoned equipment, hollow stumps and trees, old gopher burrows, and rocky crevices as den sites within an area. Nests are usually constructed from grasses and other available materials. When abandoned buildings are inhabited, nests usually are not constructed (Howard and Marsh, 1982). Dens are occupied singly or by kin-groups. The eastern spotted skunk has been collected in numbers from communal dens during the coldest days of winter (Jones et al., 1983), and the western spotted skunk also may den communally in the winter months.

Breeding in *S. gracilis* begins in September, with both adult and juvenile females participating. Delayed implantation is present, and the embryos float freely in the uterus for approximately 180 to 200 days (Schmidly, 1984b). Implantation of the embryos takes place in April and young are born in May (Howard and Marsh, 1982). The average litter size is four young.

The subspecies on the Edwards Plateau is *S. g. leucoparia* Merriam, 1890. Sexual dimorphism is present in spotted skunks, with males being larger than females. Mean external measurements of three females and two males from Mason County are, respectively: total length, 360.30, 401.50; tail length, 130.67, 123.50;
length hind foot, 41, 42; ear length, 26.33, 26.5. Selected cranial measurements of a male from Kerr County are: occipitobasal length, 55.36; zygomatic breadth, 36.23; interorbital breadth, 15.27; mastoidal breadth, 33.28; breadth braincase, 23.72; length maxillary toothrow, 16.66; least breadth bullae, 6.82; length bullae, 12.48; length bony palate, 16.68; skull depth, 19.33.


_**Mephitis mephitis**_

Striped Skunk

_Distribution._— The striped skunk ranges from Durango and Tamaulipas, Mexico northward throughout all but the most arid regions of the southwestern United States. This skunk ranges northward throughout all of the southern provinces of Canada and into southern Yukon and Mackenzie Provinces.

The striped skunk ranges throughout Texas (Schmidly, 1984b), however, museum specimens are not common. Records are available from Bexar, Coke, Coleman, Concho, Crockett, Glasscock, Hays, Howard, Kerr, Kimble, Kinney, Llano, Mason, McCulloch,
Mephitis mephitis has a long, bushy tail, a triangular shaped face, and short legs with rather long, curved claws on the front feet. The hind legs are slightly longer than the front legs, and claws on the hind legs are shorter, and straighter than claws on the front feet. *M. mephitis* is smaller than the hog-nosed skunk (*Conepatus mesoleucus*) and has a different stripe pattern. The stripe pattern is the most distinctive feature of *M. mephitis* and consists of a pair of bifurcated white stripes that extend variable lengths down the dorsal side of the animal and join in the neck and pate area. The remainder of the pelage is black in color. Ears are short and rounded, and eyes are small. The western spotted skunk is smaller in size than *M. mephitis*, and has a different color pattern consisting of several white bands and spots set against black. Striped skunks have three upper premolars, whereas hog-nosed skunks have only two.

Preferred habitats are upland pastures, sparse woodlands, and agricultural areas and fields. Other favored habitats include fencerows, edge habitats, wooded ravines, brushy areas, and rocky areas (Godin, 1982). Striped skunks may also be found around city dumps, and associated with human habitations, barns, sheds, and other structures (Godin, 1982). Mixed vegetation habitats have been identified as the most suitable habitats for *M. mephitis* by some researchers; however, other workers have found the striped skunk to be abundant in monocultural areas (Wade-Smith and Verts, 1982).

The striped skunk is omnivorous, with insects making up a major percentage of its diet. *M. mephitis* is opportunistic in foraging behavior and will take advantage of windfall resources within an area. Striped skunks also vary their diets according to resource availability throughout the year (Wade-Smith and Verts, 1982). Diet items include mice, frogs, lizards, birds, eggs, fruits, garbage, and some carrion (Jones et al., 1983). Most foraging activity is nocturnal, but *M. mephitis* occasionally may be observed moving about during daylight hours.

*M. mephitis* is active throughout the year but may den up and sleep, sometimes with other skunks, during extremely cold periods. Communal dens may contain any combination of sexes and ages of striped skunks, and the combinations may vary from day to day (Godin, 1982). True torpor is not evinced by the striped skunk, although skunks may experience mild hypothermia and lethargy (Wade-Smith and Verts, 1982). Striped skunks deposit fat during the spring and summer months, and usually lose weight during the winter months (Cuyler, 1923; Godin, 1982).

Burrows and dens are utilized by females during the breeding season, and by both sexes during the colder months of the year. Dens are often located in rocky crevices, under brush piles, in fencerows, and on slopes. In addition, dens are sometimes located in the watersheds of streams and ponds (Cuyler, 1923). Skunks frequently utilize the abandoned burrows of other animals, but, if none are available, striped skunks are capable of excavating their own burrows. Natal dens usually are shallow and relatively simple, with an enlarged nest chamber at the end of a single tunnel (Wade-Smith and Verts, 1982). Other dens may have more than one entrance and multiple tunnels (Godin, 1982; Wade-Smith and Verts, 1982). Grasses and other nesting material are used to construct a nest within the den, but females may remove part or all of the nest material before the birth of young (Wade-Smith and Verts, 1982).

Striped skunks are solitary in habit, except for family groups of a female and her young. *M. mephitis* is tolerant of the activities of conspecifics, except during the mating season. Striped skunks are often oblivious to the activities of conspecifics and other animals while foraging and moving about (Wade-Smith and Verts, 1982). Movements and home ranges are small and may be centered around dens (Godin, 1982). Males may move greater distances within an area during the mating season (Godin, 1982).

Striped skunks are polygamous in mating habit (Godin, 1982). Females are monestrous and usually breed during February or March (Wade-Smith and Verts, 1982). Striped skunks are induced ovulators (Wade-Smith and Verts, 1982). The gestation period ranges from 59 to 77 days, and most young are born during the first part of May. Litter size ranges from three to nine, with an average of about five (Schmidly, 1984b).

The subspecies of striped skunk found on the Edwards Plateau is *M. m. varians* Gray, 1837. Adult males are larger in size than females (Godin, 1982). External measurements of two adult males from the
Figure 102. Distribution of *Mephitis mephitis* on the Edwards Plateau.

Edwards Plateau are: total length, 563, 573; tail length, 286, 275; length hind foot, 63, 61; ear length, 25, 25. Selected mean cranial measurements of two male and two female striped skunks, respectively, are: occipitobasal length, 70.8, 65.52; zygomatic breadth, 42.16, 38.62; least interorbital breadth, 19.45, 17.93; mastoid breadth, 34.98, 31.51; greatest breadth brain­case, 28.38, 26.73; bullar breadth, 6.01; 6.13; bullar length, 9.94, 9.76; length maxillary toothrow, 21.23, 19.61.


*Additional records.*— Bexar Co.: San Antonio vicinity (Unspecified Locality). Crockett Co.: 14 2306000E, 3415600N; 14 3091000E, 3366400N.
Conepatus mesoleucus
Common Hog-nosed Skunk

Distribution.—The hog-nosed skunk ranges from northern Nicaragua northward throughout all but eastern Mexico, and into the southwestern region of the United States. Hog-nosed skunks range from south-central Texas, north and west into New Mexico and Arizona. These skunks are not found on most of the Llano Estacado of New Mexico and Texas, and occur as far north as the Oklahoma panhandle and southeastern Colorado.

Hog-nosed skunks are found over at least the southern two-thirds of the Edwards Plateau. C. mesoleucus occurs at least as far north as Reagan and Nolan counties on the Edwards Plateau (Manning et al., 1986), and may range throughout the entire region. Records are available from Bexar, Coke, Concho, Crockett, Gillespie, Hays, Kerr, Kimble, Llano, Mason, McCulloch, Menard, Nolan, Reagan, Tom Green, and Val Verde counties (Fig. 103).

Conepatus mesoleucus is larger than M. mephitis and has a single, solid, white stripe of pelage extending from the top of the head to the tip of the tail. The snout is relatively long with a hairless pad at the end, and the tail is relatively short, bushy, and predominately white in color. The remainder of the pelage is black in color. C. mesoleucus has one less upper premolar in its dental complement than either Mephitis or Spilogale.

Preferred habitats include rocky, upland areas and slopes, and the more xeric areas of the Edwards Plateau. I have seen these skunks adjacent to rocky, broken areas on the Edwards Plateau, and other researchers (Baker, 1956) have observed hog-nosed skunks in mesic, canyon areas. Hog-nosed skunks are uncommon in unbroken, homogeneous habitats (Leopold, 1959). Unlike the striped skunk, hog-nosed skunks are seldom found around human habitations (Schmidly, 1983).

The hog-nosed skunk is omnivorous. Diet items include insects, vegetation, spiders, snails, small mammals, and reptiles (Schmidly, 1984b). Grubs, cactus fruits, and other fruits are consumed, and, perhaps, some carrion. Foraging areas may be identified by the presence of diggings and overturned (rooted up) rocks and other items at localities where the skunks reside (Davis and Schmidly, 1994). Insects make up the major percentage of the diet throughout the year (Davis and Schmidly, 1994). The hog-nosed skunk is mostly nocturnally active. However, they also may be observed feeding during the warmest hours of the day in mid-winter (Schmidly, 1984b).

Hog-nosed skunks are solitary in habit and occupy dens. Dens may be constructed or these skunks may utilize rock piles, hollow logs, and other features for dens (Leopold, 1959). Usually only a single individual occupies each den (Davis and Schmidly, 1994). The hog-nosed skunk has been found inhabiting woodrat nests in Arizona (Hoffmeister, 1986), and may also utilize Neotoma nests as refuges throughout its range in Texas. Little is known concerning the life history of hog-nosed skunks because of their nocturnal habits.

Females produce one litter of young per year, with the number of offspring ranging from two to four. Gestation period is approximately 42 days (Howard and Marsh, 1982). Nursing young have been observed in April in Coahuila, Mexico (Leopold, 1959).

The subspecies of hog-nosed skunk on the Edwards Plateau is C. m. mearnsi Merriam, 1902. Males are slightly larger than females (Marsh and Howard, 1982). Average external measurements for males and females (Schmidly, 1977), respectively, are: total length, 602, 551; tail length, 233, 215; length hind foot, 68, 65; ear length, 27, 24. Selected cranial measurements of two adult females from the Edwards Plateau are: greatest length skull, 70.10, 76.57; zygomatic breadth, 43.46, 49.14; least interorbital breadth, 21.82, 20.29; mastoid breadth, 39.05, 42.04; length maxillary toothrow, 20.51, 22.46; length bullae, 10.32, 15.59; width bullae, 7.17, 11.45.
Figure 103. Distribution of *Conepatus mesoleucus* on the Edwards Plateau.


Additional records.— Bexar Co.: Medina River (Unspecified Locality). Crockett Co.: 14 285900E, 3402600N (TCWC); Devils River (Unspecified Locality). Gillespie Co.: 14 4777000E, 3371000N (TCWC). Kerr Co.: Unspecified Locality; 14 434300E, 3337400N (TCWC); 14 486100E, 3324700N; 14 485800E, 3315500N (TCWC); 14 438400E, 3315400N (TCWC). Llano Co.: 14 531200E, 3401900N. Mason Co.: 14 477900E, 3401000N; 14 477900E, 3382800N (TCWC). Travis Co.: 14 622000E, 3341500N. Val Verde Co.: Unspecified Locality; 14 3159000E, 3267700N (Davis and Schmidly, 1994).
**Lutra canadensis**

**River Otter**

*Distribution.*—The river otter historically was found throughout all but extreme northern Alaska and Canada, southward throughout all but the most arid regions of the conterminous United States to Florida. The present distribution of the species throughout its original range has been much reduced (Toweill and Tabor, 1982).

The river otter’s historic range upon the Edwards Plateau, as mapped by Schmidly (1984b), included approximately the eastern half of the region. Schmidly, in delineating the range of the river otter in Texas, probably referred to a statement by Bailey (1905) that reports had been obtained of the species’ occurrence from Mobeetie, in Wheeler County of the Texas Panhandle, and along the Colorado River to the south. All recent reports of the river otter have come from counties east of the Edwards Plateau within Texas (Schmidly, 1984b). Bailey reported that the river otter was found on the Colorado River in the “region of Austin.” This is the only basis for inclusion of the species in the fauna of the Edwards Plateau (Fig. 104). No residents of the area that I have queried concerning the river otter have reported its occurrence in the region, and it may now be extirpated from this portion of its former range.

*Lutra canadensis* is a rather large mustelid; the shape of the body resembles a long cylinder that reaches its greatest diameter in the thoracic region. The head is broad and flattened, ears are small and rounded, and eyes are oriented toward the top of the head. The ears and nose are valvular and may be closed whenever the animal is underwater. The fur is sleek, short, and dense. The pelage ranges in color from a chocolate brown to pale chestnut dorsally and light brown to silver gray ventrally. The tail is long, thick at the base, ventrally flattened, and terminally pointed. All five toes of the appendages are completely webbed. The appendages are short and stocky.

River otters are inhabitants of riparian areas, and may have been found along major river drainages within the Edwards Plateau. They are also found in estuaries, lakes, and other aquatic habitats (Toweill and Tabor, 1982). The species is adapted to existence in freshwater habitats, and extensive arid areas may serve as barriers to the dispersal of this species. However, considering the drainage patterns of the Edwards Plateau, opportunity for recolonization and expansion within the area would seem to exist for the eastern populations of *L. canadensis*.

River otters are exclusively carnivorous in diet. Prey consumed includes crayfish, fish, amphibians, insects, birds, and mammals. Fish are the primary dietary staple, with other items being consumed in lesser proportions, dependant upon their availability within an area (Lowery, 1974; Toweill and Tabor, 1982; Jones et al., 1983). Rough fish are consumed in the greatest amounts, possibly because they are easier for the otter to capture. Young muskrats and beavers may be eaten in spring and early summer. The river otter is active throughout the year, and is generally crepuscular in activity period. However, otters may be observed actively foraging or playing at any time of day (Jones et al., 1983).

Otters do not construct new dens, but may enlarge the abandoned dens of other animals. Abandoned beaver and muskrat lodges also are utilized as dens. Hollow logs, log jams or drift piles, rock jumbles along a watercourse, and abandoned boat houses and duck blinds are known to be utilized as dens (Toweill and Tabor, 1982). Otters occasionally build a nestlike structure of aquatic vegetation.

River otters are solitary in habit, except during mating season (Davis and Schmidly, 1994). Groups of bachelor males occur (Lowery, 1974), but these may be younger animals excluded from breeding. *L. canadensis* may emigrate from an area if either a food shortage or unfavorable environmental conditions occur. Dispersal is usually along rivers and streams within an area, and otters may range from 35 to 45 miles per year (Jones et al., 1983). The river otter also disperses overland upon occasion.

River otters breed in March or April, with copulation usually taking place in the water (Toweill and Tabor, 1982). Females reach sexual maturity at two years of age. Delayed implantation is present, and the blastocysts may not implant in the uterus for eight months or longer (Davis and Schmidly, 1994). The total gestation period is approximately 12 months. Young may be born from late March through May. Litters range in size from one to five, with two or three being the most common number of young. The female keeps the
male away from the young for about six months, and then may allow the father to take an active role in care of the offspring (Jones et al., 1983).

The subspecies that may occur on the Edwards Plateau is *L. c. lataxina* F. Cuvier, 1823. Sexual dimorphism is present in the river otter, with females being smaller than males. Average external measurements of three males from Louisiana (Lowery, 1974) are: total length, 1129; tail length, 444; length hind foot, 129; ear length, 24. Selected mean cranial measurements of four males from the same source are: greatest length skull, 111.8; mastoid breadth, 68.6; zygomatic breadth, 72.3; postorbital breadth, 21.7; interorbital breadth, 25.1; length maxillary toothrow, 39.0.

*Specimens examined* (0).

*Additional records.*—Travis Co.: Colorado River near Austin. (Bailey, 1905).
KEY TO FELIDAE

1  Greatest length of skull averaging 121 mm; premolars 2/2; total length averaging 770 mm; tail length averaging 140 mm; dorsal and lateral pelage reddish-brown with numerous black streaks and spots. ............................................ *Lynx rufus*

1' Greatest length of skull much more than 121 mm; premolars 3/2; total length averaging much more than 770 mm; tail much longer than 140 mm; dorsal and lateral pelage a uniform tan color without black streaking and spotting ........................................... *Felis concolor*

**Family Felidae—Cats**

*Felis concolor*

Mountain Lion

*Distribution.*—The original range of the mountain lion was the most extensive of any terrestrial mammal in the Americas. This species ranged from Alaska, south through all of the southern Canadian provinces, throughout the conterminous United States, Mexico, Central America, and south to southern Chile and Argentina.

The mountain lion currently ranges throughout most of the western United States from Montana south to Texas. This species is found in British Columbia and Alberta in appreciable numbers. Scattered populations may still be found in many central, southeastern, and northeastern states of the conterminous United States and in Alaska.

The mountain lion has been recorded from scattered localities throughout much of the Edwards Plateau. Because of its secretive nature, the mountain lion is rarely seen and is difficult to census in any area. Records are available from Bexar, Crockett, Hays, Irion, Kerr, Kimble, Kinney, Upton, and Val Verde counties on the Edwards Plateau (Fig. 105).

*Felis concolor* is the largest cat residing on the Edwards Plateau. Because of its large size, lack of spotted pelage in adults, and long tail, the mountain lion can be mistaken for no other species of felid. The upper parts are tawny in color, whereas the venter, throat, chin, inside of the ears, and insides of the legs are whitish in color. The back of the ears, mustache around the muzzle, and tip of the tail are black in color. The claws of the four functional digits of each foot may be retracted, and the skull is shortened and round in shape. A prominent sagittal crest is present and the dental formula is i 3/3, c 1/1, p 3/3, m1/1.

The mountain lion is encountered most often in sparsely populated areas within its range on the Edwards Plateau. Factors limiting the distribution of *F. concolor* include human interference, lack of suitable prey, or lack of stalking cover (Currier, 1983). Brushy areas, and rocky, broken terrain provide suitable habitats for this cat on the Edwards Plateau. The mountain lion and white-tailed deer, historically, share the same basic habitat types (Dixon, 1982).

The mountain lion is carnivorous in diet. Known prey items include, deer, pronghorns, peccaries, porcupines, beavers, badgers, coyotes, bobcats, raccoons, foxes, rabbits, skunks, rock squirrels, cotton rats, ground squirrels, various birds, fish, insects, and all types of domestic livestock (Currier, 1983). Mountain lions obtain prey by stalking or ambush, and after making a kill, drag the prey to a secluded spot for feeding (Young and Goldman, 1946). *F. concolor* conceals the prey beneath leaves and other available material after feeding, and may return later for another meal. The mountain lion gorges when feeding, if suitable prey is killed, and may not feed again for a few days. This cat can survive for extended periods without water (Young and Goldman, 1946). The mountain lion is active during twilight or nocturnal hours, but sometimes forages during diurnal hours (Lowery, 1974).

Dens of *F. concolor* are found in rocky, rough areas, in crevices, underneath upturned trees, or other secluded areas. If the terrain is level, areas of thick brush or other vegetation are utilized as denning sites (Young and Goldman, 1946). No nest is constructed within the den for the young.
Mountain lions are solitary in social habits. Home range size varies depending upon season, but is usually large. Home ranges of males do not overlap, but female-female home ranges overlap, and female-male home ranges overlap. Winter to spring home ranges may be 145 square kilometers, and summer to fall home ranges may be 293 square kilometers or larger (Currier, 1983). The mountain lion may wander 25 miles or more per day in search of food (Lowery, 1974). *F. concolor* marks its territory by scrapes along the boundaries; urine and feces are deposited along boundaries, as well (Currier, 1983).

Mountain lions are polygamous. The same pairs may mate for consecutive years as a consequence of the stability of their home ranges (Currier, 1983). Females can come into estrous at any time of year. Gestation period ranges from 82 to 96 days. Most births are between April and September (Currier, 1983). The number of young per litter is usually three, but litters of six have been recorded (Lowery, 1974). Young females reach sexual maturity at two to three years of age (Currier, 1983).

The subspecies of mountain lion on the Edwards Plateau is *F. c. stanleyana* Goldman, 1938. Males are slightly larger than females (Lowery, 1974). Total length of the type specimen (Young and Goldman, 1946) of *F. c. stanleyana*, an adult male from Webb County, Texas, is 2134. Currier (1983) gives the range of total lengths for males and females, respectively, as: 2200 to 2300; 2000 to 2100. Selected cranial measurements of an adult male from Val Verde County are: greatest length skull, 207.00; zygomatic breadth, 141.00; length maxillary toothrow, 60.33; width across carnassials, 78.75; length auditory bullae, 34.42; width auditory bullae,


**Felis pardalis**

Ocelot

Distribution.—The historic range of this species extended throughout the eastern and western margins of Mexico, southward well into northern South America. The species ranged from southeastern Arizona through most of Texas, excluding parts of the Llano Estacado and far western Trans-Pecos, to western Louisiana, and western Arkansas.

The ocelot has been extirpated from the Edwards Plateau region. At the turn of the century, the species occurred as least on the southern Edwards Plateau and at the western boundary of the region around the Pecos River (Fig. 106). Records are available from Crockett, Edwards, Kerr, and Val Verde counties on the Edwards Plateau.

*Felis pardalis* is about the size of the bobcat (*Lynx rufus*), but differs from that species in having a longer tail, more streamlined profile, and no terminal tufts of hair on the ears. The ground color of the ocelot ranges from whitish or tawny yellow to reddish gray and gray. Dark streaks and spots are present in the pelage and are arranged in small groups and around areas that are darker than the ground color. The venter is usually white in color, with black spots present. There are two black stripes on each side of the face, and one or two transverse black bars on the insides of the legs. The tail is usually incompletely ringed with black stripes or marked with dark bars on the upper surface.

The ocelot originally occurred in brushy areas, and around rivers and streams within its range on the Edwards Plateau. Throughout its range, the ocelot occurs from tropical forests to fairly dry scrub country (Nowak, 1991:1202). Bailey (1905) indicated that the ocelot was usually found in rough, broken, and brushy habitats of the Edwards Plateau.

The ocelot, like all felids, is a carnivore. The diet consists of rabbits, rodents and other small mammals, birds, snakes, and fish. Nowak (1991:1202) also listed young deer and peccaries as prey items of the ocelot, both of which are, or once were, common on the Edwards Plateau. Bailey (1905) indicated that the ocelot also preys upon young pigs, kids, and lambs. The ocelot is said to hide parts of its kill underneath piles of leaves and dirt. *F. pardalis* climbs well and probably feeds upon bird eggs upon occasion. Dalquest (1953) stated that *F. pardalis* seems to be diurnal in its foraging and activity periods.

Little is known concerning the habits of this cat. In South America, females occupy exclusive home ranges of about two square km, whereas, males' home ranges were several times greater and overlapped the home ranges of several females. Males also maintain home ranges that are exclusive of one another (Nowak, 1991:1202). The ocelot is shy and retiring, and is usually solitary (Hoffmeister, 1986). Contact between two individuals is not infrequent and social ties are probably maintained in this fashion (Nowak, 1991:1202). These cats likely take shelter in rocky areas and in thickets of brush. The ocelot also may rest in trees upon occasion (Bailey, 1905).

Considering the nature of home ranges of *F. pardalis*, it would seem that males are probably polygynous in mating habits. In Mexico and Texas, births occur in fall and winter months. The gestation period is 70 days in the ocelot. Litter size ranges from one to four young, with the most common number being two (Davis and Schmidly, 1994).

The subspecies on the Edwards Plateau was probably *F. p. albescens* Pucheran, 1855. Males are slightly larger than females. Average external measurements for males and females (Davis and Schmidly, 1994) respectively are: total length, 1135, 930; tail length, 355, 285; length hind foot, 157, 135.
Figure 106. Distribution of *Felis pardalis* on the Edwards Plateau.

*Specimens examined (0).*

*Additional records.*—Crockett Co.: 14 240400E, 3394800N. Edwards Co.: 14 383400E, 3321000N. Kerr Co.: 14 486200E, 3324800N; 14 486000E, 3309500N. (Bailey, 1905; Davis, 1951).

*Panthera onca*

**Jaguar**

*Distribution.*—The historic range of the jaguar included portions of southern California, Arizona, New Mexico, and Texas within the conterminous United States, and the western, eastern, and southern regions of Mexico. The range of *P. onca* once extended southward into Argentina. The jaguar subsequently has been extirpated from its range within the United States and much of Mexico since the beginning of the twentieth century.

It has been speculated that the species once occurred over much of the southern Edwards Plateau (Jones, 1993). Although this large cat was said to be found from the Medina River to the Rio Grande within the region, by 1880, the jaguar was restricted to areas south and west of San Antonio (Doughty, 1983). Allen (1896), referring to the notes of Mr. H. P. Attwater, stated that the species no longer occurred in Bexar County by 1896, but was still taken occasionally in chaparral thickets bordering the Rio Grande. Bailey listed a single specimen from within the Edwards Plateau in Val Verde County (Fig. 107).

*Panthera onca* is the largest native cat of North America, and can be mistaken for no other species. Length of head and body in the jaguar ranges from 1120 to 1993. The jaguar is conspicuously spotted, with some spots forming rosettes along the lateral sides. The tail
Figure 107. Distribution of *Panthera onca* on the Edwards Plateau

is relatively short, spotted, and usually solid black at the end. Limbs are rather short and massive, and ears are small, rounded, and black with white or buff central spots on their posterior sides. Coloration varies from pale yellow to tan or reddish yellow. Color is uniform over the median dorsal area and pales laterally to buff or white on the cheeks, side of the neck, outer surfaces of the legs, and lower parts of the flanks. The venter, throat, and insides of the limbs are white. Spotting patterns are variable and often are not the same on opposite sides of the same animal.

Jaguars are tolerant of a variety of habitats and environmental conditions, but are found most commonly in areas with considerable plant cover, a water supply, and sufficient prey (Seymour, 1989). They are found in lowland semi-deciduous forests, open tree and shrub woodland, marshland, swampy savannah, thorn scrub, and desert areas. The specimen from the Edwards Plateau was from the mouth of the Pecos River, in what could best be termed a scrubby, brush habitat.

Jaguars are carnivorous in diet, but also ingest some grass and are said to be fond of avocados (Seymour, 1989). A great range of prey items are included in the diet of *P. onca*. Peccaries, armadillos, and turtles are preferred items. Opossums, otters, ocelots, skunks, porcupines, frogs, and catfish are consumed also in the diet. The jaguar with kill cattle, burros, horses, and deer (Hoffmeister, 1986). Jaguars are primarily nocturnal in foraging habit, but may be active at different periods throughout the day and night. Activity probably depends upon habitat and prey availability. In most instances, *P. onca* preys upon animals in proportion to their abundance within the habitat (Seymour, 1989). Prey is not hidden if unconsumed
after a kill. The jaguar usually procures prey by stalking or ambush. This large cat can climb and swim quite well (Seymour, 1989), which might aid in capturing some types of prey.

Jaguars are solitary for most of the year, except for family groups of a female and her young. Jaguars have established home ranges which may be designated by scraping, urination and other scent marking, deposition of feces, and raking on trees (Seymour, 1989). Home ranges are gained through a land tenure system, wherein the first occupant of an area establishes tenure until death or movement out of the area. Home ranges may vary in size from two square km to as much as 390 square km. Home ranges of males are larger than those of females, and the male’s home range overlaps those of all females within an area. Daily travels within the home range may vary from two km to greater than 18 km. If pursued, jaguars may travel more than 65 km in a single day (Seymour, 1989).

The breeding season extends from July to September in Mexico (Leopold, 1959). Gestation period varies from 91 to 111 days. Litter size is usually two young, but may range from one to four. Young are born in a sheltered place such as a cave, underneath an upturned tree, in a thicket, among rocks, or underneath a river bank (Seymour, 1989). More than one male may follow an estrous female, but fighting between males is rare. Females care for the young alone, and will not let a male jaguar approach them. The female consumes the feces of the young up to weaning. Cubs stay with their mother for 1.5 to 2 years. Sexual maturity is attained in two to three years in females and in three to four years in males.

The subspecies on the Edwards Plateau was *P. o. veraecrucis* (Nelson and Goldman, 1933). In the jaguar, males are larger than females. External measurement are from a male and female, respectively, from Tamaulipas, Mexico (Nelson and Goldman, 1933) are: total length, 1993, 1547; tail length, 533, 432. Selected cranial measurements for an adult male (Nelson and Goldman, 1933) from Vera Cruz, Mexico are: greatest lengthskull, 279; condalobasal length, 247.4; zygomatic breadth, 180; width rostrum, 72.3; interorbital constriction, 50; mastoid width, 111.7; length maxillary toothrow, 77.5.

Specimens examined (0).

Additional records.— Val Verde Co.: 14 270400E, 3287600N. (Bailey, 1905).

*Lynx rufus*

Bobcat

Distribution.— The bobcat ranges from southern Mexico northward throughout all but the midwestern region of the United States. The range of this species extends northward to include all of the southern Canadian provinces. The bobcat may once have ranged throughout all of the conterminous United States, but habitat losses in the midwestern United States since European settlement may have contributed to its extirpation in this area (McCord and Cardoza, 1982).

The bobcat ranges throughout the Edwards Plateau (Schmidly, 19846). This cat is difficult to collect or observe because of its secretive nature and nocturnal habits. Records exist from Blanco, Burnet, Callahan, Coke, Coleman, Comal, Crane, Crockett, Edwards, Gillespie, Glasscock, Hays, Howard, Irion, Kerr, Kimble, Llano, Mason, McCulloch, Medina, Nolan, Reagan, Runnels, San Saba, Sterling, Taylor, Tom Green, Travis, Uvalde, and Val Verde counties (Fig. 108).

*Lynx rufus* is a medium-sized felid with a short tail, spotted pelage, and pointed, tufted ears. The bobcat has rather long legs and large feet in relation to its overall size. Pelage color is yellowish brown, and variously streaked or spotted with black or dark brown. The venter is white with black spots, and there are several black bars along the insides of the forelegs.

The bobcat is adapted to a wide variety of habitat types throughout its range. The only habitat that is not utilized is agricultural land that is so extensive that all rocky ledges, swampy areas, and forest and wooded tracts are eliminated (McCord and Cardoza, 1982). Preferred habitats on the Edwards Plateau include riparian and wooded areas, rocky slopes and ledges, and pasture and field-edge areas. Rocky ledges and thickets of brush and other vegetation are important terrain features (McCord and Cardoza, 1982). Bobcats are tolerant of human disturbances, and may live near humans in both rural and urban areas (McCord and Cardoza, 1982). Local disturbances elicit only limited movements within a bobcat’s territory.
Bobcats are almost exclusively carnivorous in diet, but grass is sometimes eaten. Diet items include rabbits, squirrels, rats and mice, birds and bird eggs, snakes, skunks, small raccoons, insects, and carrion (Schmidly, 1984b). The bobcat most frequently kills prey the size of large rodents, rabbits, and opossums (McCord and Cardoza, 1982). However, *L. rufus* is rather opportunistic and will take almost anything available within its habitat. Bobcats may even kill deer if these cervids are plentiful in an area and alternative prey is scarce. Most deer are attacked while they are bedded down (McCord and Cardoza, 1982). *L. rufus* is a solitary hunter most of the time, but pairs have occasionally been observed in cooperative hunting efforts (McCord and Cardoza, 1982). Bobcats prefer broken rocky ledges and rock piles as denning sites. Other suitable den sites include brush piles, hollow trees, stumps, mott areas, and caves (McCord and Cardoza, 1982). In addition, I have observed bobcats denning in abandoned houses and barns. Dens, refuges, and resting sites are usually unimproved by the occupant.

The bobcat is rather solitary in nature, except during the mating season, when several males may follow an estrous female (McCord and Cardoza, 1982). Bobcats maintain territories based upon a land-tenure system with small or no overlap between individuals (McCord and Cardoza, 1982). Territories are marked with urine, anal gland secretions, and, sometimes, with feces. Marks are concentrated around dens, and the periphery of a territory may only be marked at a few
locations around its circumference. Trails that are often utilized by the territorial resident are more frequently marked (McCord and Cardoza, 1982). Bobcats may travel from two to five miles each night during foraging excursions, but the exact size of their home ranges depends upon season of the year and prey availability (Schmidly, 1984b).

Females are seasonally polyestrous and may come into heat several times if not successfully mated (Jones et al., 1983). A single litter is produced each year. Evidence is not conclusive concerning whether females are induced or spontaneous ovulators (McCord and Cardoza, 1982). Breeding peaks in February and March. The gestation period is about 10 weeks in duration (Jones et al., 1983). Young usually are born in the months of April and May, and litter size ranges from one to five (Schmidly, 1984b). Fecundity depends to some extent upon the available prey base in an area and, concomitantly, to the nutritional state of the females (McCord and Cardoza, 1982). Females usually breed for the first time between their first and second year of age. Males show little evidence of spermatogenesis until their second year of life.

Only a single subspecies of bobcat is found in Texas; L. r. texensis J. A. Allen, 1895. Males are larger than females in most measurements (Schmidly and Read, 1986). Average external measurements of males and females (Schmidly, 1984b), respectively, are: total length, 870, 770; tail length, 150, 140; length hind foot, 170, 160. Selected mean cranial measurements of seven males and 11 females, respectively, (Schmidly and Read, 1986) are: greatest length skull, 125.59, 121.40; zygomatic breadth, 92.31, 83.76; squamosal breadth, 54.63, 52.52; postorbital constriction, 35.48, 36.84; interorbital constriction, 23.43, 21.43; length of nasals, 26.36, 24.23; length maxillary tootthrow, 37.45, 36.50; mastoid breadth, 56.28; 52.21; length auditory bullae, 31.65, 28.92; width auditory bullae, 15.22, 14.90.

Specimens examined (84).—Burnet Co.: 14 573300E, 3382200N, 1 (SWTU). Coke Co.: 14 338600E, 3515000N, 1 (ASNHC); 14 330100E, 3510500N, 1 (ASNHC). Comal Co.: 14 563400E, 3305300N, 1 (SWTU). Crane Co.: Hooper Ranch (Unspecified Locality), 4 (ASNHC). Crockett Co.: 14 230600E, 3409600N, 2; 14 246300E, 3360200N, 1 (ASNHC). Glasscock Co.: 14 256200E, 3535800N, 1 (ASNHC); 14 251600E, 3528200N, 1 (ASNHC); Arlis Ratcliff Ranch W Glasscock, 2 (ASNHC); O'Bannon Ranch, 1 (ASNHC). Howard Co.: 14 267800E, 3572200N, 1. Irion Co.: 14 305900E, 3477300N, 1 (ASNHC); 14 331800E, 3480000N, 3 (ASNHC); 14 327200E, 3481700N, 1 (ASNHC); Hemphill Ranch, 7 (ASNHC). Kimble Co.: 14 436200E, 3372800N, 1 (MWSU); 14 444200E, 3372800N, 1 (MWSU). Reagan Co.: 14 297200E, 3486400N, 1 (ASNHC); 14 266100E, 3480800N, 2; 14 277200E, 3469500N, 1 (ASNHC); 14 269200E, 3456600N, 1 (ASNHC); 14 238400E, 3452700N, 1 (ASNHC); 14 256400E, 3456700N, 1 (ASNHC); 14 280500E, 3476200N, 2 (ASNHC); Rocker B-upper Centralia, head-of-river pasture, 30 (ASNHC). Runnels Co.: Murfield Ranch (Unspecified Locality), 1 (ASNHC); Spreen Ranch, 1 (ASNHC). Sterling Co.: Unspecified Locality, 5 (ASNHC); Foster Ranch, 4 (ASNHC). Taylor Co.: 14 417200E, 3581800N, 1 (ASNHC). Val Verde Co.: 14 309200E, 3345400N, 1 (MWSU); 14 257400E, 3341600N, 1.

GOETZE—MAMMALS OF THE EDWARDS PLATEAU

ORDER ARTIODACTYLA—EVEN-TOED UNGULATES

KEY TO ARTIODACTYLS

1 Upper incisors present; cheekteeth bunodont; canines well developed; sagittal crest present; body not especially modified for cursorial locomotion; pig-like snout ................................................................. *Tayassu tajacu*

1' Upper incisors absent; cheekteeth selenodont; canines absent; sagittal crest absent; body modified for cursorial locomotion; snout not pig-like .................................................. 2

2 Horns nondeciduous; no rostral fenestration on skull; total length 1980 mm or greater; tail short and with a terminal brush of hair (ox-like); forequarters much more massive in appearance than hindquarters ................................................................. *Bos bison*

2' Horns deciduous (at least in part); rostral fenestration present on skull; total length less than 1980 mm; tail well haired along entire length with no terminal brush; forequarters not especially massive; head held higher than shoulder level .................................................................................................................................. 3

3 Frontal appendages (horns) composed of fused hairs; horns arise from skull above the posterior plane of the orbits; horns present on both sexes; horns of males usually only with one main beam and a single, anteriorly directed tine; only horn sheath shed annually; rostral fenestration long and narrow; tail relatively small and narrow; two prominent white patches present on the ventral side of the neck; black mane present on the dorsal side of the neck ................................................................. *Antilocapra americana*

3' Frontal appendages (antlers) composed of bone; antlers arise from skull well posterior to the orbits; antlers usually present only on males; Antlers (at least of older males) usually with a single main beam and multiple, vertically directed tines; entire antler shed annually; rostral fenestration nearly as broad as long; tail extending to the bottom of the rump and broad at the base; one white patch present on ventral side of the neck; no mane present ................................................................................................................... *Odocoileus virginianus*

Family Dicotylidae—Peccaries

*Tayassu tajacu*
Collared Peccary

*Distribution.*—The collared peccary ranges from southwestern New Mexico, and much of southern Arizona throughout the eastern and western regions of Mexico and southward into South America. The collared peccary originally ranged throughout most of Trans-Pecos and south-central Texas to the Red River of Oklahoma in the north, and the Llano Estacado to the northwest.

The collared peccary once ranged at least as far east as Kerr County (Allen, 1986) on the Edwards Plateau, but settlement of the area and habitat alterations have pushed the range of this species somewhat farther west within the region. The species now occurs in scattered herds on approximately the western half of the Edwards Plateau. Specimens are available from Coke, Crockett, Edwards, Irion, Reagan, Sutton, Tom Green, Upton, and Val Verde counties within the region (Fig. 109).

*Tayassu tajacu* is a rather small, pig-like ungulate. The collared peccary differs from *Sus scrofa* (feral pig) in characters such as only three toes on the hind feet, only two upper incisors and six upper molariform teeth, as opposed to four hind toes, three upper incisors, and seven upper molariform teeth in *S. scrofa*. The canine teeth of *T. tajacu* project vertically as opposed to laterally in *S. scrofa*. Pelage is coarse, and rather long in *T. tajacu* and is black in color, with interspersed white hairs. A collar of white or yellowish pelage extends...
from over the shoulders to the throat. A distinct mane of longer hairs is present over the top of the head and extends to the rump. The tail is short and stubby and the nose is pig-like. Ears are prominent and rather rounded at the tips.

Collared peccaries inhabit desert shrub, and brushy areas throughout their range in the United States. Areas with dense brush cover are preferred on the Edwards Plateau. In western Texas, peccaries frequently are encountered in dry washes and along dry stream beds. Dense thickets of brush and rocky areas are utilized for escape cover and resting areas during periods of inactivity.

The collared peccary is primarily herbivorous. Insects and other animal matter are consumed in only minor percentages. Pecaries are browsers and consume forbs, cacti, fruits, and browse plants for the major percentages of the diet (Corn and Warren, 1985). Prickly pear makes up the largest part of the diet during most seasons of the year. This may relate to the necessity of *T. tajacu* to obtain a major part of its daily water requirement from succulent vegetation within an area, if free water is not available (Corn and Warren, 1985). Plants associated with collared peccary habitats and diet include mesquite, catclaw, ocotillo, scrub oak, juniper, hackberry, and various grasses and forbs. Collared peccaries forage and are active mostly during early evening and nocturnal hours.

Collared peccaries are herd animals and have rather specific home ranges within an area. Number and size of herds depends to some extent upon forage conditions, predation risks, and seasonality (Robinson and Eisenberg, 1985). Occasionally, different herds will

Figure 109. Distribution of *Tayassu tajacu* on the Edwards Plateau.
aggregate around a locally abundant food resource such as mesquite groves or large clumps of cacti (Robinson and Eisenberg, 1985; Hoffmeister, 1986). Territories of herds usually cover a little over one square mile, but may vary according to local conditions (Oldenburg et al., 1985) and, aside from occasional feeding aggregations, different herds are temporally separated in an area even if their territories overlap. The herds are close knit, but some males may leave the herd and either join another group or may begin herds of their own within an area (Hoffmeister, 1986). Fighting among members of herds is infrequent and of short duration, so some form of social hierarchy may be established within the herd.

The collared peccary is a promiscuous breeder, and may mate throughout the year (Schmidly, 1977). The gestation period is approximately 142 to 148 days in length. Litter sizes range from one to five young, however, two offspring is the usual number. Young are weaned when about 45 days of age and stay close to their mother for up to three months. Males take no part in care of the offspring.

The subspecies of collared peccary on the Edwards Plateau is *T. t. angulatus* (Cope, 1889). Sexual dimorphism is not apparent in this species. External measurements of an adult female from Val Verde County are: total length, 830; hind foot, 80; ear length, 90. Selected cranial measurements for this same individual are: greatest length skull, 224; zygomatic breadth, 100.10; length molariform teeth, 58.66; length maxillary toothrow, 83.88; length auditory bullae, 21.13; width auditory bullae, 19.46.


*Family Cervidae—Cervids*  
*Odocoileus virginianus*  
*White-tailed Deer*

**Distribution.**—The white-tailed deer ranges from northern South America, northward throughout Central America, Mexico, and into the conterminous United States. The range of the white-tailed deer includes all or most of 45 states within the United States. The white-tailed deer is absent in Utah, and rare in Nevada and California. This deer ranges northward into all of the southern provinces of Canada.

The white-tailed deer has a ubiquitous distribution in Texas (Hesselton and Hesselton, 1982; Schmidly, 1983). This species may be expected to occur in all counties of the Edwards Plateau. Records are available from Bexar, Blanco, Callahan, Coke, Coleman, Comal, Concho, Crockett, Edwards, Gillespie, Glasscock, Hays, Kerr, Kimble, Llano, Mason, Medina, Nolan, Reagan, Real, San Saba, Schleicher, Sterling, Tom Green, Travis, and Val Verde counties (Fig. 110).

*Odocoileus virginianus* occasionally may be confused with introduced species of deer on the Edwards Plateau. Characters to aid in identifying the exotic deer species are given in the section concerning introduced species on the Edwards Plateau. White-tailed deer in adult pelage are grayish-brown to reddish-brown dorsally, with white pelage on the ventral side, inside the legs, underneath the tail, on the neck, and on the rump. The tail is broad, relatively long (compared to a mule deer), and fringed with white laterally. A white ring is found around the eyes, and a white bar is present across the rostrum; a white patch is located on the throat of *O. virginianus*. Each side of the chin has a black labial spot. The antlers of males arise from a single, main beam and antler tines are not dichotomous or otherwise branched.

White-tailed deer occur in varied habitats including riparian areas, wooded uplands, rocky, wooded slopes, and in edge habitats and around cultivated field edges. *O. virginianus* is a common visitor even of towns and has frequently been observed within the city limits.
of many communities on the Edwards Plateau. White-tailed deer have benefited from human activities since historic times in the United States (Smith, 1991). Forestry activities, logging, clearing areas for cropping practices, grazing of domestic livestock, burning, irrigation in xeric western areas, planting of shelter belts and other alterations of climax communities have actually resulted in an expansion of the range of *Odocoileus virginianus* and an increase in population densities in many areas (Hesselton and Hesselton, 1982; Bryant, 1991; Smith, 1991).

White-tailed deer are herbivorous in diet and are both browsers and grazers. Food items vary according to habitat, and deer are selective foragers whenever the food supply is abundant (Hesselton and Hesselton, 1982). Diets are seasonally variable (Wade et al., 1984; Boyd and Cooperrider, 1986). Greater amounts of succulent vegetation are consumed during the spring and early summer months. During the autumn months, deer consume more soft and hard mast in their diets (Smith, 1991). Winter diets are determined largely by resource availability. Acorns are consumed in large amounts in the autumn months. Woody browse, dried leaves of deciduous trees, sedges, grasses, and mushrooms are included in winter diets (Smith, 1991). Cultivated cereal grains, hay crops, and orchard fruits are consumed (Jones et al., 1983), and white-tailed deer may cause considerable damage to crops if a large deer population is present in the affected area. White-tailed deer are most active during early morning and late afternoon to early evening hours. *O. virginianus* also sometimes feeds during the night and in the middle of the day (Jones et al., 1983).
Deer usually bed down in dense thickets of brush, juniper and other vegetation within their home ranges during the daylight hours (Bryant, 1991; Davis and Schmidly, 1994). A diverse vegetation structure is essential for excellent white-tailed deer habitat. Vegetation is utilized for hiding, escape, and thermal cover, as well as for food (Boyd and Cooperrider, 1986).

White-tailed deer in Texas are decidedly sedentary, and occupy well-established home ranges (Schmidly, 1983). Home range size may range from 24 to 138 ha for females and 105 to 256 ha for males (Inglis et al., 1979). White-tailed deer seldom move more than 3.5 km from trapping and marking sites during their lifetime (Inglis et al., 1979). Habitat characteristics determine the sizes and shapes of home ranges. Subdominant and dominant floater males are exceptions with regard to home range. These types of males have no well established home ranges, but instead, have relatively fixed action areas of travel (Inglis et al., 1979).

Females are polyestrous, but come into heat only during a narrow range of months (Lowery, 1974). Females remain in estrous for about 24 hours, and if not bred, come into heat again in about 28 days. Males are polygamous in mating habit. The gestation period ranges from 187 to 222 days (Smith, 1991). The major breeding season occurs in the months of October through January. The number of young varies from one to three, with twins being common in middle-aged does under favorable environmental and nutritional conditions (Smith, 1991). Does leave their fawns at specific locations within the home range after their birth and until the fawn is approximately three to four weeks old. At this age, the fawns begin to accompany their mothers on foraging excursions (Smith, 1991). The doe and her offspring may rejoin a maternal group when the fawns are approximately two months old.

Carr and Hughes (1993) used mtDNA techniques to study white-tailed and mule deer populations on the Stockton Plateau and Trans-Pecos of Texas and found some genetic introgression from mule deer into white-tailed deer in an area of sympathy. Individuals of intermediate morphotype should be sought in the future, both from this area and others in the state of Texas.

The subspecies of white-tailed deer on the Edwards Plateau is probably O. v. texana (Mearns, 1898). Hunting pressures and other factors have resulted in the reintroduction of white-tailed deer from areas outside of the Edwards Plateau, and more than one subspecies may now reside on the Edwards Plateau. Adult male O. v. texana are larger than adult females (Smith, 1991). The range in external measurements (Schmidly, 1983) is: total length, 1370-1980; tail length, 152-292; length hind foot, 457-520; ear length, 139-228.


Additional records.—Bexar Co.: Unspecified Locality. Blanco Co.: 14 566800E, 3351300N; Carl Smith Ranch (TCWC); 14 556900E, 3349500N.
Family Antilocapridae—Pronghorn
Antilocapra americana

Pronghorn

Distribution.—The pronghorn originally ranged from Durango, Mexico, northward throughout western Texas, and all of the central Great Plains states. The species ranged northward as far as Alberta, Saskatchewan, and Manitoba, Canada, and eastward to the western border of Minnesota. The species occurred as far west in the United States as the Pacific Coast states, Nevada, and in scattered places in the Rocky Mountain region.

The pronghorn once was common on the Llano Estacado, Trans-Pecos, and at least the western portions of the Edwards Plateau. Literature records are known for specimens from at least as far east on the Edwards Plateau as Irion County (Fig. 111), but numbers were greatly reduced by the early twentieth century. The species now is probably most common in the extreme northwestern Edwards Plateau adjacent to the border of the Kansan Biotic Province.

Antilocapra americana is one of the smallest native ungulates in North America, and is distinctive in appearance. Horns may be present on both sexes; the horns of males have anterior points and terminal hooks. The horns are laterally compressed at the bases, but circular in shape at the hooks above. Horns are supraorbital in position. The torso is rather barrel-shaped and the legs are long and slender. Dew claws are absent on the feet of A. americana. Interdigital glands are present on the feet and produce sebum to condition the hooves. Two large, white rump patches are present, and the tail is short. The belly, inside of the legs, and patches on the face and neck are white. Ears are large and terminally pointed. Hooves are cloven and are black in color. Most of the dorsum is tan to brown in color, joining with white patches on the sides. The nose pad is black, as are the tongue, eyes, eyelashes, and patches below the ears. A black mane is present from between the ears and extending down to the base of the neck.

The pronghorn is well adapted to existence upon the open plains environments of the central and western United States. Kitchen and O’Gara (1982) stated that the species is found in 26 different prairie and shrubland habitats within its range. Some important habitat features include a low, rolling topography, a mixture of forage types within the habitat, at least 50 percent ground cover of plants, and a relatively unobstructed view of the terrain. Pronghorns occur in desert habitats away from a ready source of water in parts of the southwest. Water is not essential to survival as long as sufficient succulent forage is available (O’Gara, 1978).

Pronghorns are herbivores and utilize a large percentage of browse in their diets. The diet includes various forbs, grasses, shrubs, domestic crops, cacti, and other plant items (Kitchen and O’Gara, 1982). Forbs are eaten in all seasons except fall, and grasses only make up a significant portion of the diet in the spring months. Forbs are not consumed in the fall months because of a lower nutritive value during this season. Pronghorns do not compete directly with cattle because of the heavy reliance upon browse by A. americana. Pronghorns eat some types of plants, such as sagebrush, that are quite unpalatable to domestic cattle. More direct competition occurs between pronghorn antelope and domestic goats and sheep (O’Gara, 1978). Pronghorns are primarily diurnal. Most foraging is conducted during early morning and late evening hours, with the middle portion of the day given to resting and rumination (Kitchen and O’Gara, 1982).

Pronghorns are social animals and form herds. Herd size depends upon habitat quality, density of animals, season of the year, and other factors. Females and young form herds that may also include young males. Older males appear to be territorial in nature.
within an area and often are solitary. Females are free to move between the territories of dominant males; a harem system is usually not maintained. Dominance hierarchies are established among old males and also within the mother and young herd groups. Females are usually subordinate to males (Kitchen and O'Gara, 1982). Young males may form small bachelor herds of their own and remain in the vicinity of the matriarchal herds. Level and extent of aggressive behavior that males utilize in defending their territories depends upon seasonality, age, and sex of intruders. Except during years of low vegetation productivity, seasonal movements were probably not common in the southwestern portion of the pronghorn’s range and upon the Edwards Plateau. These movements to differing forage areas are more common in the northern portion of the species’ range.

Herding behavior apparently aids in escape from predators. When danger is discovered, the entire herd runs from the area in an elliptically shaped formation (Kitchen and O’Gara, 1982). This may help to confuse predators and reduce losses to the herd. Adult females and young males and females also practice predator harassment, driving coyotes and other predators away from the herd (Lipetz and Bekoff, 1980).

Pronghorns are polygamous in mating habit. Females become sexually mature at about 16 months of age, but sometimes breed as early as five months of age (O’Gara, 1978). Gestation period averages 252 days, and two young is the usual number of offspring per litter. The female usually separates herself from the herd and finds a suitable birthing location when parturition is near. Young are born while the female stands upon
her feet, and the young simply fall to the ground (Jones et al., 1983). Females remain separated until the young are able to run with the herd without undue tiring. The female and her offspring then rejoin the matriarchal herd.

Pronghorns have been widely reintroduced over portions of their former ranges, with restocked animals coming from varied locations, and, hence, subspecies. The original subspecies on the Edwards Plateau was *A. a. mexicana* Merriam, 1901. Sexual dimorphism is not pronounced in this species. Average external measurements of a buck and doe from Trans-Pecos, Texas (Schmidly, 1977), are: total length, 1325; tail length, 62; length hind foot, 388; ear length, 149.

Specimens examined (1).—Reagan Co.: 14 272700E, 3468500N, 1 (ASNHC).

Additional records.—Crockett Co.: 14 241400E, 3392600N. Irion Co.: 14 326700E, 3459700N. Menard Co.: 14 394200E, 3410800N. Sterling Co.: 14 314100E, 3504800N. Sutton Co.: 14 351800E, 3552900N. Val Verde Co.: 14 289500E, 3288600N. (Bailey, 1905; Murray, 1932; Boyd, 1994).

Family Bovidae—Bovids

*Bos bison*

*Bison*

Distribution.—The historic range of the bison was centered on the Great Plains of North America, and extended northward into Alberta, Saskatchewan, and Manitoba, Canada. The bison ranged as far south as north-central Mexico, and eastward to New York and Georgia. Westward distribution was determined to some extent by the Rocky Mountains and by desert areas. Elevation appears to have had small effect, overall, on the distribution of bison.

The bison occurred throughout most of Texas, except the immediate gulf-coastal area, and all of the Edwards Plateau region. The species was subsequently eliminated as a free-ranging species by the close of the nineteenth century, but still persists within the region on privately owned lands. Based upon a census of exotic ungulates in Texas (Traweek, 1989) bison may be found in Bandera, Blanco, Burnet, Callahan, Coke, Coleman, Comal, Gillespie, Kendall, Kerr, Kinney, Medina, Real, Sutton, Taylor, Uvalde, and Val Verde counties (Not Mapped). Also, I observed a small herd of the animals on private lands in Hays County in 1993.

*Bison bison* is the largest native ungulate to occur on the Edwards Plateau and is distinctive in appearance. The head is massive and heavy with a short, broad nasal area. Horns are present on both sexes and rise laterally from the head and curve inward over the head. Overall, the color is dark brown to black. Pelage is darker and longer over the head, shoulders, and front appendages. A distinctive hump is present over the front shoulders and the hindquarters are lighter in color and smaller in appearance giving the bison a sloping profile. The legs are relatively short and the hooves are rounded and black in color. The nose pad, lips, and tongue are black in color. The tail is rather short and has a tufted tip. A dark band of hair often is present over the mid-dorsum giving the appearance of a mane, although the hairs in this region are scarcely longer then in surrounding areas.

The bison is a grazing animal, and was found in greatest numbers in the plains regions and open, edge habitats throughout its original range. However, valley areas in mountainous regions also provided suitable habitat for the bison, and any area with sufficient palatable forage and water was potential habitat for this species within its original range (Meagher, 1986). The bison can withstand extremes of both hot and cold temperatures, and thus is not limited in habitat selection by this environmental factor. Bison are primarily diurnal in foraging and activity period.

The bison is herbivorous in diet, and consumes mostly grasses and sedges. Percentage of grasses, sedges, and forbs in the diet may be a consequence of availability at a particular site. Bison generally are less selective in forage selection when compared to other ungulates under similar environmental conditions (Reynolds, Glaholt, and Hawley, 1982). Bison consume almost two percent of the body weight per day in dry-matter forage (Meagher, 1986). When stocked upon ranges with other species, the diet of B. bison and domestic cattle is most similar. Under low to moderate stocking rates, however, competition is insignificant. White-tailed deer, pronghorn, sheep, and goats do not compete significantly for forage with *B. bison*; probably because the aforementioned species consume greater percentages of forbs than does *B. bison* under
ordinary conditions (Reynolds, Gla holt, and Hawley, 1982). Bison have a higher digestibility rate of most forages than domestic cattle.

The bison is a gregarious herd animal, forming herds according to sex, age, season, foraging conditions, and habitat (Meagher, 1986). Herds usually consist of female and young groups, along with some younger bulls. Except during the rutting season, the older bulls tend to form small herds of their own away from the mother-young groups.

Dominance relationships determine the position of individual bison within a herd. The expression of intraspecific dominance appears in calves after the first few weeks of age (Reynolds, Gla holt, and Hawley, 1982). Dominance hierarchies are established both among and between bulls, calves, and cows of a herd. Calves are subordinate to cows, and cows usually are subordinate to bulls. Bulls may actively dispute postions within the hierarchy at any time, but aggressive contests are more common during periods of rut (Reynolds, Gla holt, and Hawley, 1982). Cows have been observed defending calves of a herd from predators, but bulls have not been noted to protect calves (Meagher, 1986).

Bulls usually do not mate with cows until about six years of age (Meagher, 1986). Breeding season may extend from June through September, depending upon location, but conception may occur at anytime of the year. Females are best described as seasonally poly­estrous. Gestation period has been estimated at 285 days (Meagher, 1986). Calving usually occurs from April to June. Bison demonstrate birth synchrony, possi­bly due more to climatic factors than to predation ef­fects (Rutberg, 1984). One calf usually is born per year, and rarely, twins. Calves are precocial at birth and usually begin nursing within 30 minutes of birth (Meagher, 1986).

I follow Jones and Jones (1992) in the use of the generic name *Bos* on the basis of priority. The subspecies on the Edwards Plateau is *B. b. bison* (Linnaeus, 1758). Sexual dimorphism is evident, with males being larger than females. Ranges of external measurements for males and females respectively (Meagher, 1986) are: total length, 3040 to 3800, 2130 to 3180; tail length, 330 to 910, 300 to 510; length hind foot, 580 to 680, 500 to 530.
INTRODUCED SPECIES

The following accounts describe species of mammals that have been introduced by humans on the Edwards Plateau. Information on distribution within the region, descriptions of the exotic species, and relevant natural history information is included in each account, as appropriate. Data on distribution was obtained from mammal collections, local residents, literature sources, and a survey of exotic big game of Texas by M. S. Traweek (1989).

Family Muridae—Mice and Rats

*Rattus norvegicus*

Norway Rat

**Distribution.**—The Norway rat occurs throughout the Edwards Plateau region, especially in urban areas, and in close association with man in rural settings. This rat may be limited in distribution in more xeric areas of the region by lack of food and water sources. I have examined no specimens of the Norway rat from the region, although local residents and pest exterminators state that the species is almost as common as the roof rat in urban areas. The lack of representation in collections is probably due to researchers' bias against preparing this species for museum collections. Bailey (1905) was of the opinion that the Norway rat was commensal with man in most cities and towns in Texas.

*Rattus norvegicus* differs from similar-sized native rats, such as woodrats and cotton rats, in having a nearly naked, distinctly annulated tail, and three transverse rows of cusps on the molar teeth. The Norway rat differs from the similar-appearing roof rat (*R. rattus*) in having parallel temporal ridges, tail shorter than the head and body length, greatest distance between temporal ridges usually less than 13 mm, and first upper molar often without a distinct notch on anterior cusp row. The roof rat has temporal ridges bowed-outwards on the parietals, tail longer than the head and body, greatest distance between temporal ridges usually 13 mm or more, and first upper molar with distinct notch on anterior cusp row. Dorsal color is uniformly grayish brown or blackish brown. The venter is gray to yellowish-white in color. Ears of *R. norvegicus* are small and covered with short hairs.

The Norway rat inhabits dwellings, warehouses, barns, grain-storage facilities, garbage dumps, and other areas in association with the activities of humans. The Norway rat is often found in sewers, but may inhabit cultivated fields and meadows during the summer months (Sealander and Heidt, 1990). *R. norvegicus* is omnivorous in diet. Vegetation makes up a major portion of the diet, but the Norway rat shows a strong preference for animal matter, if available (Jackson, 1982); young poultry and eggs are eaten. Garbage and cereal grains are readily consumed, and the Norway rat will occasionally bite sleeping humans (Sealander and Heidt, 1990).

*Rattus rattus*

Roof Rat

**Distribution.**—The range of this species, as mapped by Schmidly (1983), includes the entire Edwards Plateau region. Records exist from Bexar, Hays, Kerr, McCulloch, and Travis counties within the region.

*Rattus rattus* has been compared to *R. norvegicus* in the previous account. The ears of *R. rattus* are large, nearly naked, and may be extended over the eyes; as opposed to the shorter, haired ears of *R. norvegicus*. The eyes of the roof rat are rather large and prominent compared to the small eyes of *R. norvegicus*. The dorsal fur is grayish brown to black, and the venter is yellowish white to white in color.

The roof rat is a commensal species and is similar in habitat preference to the Norway rat. However, where both species of *Rattus* are present at a single locality, the Norway rat is dominant. Roof rats are either driven from the area, or are spatially and temporally separated within the habitat. If both species occur in a residence, the roof rat is more prone to inhabit attics and upper areas. The Norway rat will reside in lower levels, basements, and sewer systems (Lowery, 1974; Sealander and Heidt, 1990). Roof rats are also found associated with lush vegetation around highway rights-of-way and urban housing areas (Jackson, 1982). The roof rat is omnivorous. Diet items include various fruits, nuts, cereal grains, and vegetables. Animal material is also consumed, if available.
**Goetze—Mammals of the Edwards Plateau**

**Mus musculus**

House Mouse

*Distribution.*—The house mouse has a ubiquitous distribution on the Edwards Plateau, usually associated with human activities. Specimens exist from Blanco, Coke, Comal, Runnels, and Tom Green counties in the region.

*Mus musculus* has a tail that is longer than its body. The tail is sparsely haired and conspicuously annulated. The pelage of *M. musculus* varies from gray to brown in color dorsally and is grayish ventrally. The ears are rather large and almost naked of hair. *M. musculus* has a conspicuous notch behind the anterior, distal end of the upper incisors and lacks the anterior, longitudinal grooves found in the upper incisors of *Reithrodontomys*. Cheek teeth of *M. musculus* have the cusps arranged in transverse rows as opposed to the alternating cusp patterns of *Reithrodontomys* and *Peromyscus*.

The house mouse is common in and around human habitations throughout the Edwards Plateau. Feral populations also exist in weedy, overgrown areas, such as railroad rights-of-way and oldfields. Populations of the house mouse fluctuate through the seasons, and high numbers of *M. musculus* can occur in an area (Lowery, 1974).

**Family Myocastoridae—Myocastorids**

**Myocastor coypus**

Nutria

*Distribution.*—The nutria ranges over the eastern half of the Edwards Plateau, at least as far west as Kimble and Mason counties, and is expanding its range farther west and along the Pecos River system in Val Verde County (Hollander et al., 1992).

*Myocastor coypus* is a large rodent, with yellowish-brown pelage and white coloration around the nostrils, mouth, and chin. The hind feet have webbing between the toes and the tail is long, scaly, and rounded. The ears are short and rounded, and are almost hidden in the fur. The mammae of female nutria are located high on the lateral sides of the animal, as opposed to those of native North American rodents. The only mammal on the Edwards Plateau that the nutria may be confused with is the beaver. Beavers are larger than nutria, and have conspicuous, dorso-ventrally flattened, and paddle-like tails.

Nutria are found in rivers, lakes, ponds, and streams on the Edwards Plateau. *M. coypus* is adept at moving about on land, but spends most of its time in water, even feeding while floating in water (Lowery, 1974). Nutria often disperse overland through areas, and I have observed a specimen struck by an automobile south of Eden, Texas, in Concho County; no streams or ponds were evident in the immediate vicinity. *M. coypus* is a vegetarian and feeds upon a variety of emergent vegetation, and sometimes, upon agricultural crops, such as sugar cane and rice (Swank and Petrides, 1954; Lowery, 1974). Dens are constructed in mud banks along watercourses and ponds (Schmidly, 1984b), and this burrowing activity may cause damage to manmade water impoundments.

**Family Canidae—Canids**

**Canis familiaris**

Feral Dog

*Distribution.*—The feral dog occurs throughout the Edwards Plateau. *C. familiaris* often is closely associated with urban areas, farms, and other human habitations.

*Canis familiaris*, because of selective breeding by humans through the centuries, has so many different morphotypes as to defy generalized description. The only other canid presently occurring on the Edwards Plateau that *C. familiaris* may be mistaken for is the coyote. Howard (1949) found the muzzles of coyotes are longer and narrower than those of domestic dogs of similar size. Ratio of palatal width to length of upper molariform toothrow helps to separate *C. latrans* from feral dogs. If the toothrow is 3.1 times the palatal width, the specimen of concern is a coyote (Howard, 1949). The skull profile is relatively flat in the coyote, whereas the skull is often domed in *C. familiaris*. Coyotes generally have moderately long, bushy tails, thick, fur, and upright, pointed ears. Feral dogs are more variable in external appearance.

Feral dogs inhabit all ecological areas on the Edwards Plateau, ranging from woodlands, slope habitats, valley habitats, agricultural areas, and riparian areas. Feral dogs are omnivorous and consume varied fruits and vegetables, rodents and other small mammals,
birds, various insects, and carrion. These dogs may cause economic losses when they become associated into packs. *C. familiaris*, when in packs and sometimes when solitary, is known to prey upon calves, sheep, goats, and deer.

**Family Felidae--- Cats**  
*Felis catus*  
Feral Cat

*Distribution.*—Feral cats are found throughout the Edwards Plateau, often associated with urban areas and other centers of human activity. I have seen these cats in Kimble, Mason, Crockett, and Val Verde counties.

Feral cats may be readily identified by their small size, long tails, and variable coloration. The skull of *F. catus* differs from the bobcat in possessing an extra premolar on each side of the upper jaw.

Feral cats occur in habitats ranging from upland woods, meadows, riparian areas, and rocky habitats. These cats are carnivorous and are great decimators of wildlife (Schmidly, 1983). Songbirds, upland game birds such as quail, rodents, cottontail rabbits, eggs, snakes, insects, and other animals are included in the diet of feral cats. *F. catus* is primarily solitary in the wild.

**Family Suidae--- Pigs**  
*Sus scrofa*  
Feral Pig

*Distribution.*—Feral pigs occur in wooded and brushy areas throughout the southern and eastern portions of the Edwards Plateau, as far north as Coleman, Runnels, and Sterling counties, and westward to the Pecos River in Val Verde and Crockett counties (Mayer and Brisbin, 1991).

*S. scrofa* may be distinguished from collared peccaries by numerous characteristics. Feral pigs are larger in size, as adults, have conspicuous tails (which collared peccaries lack), usually are more sparsely haired, and lack a white collar around the shoulders that peccaries possess. Feral pigs also have four toes on the hind legs, whereas peccaries have only three. *S. scrofa* has three pairs of mammae; peccaries have two pairs of mammae. The snout is pig-like and terminates with a rounded, cartilaginous pad in both *S. scrofa* and the collared peccary. The ears are usually rather large, erect, and pointed in feral pigs.

Feral pigs occupy white-tailed deer habitats in Texas (Mayer and Brisbin, 1991). Most common habitats on the Edwards Plateau would be upland wooded areas, riparian and streamside areas, and the margins of agricultural lands. Feral pigs are occasionally struck by automobiles, and I have seen one individual dead on a roadway northwest of Kerrville, Texas, in Kerr County. The surrounding habitat was brushy pasturelands and smilax vines forming dense thickets. *S. scrofa* is omnivorous and consumes fungi, tubers, green vegetables, grains, nuts, fruits, cultivated crops, invertebrates, small vertebrates, and carrion (Nowak, 1991). Feral pigs are considered pests in some areas in Texas because they prey upon range calves and goats. Most foraging is conducted during crepuscular and nocturnal hours (Nowak, 1991).

**Family Cervidae--- Cervids**  
*Cervus axis*  
Axis Deer

*Distribution.*—Axis deer are relatively common in eastern and southcentral portions of the Edwards Plateau, including Bandera, Bexar, Comal, Concho, Gillespie, Kendall, Kerr, Kimble, Kinney, and Real counties (Traweek, 1989). Upland woods are the most favored habitats for this species in the area.

*Cervus axis* varies in color from rufous fawn to yellowish-brown, to brown. A dark dorsal stripe is present in axis deer, and adults are spotted with white on the sides. No mane is present in this species of deer. The underparts and underside of the tail are white. Antlers of *C. axis* are three-tined, with the brow tine nearly forming a right angle with the beam.

Axis deer inhabit grasslands and open woodlands (Nowak, 1991). Within Texas, meadows and glades are inhabited, and rough, broken terrain is generally avoided (Davis and Schmidly, 1994). Axis deer are predominantly grazers, but do consume some browse items and forbs. Mesquite leaves are probably consumed in significant amounts during the drier seasons of the year. These deer also consume fruits (Nowak, 1991).
**Cervus dama**  
Fallow Deer

*Distribution.*—The fallow deer is found, mostly in confinement, in the eastern half of the Edwards Plateau at least as far west as Tom Green and Irion counties (Traweek, 1989). This deer is relatively numerous in Bandera, Blanco, Comal, Kendall, Kerr, and Real counties.

*Cervus dama* is grayish-brown dorsally, with white underparts. White spots are present in adults. Spots on the lower sides and haunches fuse into a white line. A black dorsal stripe extends from the nape of the neck to the tip of the tail. A white rump patch is present. Antlers are found only on males, and are quite different from those of *O. virginianus*. The antlers of the fallow deer are flattened and palmate with numerous terminal points.

Preferred habitat for this species on the Edwards Plateau is woodland. The fallow deer consumes a greater percentage of grasses in its diet than the whitetailed or mule deer, but may still compete for forage with the aforementioned species in certain areas. Because of its preference for grasses, the fallow deer competes more directly with domestic livestock (Feldhaer et al. 1988).

**Cervus nippon**  
Sika Deer

*Distribution.*—The sika deer occurs primarily in the eastern and southern portions of the Edwards Plateau. Sizable populations may be found in Bandera, Blanco, Comal, Kerr, Real, and Sutton counties (Traweek, 1989).

*Cervus nippon* ranges in color from chestnut-brown to reddish-olive. Numerous white spots are present on the sides and are arranged in seven to eight rows. The chin, throat, and belly are off-white or gray. A large, white, erectile rump patch is present. Both sexes have a conspicuous, dark, neck mane in the winter season. Antlers are narrow and erect and have two to five points each.

Favored habitats on the Edwards Plateau are upland woods and edge habitats along streams. Sika deer are highly adaptable in their feeding habits and consume a wide variety of vegetative species (Feldhamer, 1982). Plant items consumed include poison ivy, greenbrier, pokeweed, and American holly. Diets are seasonally variable (Feldhamer, 1982). During the spring and summer months, sika deer are partial to emerging agricultural crops.

**Cervus elaphus**  
Wapiti or Elk

*Distribution.*—The wapiti or elk may be found mostly on privately-owned ranches and estates. Elk may be found in small numbers in Bexar, Blanco, Comal, Edwards, Hays, Kendall, Kerr, Kinney, Llano, Medina, Real, Sutton, Tom Green, Uvalde, and Val Verde counties (Traweek, 1989).

*Cervus elaphus* is the largest cervid on the Edwards Plateau, and has a conspicuous, dark mane that extends down to the brisket area. The overall color is a dark brown to red. A rump patch is present and is deep yellow to almost orange. The rump patch fades to a cream color in winter. The antlers of bulls sweep upward and backward and usually have six tines. The only artiodactyl that approaches the size of the elk (excluding domestic cattle, horses, and bison) on the Edwards Plateau is the nilgai antelope, which is quite different in appearance.

**Family Bovidae—Bovids**

**Boselaphus tragocamelus**  
Nilgai

*Distribution.*—The nilgai is found in approximately the eastern half of the Edwards Plateau. Records are available for Kerr, Medina, Real, and Uvalde counties (Traweek, 1989).
Boselaphus tragocamelus is one of the largest exotic mammals on the Edwards Plateau. Males may stand as high as 153 cm at the shoulder. The upper parts of males are usually iron gray in color. The underside of the tail, stripes inside the ears, rings on the fetlocks, and venter are white in color. The head and limbs are tawny in color. The tip of the tail, and a throat tuft found on males are black in color. Females are more lightly colored than males. The forelegs are longer than the hindlimbs. Horns are found only on males and are short and unbranched.

Upland woods are the most common habitat of this species in Texas (Sheffield et al., 1983). The nilgai has acute hearing and sight, and is a rapid runner (Nowak, 1991). The preferred foods, in order of importance in the diet, are grasses, forbs, and browse items (Sheffield et al., 1983). Digestive efficiency of nilgai antelope, domestic cattle, and goats is approximately equal when tested on diets of browse, hay, and pelleted feed rations (Priebe et al., 1987). Nilgai antelope, cattle, and goats are all able to digest vegetation more efficiently than white-tailed deer. The nilgai is a rather calm, docile animal. An adult male observed in Kerr County moved away only after fifteen minutes of close observation; and then in a slow, casual fashion.

Ammotragus lervia
Barbary Sheep

Distribution.—The Barbary sheep is found in free-ranging populations in the western and central portions of the Edwards Plateau (Traweek, 1989). Appreciable numbers of Barbary sheep may be found in Bandera, Blanco, Comal, Edwards, Kerr, Kimble, Kinney, Llano, Medina, Real, Uvalde, and Val Verde counties (Traweek, 1989).

Ammotragus lervia is rufous or tawny brown, with occasional dark brown areas about the head and forequarters. The chin, belly, and inside of the legs are whitish, and a circular spot of white hairs frequently occurs on the head between the horns. A mane extends from under the throat down the front of the neck to the chest; the mane then bifurcates and extends down the forelegs, where it is termed chaps. Other goats may have manes, but only the Barbary sheep has chaps on the forelegs. Horns are present on both sexes and are relatively large and long, with a moderately high spiral angle. The horns have a broad frontal surface, exhibit heteronym winding, and have numerous sulci or rings. Forequarters are more massive than the hindquarters, and legs appear to be short and stocky. Hooves are large, blunt and well developed.

The preferred habitat of A. lervia is steep, rocky, broken, precipitous terrain (Gray and Simpson, 1980). Woody browse is the most important forage class in the spring, summer, and fall months. Browse and grasses are equally important during winter months. Forbs may be the most important food items consumed on the Edwards Plateau (Ramsey and Anderegg, 1972). The Barbary sheep can survive for extended periods on metabolic water and moisture obtained from dew condensed on vegetation (Nowak, 1991).

Antilope cervicapra
Blackbuck

Distribution.— Most populations of the blackbuck are confined to private ranches on the Edwards Plateau (Traweek and Welch, 1992). Substantial populations of the blackbuck may be found in Bandera, Bexar, Blanco, Edwards, Hays, Kerr, Real, Sutton, Uvalde, and Val Verde counties on the Edwards Plateau. The species is managed for hunting purposes in the area.

Antilope cervicapra is a small antelope, and the color differs between males and females. Males are a dark brown color on the back, sides, and outside of the legs, whereas females are yellowish fawn on the dorsal side, and head. The venter, insides of the legs, and eye ring are white in color. Only the males bear horns. The horns are unbranched, ringed at the base, and twisted spirally up to five turns. The muzzle is narrow and shear-like, the tail is short, and the hooves are delicate and sharply pointed.

The blackbuck occurs in open, plains habitats, but also inhabits upland woods. A. cervicapra is a rapid runner and utilizes its great speed to escape predators (Nowak, 1991). The preferred diet of the blackbuck is composed almost exclusively of grasses (Nowak, 1991). Grasses, cereal grains, and some forage crops are consumed on the Edwards Plateau.
SPECIES OF UNVERIFIED OCCURRENCE

The following abbreviated species accounts are of mammals not presently represented by museum records from the Edwards Plateau. Most of these mammals occur immediately adjacent to the region, and may well range upon the Edwards Plateau upon occasion.

*Cryptotis parva*
Least Shrew

This species is found immediately north and east of the Edwards Plateau; records of occurrence are available from Tom Green and Travis counties adjacent to the Edwards Plateau. The least shrew inhabits areas of dense grasses and vegetation, and riparian and other wooded areas where leaf litter covers the soils. Although once an inhabitant of the Edwards Plateau during the Pleistocene (Toomey et al., 1993), *C. parva* is probably excluded from the region because of unsuitable climatic and edaphic conditions.

*Nyctinomops macrotis*
Big Free-tailed Bat

The reputed range of this species extends throughout the southern and western portions of the Edwards Plateau, but no specimens are available to verify this distribution. The nearest records are from Brewster County, southeast of the Edwards Plateau, and Lubbock County, north of the Edwards Plateau (Schmidly, 1991). This species roosts in caves, along rocky cliffs, and in buildings.

*Eumops perotis*
Western Mastiff Bat

The western mastiff bat has been reported from west of the Pecos River in Val Verde County on the Stockton Plateau (Schmidly, 1991). The western mastiff bat no doubt forages on the Edwards Plateau, as it has been reported from Langtry and Pumphill, just west of the Pecos River, in Val Verde County. This species is often found roosting in precipitous cliffs and canyons, and occasionally, buildings.

*Glaucomys volans*
Eastern Flying Squirrel

Flying squirrels may occur on the extreme eastern Edwards Plateau along the Balcones Fault. The nearest records are from McLennan County to the north and Bastrop County just east of the Edwards Plateau (Davis and Schmidly, 1994). *G. volans* is most commonly found in wooded, riparian habitats and in the piney woods region of eastern Texas.

*Geomys personatus*
Texas Pocket Gopher

The Texas pocket gopher may occur in scattered populations in Val Verde and Kinney counties on the Edwards Plateau (Jones and Jones, 1992). *G. personatus* is widespread in South Texas, but prefers deep, sandy soils. The gravelly soils of the Edwards Plateau may be unsuitable.

*Perognathus flavescens*
Plains Pocket Mouse

The plains pocket mouse is found in the High Plains, Toya Basin, and parts of the Trans-Pecos of Texas. This pocket mouse occurs in Midland County immediately north of the Edwards Plateau, and may range onto the region (Jones et al., 1991). *P. flavescens* favors sandy habitats, so may be excluded from the Edwards Plateau by soil substrate.

*Dipodomys spectabilis*
Banner-tailed Kangaroo Rat

The banner-tailed kangaroo rat may occur on the Edwards Plateau in the extreme western counties. This species has been reported from Ector County just west of the Edwards Plateau (Choate et al., 1992). The banner-tailed kangaroo rat requires soils friable enough to excavate burrows and mounds, and may be limited by the shallow, rocky soils of the Edwards Plateau.

*Spilogale putorius*
Eastern Spotted Skunk

This species may occur on the extreme eastern Edwards Plateau around the Balcones Fault zone. This skunk has been reported from Travis County, just east of the region (Schmidly, 1984b). The eastern spotted skunk may be found in wooded areas, grasslands, and rocky areas.
Odocoileus hemionus
Mule Deer

The mule deer occurs west of the Pecos River in Val Verde County and may range onto the extreme western Edwards Plateau in Crockett, Midland, and Val Verde counties (Choate et al., 1992; T. L. Zorn, pers. comm.; P. Christmas, pers. comm.). O. hemionus favors rocky, slope habitats dominated by juniper trees, so suitable habitat is to be found upon the Edwards Plateau.

ADDENDUM

Since this work has gone to press, a revised checklist of North American mammals north of Mexico, 1997, has been published by Jones et al. (1997). Some nomenclatural differences noted between the aforementioned checklist and this work include the use of the familial name Tayassuidae for the collared peccary and separation of skunks from the family Mustelidae and subsequent placement of these taxa into the family Mephitidae (Jones et al., 1997). The generic name of the northern river otter is listed as Lontra, and the desert pocket mouse has been divided into two species. The species which occurs on the Edwards Plateau is listed as Chaetodipus eremicus. The author wishes to acknowledge the newer checklist and its availability. A few older nomens are retained within this work for the sake of consistency throughout the text.

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30 March 1998
SUMMARY AND CONCLUSIONS

Seventy-six species of native mammals presently reside on the Edwards Plateau. The presence of two species of mammals, the hairy-legged vampire bat and white-nosed coati, on the Edwards Plateau is based upon extralimital records. At least six species of mammals have been extirpated from the region since the late nineteenth and early twentieth centuries. Fourteen species of mammals have been introduced by Europeans and now occur in significant numbers. Counting the extralimital and exotic mammals, 92 species reside on the Edwards Plateau, and are discussed within this work. Many other ungulate species have been introduced on the Edwards Plateau but are, at present, primarily confined within private game ranches.

The diverse mammalian fauna of the Edwards Plateau has no endemic members. This diversity of mammals can, in part, be attributed to the ecotonal nature of the region. Certain vegetational components reach distributional limits on the Edwards Plateau. The western Edwards Plateau has a strong creosote element that is lacking on the remainder of the region, and the eastern Edwards Plateau has bald cypress trees along some of its rivers and streams that the western section lacks. Rainfall increases in a noticeable gradient from west to east, with the Balcones Fault zone moderating moisture levels because of invection to the south. Rivers such as the Concho, Frio, Guadalupe, Llano, and Medina have their headwaters on the central and northern Edwards Plateau, whereas most of the western Edwards Plateau is without such watercourses. Exceptions to this are the Devils, Pecos, and Rio Grande rivers on the western Edwards Plateau. Soils are mostly shallow entisols and mollisols and are formed over beds of Cretaceous age limestone. Topography of the area varies from almost level valley areas and gently rolling hills in the northwest to steep, deeply cut canyon lands in the southern and eastern Edwards Plateau. All of these factors contribute to the ecotonal characteristics of the region.

Native mammals currently residing on the Edwards Plateau belong to seven distinct faunal elements. The two faunal elements with the greatest number of species are the Chihuahuan and Widespread faunal elements, with 28 and 20 species, respectively. The Eastern and Neotropical faunal elements each contribute eight species to the total, and the Campestrian faunal element contributes seven species to the total mammalian fauna of the Edwards Plateau. The Local faunal element consists of three autochthonous species of mammals, and two species belonging to the Austral faunal element occur on the Edwards Plateau.

Distinct patterns of distributions of species are sometimes shown by utilizing areal biogeographic techniques. Several Chihuahuan species reach distributional limits on the western Edwards Plateau. Possible source areas for the mammalian faunal of the Edwards Plateau can be delineated by determining the center of coincidence for each faunal element. The four most likely historical source areas for the mammalian fauna of the Edwards Plateau are Coahuila, Mexico, the Llano Estacado, East Texas, and South Texas.

Cluster analyses were performed on the native, resident mammalian fauna of the Edwards Plateau and surrounding areas, and slightly different source areas were determined for the current mammalian fauna of the Edwards Plateau. A hypothesis that the Edwards Plateau is a barrier to the dispersal of some mammalian species was tested first by dividing the Edwards Plateau into two approximately equal quadrats on each side of the 100th meridian and determining the presence or absence of native mammals within either quadrat. If no such barrier existed, it was reasoned that each quadrat should be identical, or close to identical, in its mammalian species complement. As a result of this analysis, the Edwards Plateau was hypothesized to constitute a barrier to the dispersal of some mammals and, consequently, the entire Edwards Plateau, and each quadrat of the Edwards Plateau, was compared by UPGMA cluster analysis utilizing Dice’s similarity coefficient and found to differ in regard to their mammalian faunas. If no such barrier existed, it was reasoned that each quadrat should be identical, or close to identical, in its mammalian species complement. As a result of this analysis, the Edwards Plateau was hypothesized to constitute a barrier to the dispersal of some mammals and, consequently, the entire Edwards Plateau, and each quadrat of the Edwards Plateau, was compared by UPGMA cluster analysis utilizing Dice similarity coefficients and Euclidean distance measures to the surrounding regions in order to determine possible source areas of the contemporary mammalian fauna.

The entire mammalian fauna of the Edwards Plateau was most similar to the Rolling Plains region; and secondarily with the Llano Estacado. Mammals of the eastern quadrat of the Edwards Plateau clustered with the mammalian fauna of the Rolling Plains in every case, but the western quadrat of the Edwards Plateau, with
Euclidean distance clustering, was equally similar to the Rolling Plains and Trans-Pecos regions. In order to determine what caused this type of grouping for the western quadrat, I compared only the rodents of each region and quadrat of the Edwards Plateau with UPGMA cluster analysis. Rodents of the eastern Edwards Plateau were most similar to rodents of the Rolling Plains Region, whereas Rodents of the western Edwards Plateau were most similar to the rodent fauna of the Trans-Pecos Region. These results support the hypothesis that the Edwards Plateau is a barrier to dispersal at least to some of the western mammals. Rodents and other sedentary mammals are probably most affected by the marginal environments of the Edwards Plateau.

Artificial quadrats of rainfall amounts (based upon 30 year average rainfall isoclines) were constructed and the mammals within each quadrat were compared by cluster analysis to determine possible differences. The westernmost quadrat was distinct from the other quadrats and the fauna of the extreme eastern quadrat shared a relatively low similarity value and a higher distance value with two central quadrats. This seemed to indicate that differences in mammalian distributions related to rainfall and moisture were most prevalent on the extreme western and eastern Edwards Plateau.

Vegetation associations also were combined and treated as sampling quadrats. UPGMA clustering of these vegetation associations resulted in dendrograms uniting the western vegetation associations separately with the other three quadrats (vegetation associations). The central and southeastern Edwards Plateau were united and the Llano Uplift region of the northeastern Edwards Plateau clustered separately in this analysis. The separate clustering of the Llano Uplift region may be due to a sampling error, as that particular vegetation association possessed the fewest species of mammals on the Edwards Plateau.

Humans have inhabited the Edwards Plateau region since at least the early Holocene. Although the aboriginal inhabitants utilized mammals for food and other essential materials, the most dramatic utilization of the mammalian fauna occurred as a consequence of settlement of the region by Europeans. Some marginal, neotropical species, such as the jaguar and ocelot, were extirpated from the region, and the North American bison was hunted to extinction by the latter part of the nineteenth century. European settlers also altered the original environment of the Edwards Plateau by cultural and pastoral practices. Europeans also introduced several species of mammals in the region, such as the house mouse, roof rat, Norway rat, domestic dog, domestic cat, and domestic livestock which have had varied affects upon the native mammalian species. Mammals remain an important part of the economy of the humans residing on the Edwards Plateau. Not only does domestic livestock provide a substantial income for many residents, but lease hunting of deer, fur trapping, and ranch-raising of exotic ungulates supplements the income of landowners on the Edwards Plateau. Aesthetic value of the deer and other animals of the Edwards Plateau also helps to bolster a tourist industry, aided by the many city, state, and federal parks located throughout the Edwards Plateau.

I surveyed the major mammal collections, and some smaller regional collections, at Texas universities for specimens of mammals from the Edwards Plateau, and attempted to gather all of the relevant literature concerning the natural history and distributions of Edwards Plateau mammals. This work provides a baseline source for future studies of the mammalian fauna of the Edwards Plateau and adjacent areas. Mammalian distributions are dynamic over time and habitat alterations and other factors will change the status of some species within the region.

The systematic status of many mammals occurring on the Edwards Plateau should be studied in the future. Examples of taxa which may provide worthwhile systematic research include the black-tailed jackrabbit, eastern and western cottontail, swamp rabbit, rock squirrel, silky pocket mouse, hispid cotton rat, southern plains woodrat, eastern woodrat, and long-tailed weasel. The exact subspecific status of most of the mammals on the region is, at best, poorly known. Distributions of species such as the eastern mole, desert shrew, ghost-faced bat, big brown bat, northern yellow bat, rock squirrel, swamp rabbit, eastern gray squirrel, western harvest mouse, northern grasshopper mouse, woodland vole, American badger, river otter, mountain lion, and collared peccary should be studied in greater detail in order to determine the exact status of these species. Much research remains to be conducted upon various aspects of the systematics and ecology of the mammalian fauna of the Edwards Plateau, and it is hoped that this work will serve as a point of departure for many of those future studies.
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