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SMALL MAMMAL INVENTORY CITY OF BOULDER OPEN SPACE DEPARTMENT

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INTRODUCTION

About 15,000 years ago, as the last major glaciation began to recede, the modern landscape of Colorado began to take shape (Armstrong 1972). In response to warming conditions some mammals left and others have moved in, and the wide array of species that have come to occur in Colorado have responded to different opportunities at different times (Armstrong 1972). Armstrong (1972) identified nine mammalian faunal elements based on the character of overall and Colorado ranges of constituent species, and six of these faunal elements are of interest to us in Boulder County. The most recent arrivals tend to occur in the plains riparian ecosystem, and include the Eastern (North American) and Neotropical species (Armstrong and Freeman 1984). The Cordilleran (Rocky Mountain) and Boreocordilleran (Canada and Upper Midwest/Mountain) species are in the higher forested ecosystems, and the Campestrian (Great Plains) species occur mostly on plains grasslands, or grassland/woodland ecotone. By contrast the Chihuahuan (Mexican Plateau) species tend to be concentrated in the foothills scrub habitats, and may be relict from a warmer and drier time some 5000 years ago (Armstrong and Freeman 1984). A seventh category, widespread species, are not identifiable with any geographic region (see Armstrong, 1972; 354-357, for detailed descriptions of each faunal element).

Three basic approaches can be taken in the study of biogeography (why species occur where they do); geographical, ecological, and

historical (Simpson 1965). The objectives of this study are to use an ecological approach that will (1) provide natural history baseline data upon which further ecological or evolutionary studies may be based (2) provide a species list of mammals for habitat types that are representative of Open Space properties (3) determine density or relative abundance for each species (4) provide information about small mammal populations in areas of special concern (when possible) and (5) conduct visual surveys of amphibians and reptiles on study areas.

This study originally was designed for collecting baseline ecological data, and the results must be interpreted as a whole. Any attempt to interpret results for a specific property or habitat-type for land use applications would be ~~in~~ inconsistent with the original design of the study. Data gathered from a particular property or habitat may be of interest to the Department, but this study, by its stated objectives, cannot answer land use questions about specific areas. The most important value of this study is in defining specific questions for further study.

METHODS

Methods ~~are~~^{were} essentially the same as employed successfully in previous studies of mammals in the Boulder Mountain Parks, the Cottonwood Grove, and units of the National Park Service (Armstrong 1979, Armstrong and Freeman 1982, and 1984).

Figure 2 Transect locations Boulder Valley Ranch
 (= indicates a standard transect location)

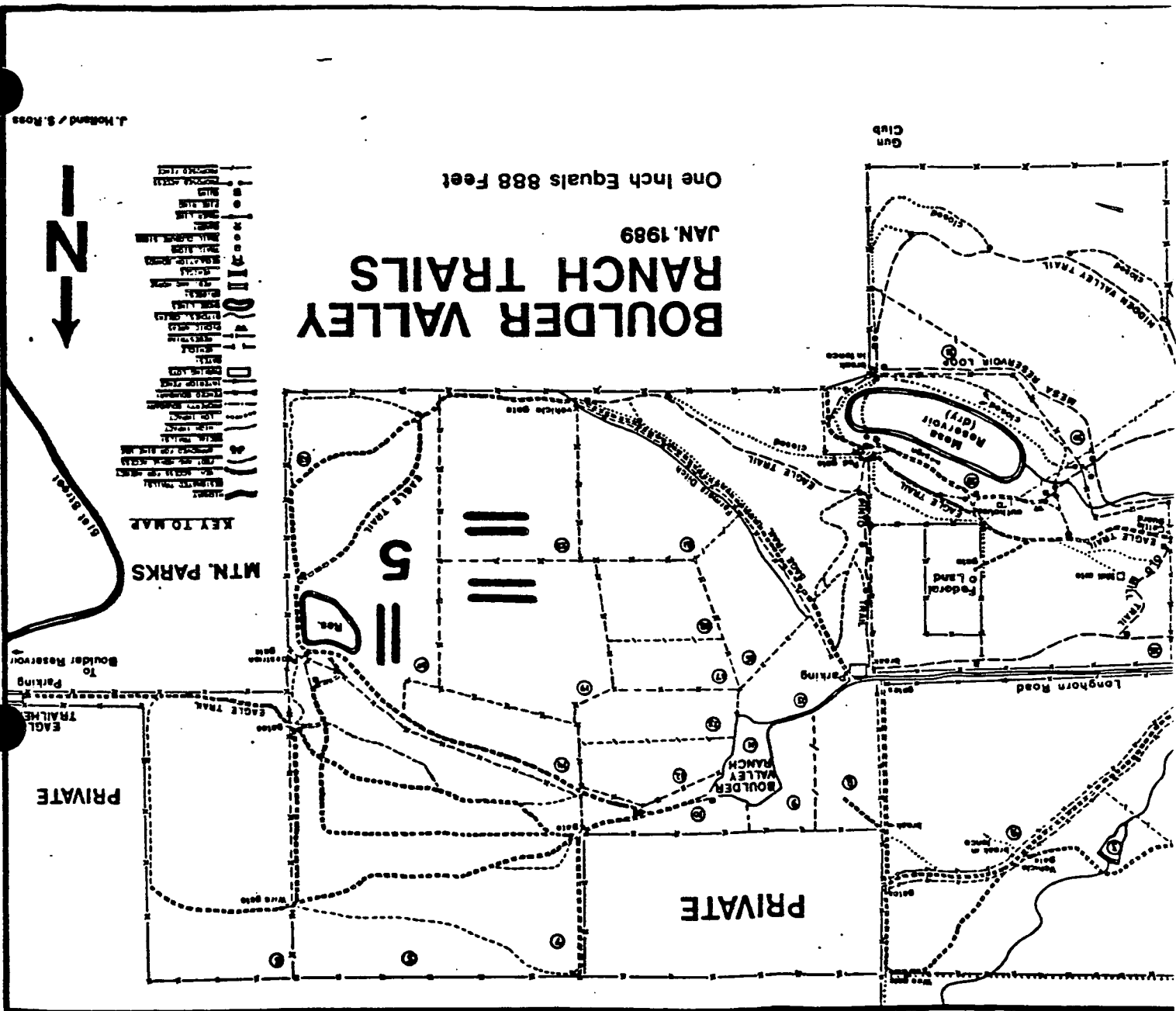


Figure 3 Transect locations Stengel I

( indicates a standard transect location)

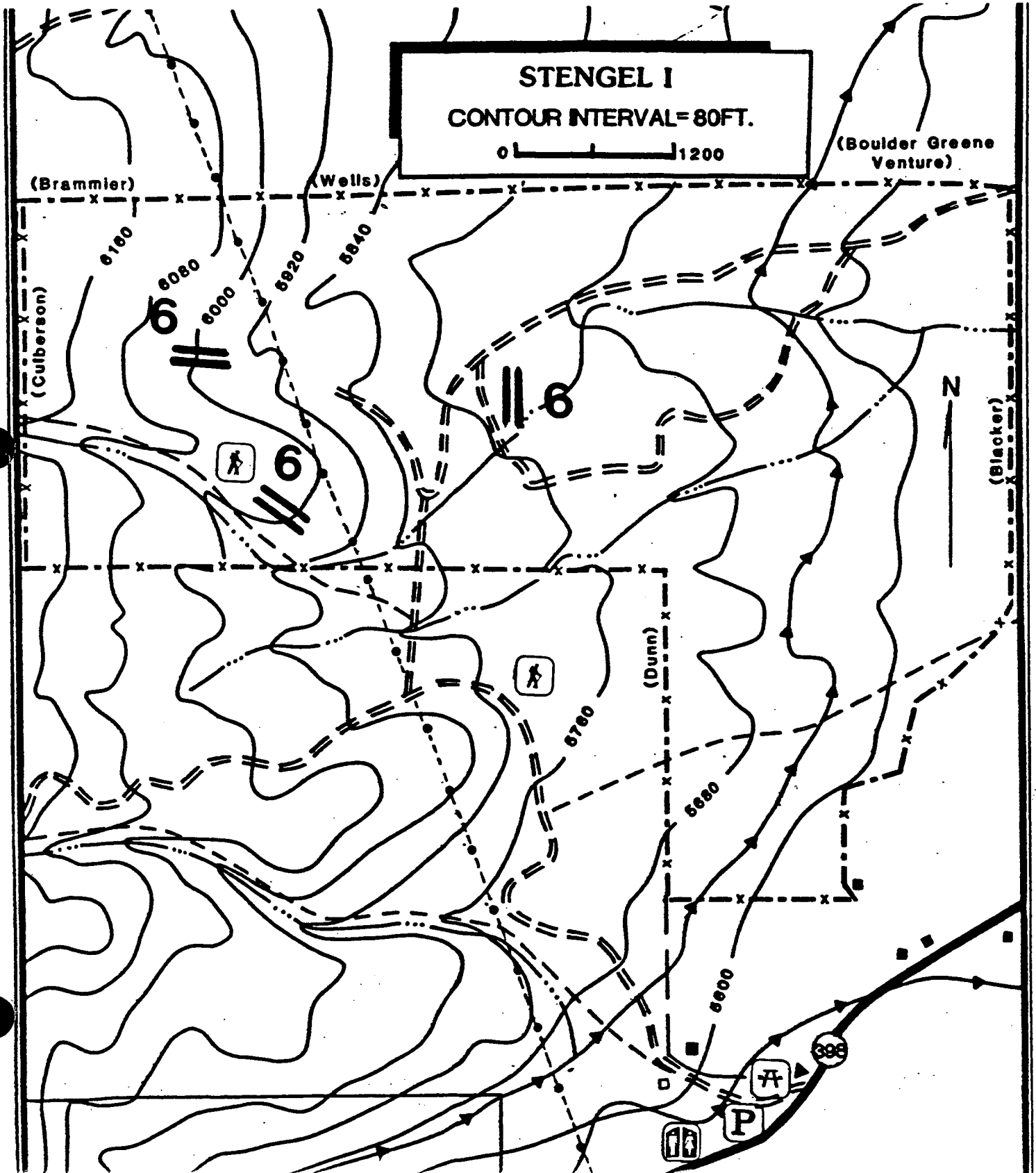
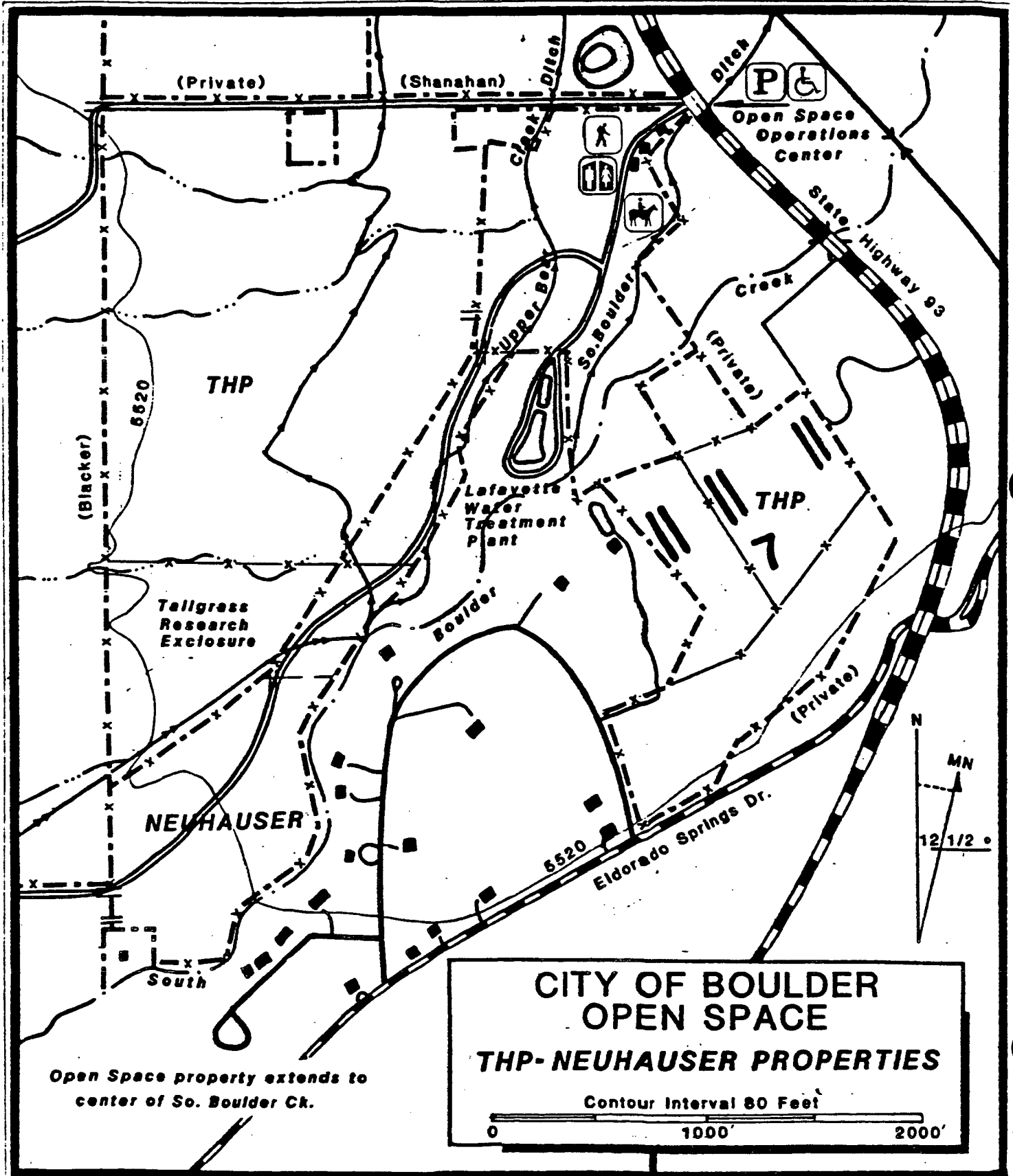


Figure 4 Transect locations Tall Grass Prairie (TG3)

( indicates a standard transect location)



Open Space property extends to center of So. Boulder Ck.

**CITY OF BOULDER
OPEN SPACE
THP-NEUHAUSER PROPERTIES**

Contour Interval 80 Feet

0 1000 2000'

All methods ~~are~~^{were} as non-manipulative as possible; therefore, the only animals that ~~will be~~^{were} live trapped for identification ~~will be~~^{were} nocturnal small mammals. At each field site a pair of transects each with 25 trapping stations set 5 meters apart was established. The transects were located 10 meters apart and two live traps were set at each trapping station. A grid of 10x10 trapping stations 15 meters apart was used on the midgrass prairie habitat to determine species density per unit area. A grid was used on this habitat because it was felt to be representative of the majority of Open Space habitat. (A few of the transects at Tracy Collins were not of the standard configuration see Table 2 for trap-nights). Each trap was provided with polyester batting for bedding, and baited with a combination of peanut butter and oatmeal. The traps were opened at dusk and checked and closed at dawn three or four days a week for three or four weeks at each study site. Captured mammals were identified, sexed, weighed, aged, their reproductive condition noted, trap location recorded, given a numbered ear tag, and then released. Transect locations are shown in Figures 1-4. Each trapping station is permanently marked with steel markers and can be relocated readily from the figures with a metal detector.

Setting mistnets for bats was considered a health risk by the City of Boulder and was not attempted. Reptiles, amphibians, and larger mammals were observed when appropriate, but the majority of field time was spent live trapping. Pitfall trapping using a

Table 1. Selected study habitats (Adapted from Armstrong 1972)

<u>Habitat Type</u>	<u>Location</u>
Plains Mid-grass	- Tracy Collins
Plains Tall Grass	- T63
Plains Riparian	- Tracy Collins
Plains Meadow/Wetlands	- Boulder Valley Ranch
Woodland/Grassland Ecotone	- Stengle /Tracy Collins
Foothills Scrub	- Stengle
Ponderosa Pine	- Stengle
Agricultural (hay) Meadow	- Boulder Valley Ranch

standard array (Bury and Corn 1987) was attempted briefly in an effort to capture species that are trap shy.

Habitats (Table 1) were chosen based upon areas that have not been investigated in previous studies for local governmental agencies (Armstrong and Freeman 1982, 1984), habitats that represent the largest physical areas of City Open Space properties, or habitats of special concern to the Open Space Department. There are a number of problems associated with using such broad categories of community types. In many cases the descriptions are based only upon the most prevalent vegetation and are not a good descriptor of each habitat type (Armstrong 1972). When possible transects were located on vegetation maps (Bunin 1985), and plant association are noted in Table 3.

RESULTS AND DISCUSSION

Trapping began on May 10, 1989, and ended on September 20, 1989. During that period of time traps were open for 50 nights representing 11,804 trap nights. Ten different species (136 individuals) were captured in the traps 343 times. Species lists for each habitat type are shown in Figure 5. A representation of species across habitats is shown in Table 2, included in the table is either their density per unit area or captures per trap night (relative density). See Appendix A for a complete list of potential mammalian fauna for Boulder County, species accounts for observed species is included in Appendix B. If we exclude

bats and extirpated species from the calculations, 27% of the potential mammalian fauna was observed or captured during the study period. Notice (Table 2) that only one species (Peromyscus maniculatus) was found in more than two habitats, five species were found in just two of the habitats, and four species were found in a single habitat. This reflects a pattern observed in the distribution of mammals in Colorado. Forty-nine percent of the fauna (53 species) occur in only one or two habitat types, eighty-eight species occur in five or fewer habitat types (Armstrong 1972). The numbers of individuals captured during this study appear to be low compared to other studies completed in the county (Armstrong and Freeman 1982, Armstrong and Freeman 1984). In 1850 trap nights Armstrong and Freeman (1982) captured eight species, and 214 individuals. Due to the annual and multiannual cycling of some rodent populations, and the fact that all of the mentioned studies were accomplished at different times of the year it is not possible to make comparisons among studies. Traditionally population numbers appear to be low during the spring and early summer months and increase during the fall (Sadleir 1965). However, Brown (1980) found populations of deermice in the Rocky Flats area that did not follow reported seasonal or annual patterns, but did find populations of Western Harvest Mice that showed seasonal variation with the highest densities occurring in the fall.

The faunal relationships of species captured are indicated in Table 2. Note that the Eastern, Chihuahuan, and Campestrian

Table 2 Species Occurrence by Habitat Type. Legend

Results reported as individuals / trap-night

* Indicates individuals / hectares

Faunal Element

E = Eastern

C = Cordilleran

P = Plains (Campestrian)

CH = Chihuahuan

W = Widespread

B = Boreocordilleran

Table 3 Site and Transect Locations

- Site #1 Mixed Grass 10X10 Grid (Tracy Collins) Widely distributed on Open Space properties below the Forest/Grassland Ecotone. Includes mid-height species such as western wheatgrass with short grasses like blue gramma.
North Facing Slope
2,084 Trap-nights
- Site #2 Riparian area of Coal Creek (Tracy Collins) Overstories of cottonwoods, willows, and river birch. Total cover by vegetation is high.
Traps perpendicular to creek
340 Trap-nights
- Site #3 Plains Meadow 5X5 Grid (Tracy Collins)
50 Trap-nights
- Site #4 Foothills Scrub (Tracy Collins) Mountain shrub thickets are characterized by a number of species that thrive on mesic soils, such as American plum, chokecherry, ninebark, and hawthorn.
165 Trap-nights
- Site #5 Plains Wetlands (Boulder Valley Ranch) Dominated by baltic rushes, and sedges, area also included some

Habitat Type	Cyrtosia	Bacva	Thomaya	Taloides	Cercanathus	Hialdus	Rethrodontomya	Reolotis	Percnyacus	Anticulatus	Neotoma	Mexicana	Miscotus	Penaylanicus	Miscotus	Schroabarc	Mus	Musculus	Zapus	Dudsonius	Zapus sp.
Plains Midgrass			1/2.25 *						23/2.25 *												
Plains Tallgrass	5/4200						2/4200		5/4200					1/4200		4/4200		2/4200			
Plains Wetland																					
Plains Riparian									29/340										3/340		3/340
Foothills Scrub																					
Stengle						1/1200			5/800												
Tracy Collins									36/165			1/165									
Woodland/Grassland						1/1200			6/1200												1/1200
Ecotone																					
Ponderosa Pine							2/800		4/800												
Faunal Element	E		C		P		CH		W		CH			B	P				Introduced		E

cattails, spike-rush and foxtail barley.

2300 Trap-nights

Site #6 Woodland/Grassland Ecotone This type is codominated by skunkbrush sumac, mountain mahogany, and big bluestem. Shrubs contribute between 5 and 25% of the canopy cover.

Transect #1 Foothills Scrub East Facing Slope

800 Trap-nights

Transect #2 Woodland/Grassland Ecotone

1200 Trap-nights

Transect #3 Ponderosa Pine Woodland

800 Trap-nights

Site #7 Tall Grass Prairie. Characterized by little bluestem, and big bluestem, with an understory of shortgrasses, and midgrasses such as blue gramma or side-oats gramma.

4200 Trap-nights

faunal elements are represented by two species, and the remainder are all represented by just one species.

No species were live-trapped at the Plains Wetland Habitat type, or in the hay meadow on the same property at Boulder Valley Ranch. The absence of animals poses an interesting question. The general area was subject to bubonic plague several years ago and many of the prairie dog communities were severely affected. How this might have influenced the small mammal populations is not known. In addition, the meadow and the wetland are exposed to fluctuating water tables due to flood irrigation techniques used on the property. Such practices may or may not influence the distributions of mammals, and is an interesting subject for further study.

Transects at the tall grass habitat site were placed in three different areas of the prescription burn at T63, ungrazed/unburned, ungrazed/burned, and grazed\ unburned. This information could be used with information about percent ground cover and seed bank comparisons currently being collected by the University of Colorado (Dr. Jane Bock). With further work it may be possible to determine effects of the burn on mammalian habitat diversity and species density.

A list of amphibian and reptile species occurring in Boulder County is included as Appendix C . An observed species is denoted with an asterisk, and location of observation are recorded. No

Figure 5 Species List by Habitat Type

* Indicates a capture or observation

PLAINS MIDGRASS

Order Insectivora

Cryptotis parva Least Shrew

Order Chiroptera Bats

Myotis ciliolabrum Small-footed Western Myotis

Order Lagomorpha Rabbits and Allies

* Sylvilagus audubonii Desert Cottontail

Lepus townsendii White-tailed Jackrabbit

Lepus californicus Black-tailed Jackrabbit

Order Rodentia Rodents

Spermophilus tridecemlineatus 13-lined Ground Squirrel

Spermophilus spilosoma Spotted Ground Squirrel

Cynomys ludovicianus Black-tailed Prairie Dog

* Thomomys talpoides Northern Pocket Gopher

Geomys bursarius Plains Pocket Gopher

Perognathus fasciatus Olive-back Pocket Mouse

Perognathus flavescens Plains Pocket Mouse

Perognathus flavus Silky Pocket Mouse

Perognathus hispidus Hispid Pocket Mouse

Dipodomys ordii Ord's Kangaroo Rat

Reithrodontomys montanus Plains Harvest Mouse

Reithrodontomys megalotis Western Harvest Mouse

* Peromyscus maniculatus Deer Mouse

Onychomys leucogaster Northern Grasshopper Mouse

Microtus ochrogaster Prairie Vole

* Mus musculus House Mouse

Order Carnivora Carnivores

* Canis latrans Coyote

Canis lupus Gray Wolf

Vulpes velox Swift Fox

Ursus arctos Grizzly Bear

Mustela frenata Long-tailed Weasel

Mustela nigripes Black-footed Ferret

Taxidea taxus Badger

* Mephitis mephitis Striped Skunk

Order Artiodactyla Even-toed Ungulates

Cervus elaphus Wapiti or American Elk

Antilocapra americana Pronghorn

Bison bison Bison

Odocoileus virginianus

* Odocoileus nemionus

PLAINS TALL GRASS

Order Insectivora

* Cryptotis parva Least Shrew

Order Chiroptera Bats

Myotis ciliolabrum Small-footed Western Myotis

Order Lagomorpha Rabbits and Allies

Sylvilagus audubonii Desert Cottontail

Lepus townsendii White-tailed Jackrabbit

Lepus californicus Black-tailed Jackrabbit

Order Rodentia Rodents

Spermophilus tridecemlineatus 13-lined Ground Squirrel

Spermophilus spilosoma Spotted Ground Squirrel

Cynomys ludovicianus Black-tailed Prairie Dog

Thomomys talpoides Northern Pocket Gopher

Geomys bursarius Plains Pocket Gopher

Perognathus fasciatus Olive-back Pocket Mouse

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* Peromyscus maniculatus Deer Mouse

Onychomys leucogaster Northern Grasshopper Mouse

* Microtus ochrogaster Prairie Vole

* Microtus pennsylvanicus Meadow Vole

* Mus musculus House Mouse

Order Carnivora Carnivores

Canis latrans Coyote

Canis lupus Gray Wolf

Vulpes velox Swift Fox

Ursus arctos Grizzly Bear

Mustela frenata Long-tailed Weasel

Mustela nigripes Black-footed Ferret

Taxidea taxus Badger

Mephitis mephitis Striped Skunk

Order Artiodactyla Even-toed Ungulates

Cervus elaphus Wapiti or American Elk

Antilocapra americana Pronghorn

Bison bison Bison

Odocoileus virginianus

* Odocoileus nemionus

PLAINS RIPARIAN

Order Marsupicarnivora

Didelphis virginiana Virginia Opossum

Order Insectivora

Sorex cinereus Masked Shrew

Cryptotis parva Least Shrew

Order Chiroptera Bats

Myotis lucifugus Little Brown Bat

Myotis volans Long-legged Myotis

Myotis ciliolabrum Small-footed Western Myotis

Lasionycteris noctivagans Silver-haired Bat

Eptesicus fuscus Big Brown Bat

Lasiurus cinereus Hoary Bat

Order Lagomorpha Rabbits and Allies

* Sylvilagus floridanus Eastern Cottontail

Order Rodentia Rodents

Sciurus niger Fox Squirrel

Castor canadensis Beaver

* Peromyscus maniculatus Deer Mouse

Microtus pennsylvanicus Meadow Vole

Microtus ochrogaster Prairie Vole

* Mus musculus House Mouse

Onychomys leucogaster Muskrat

* Zapus hudsonius Meadow Jumping Mouse

Erethizon dorsatum Porcupine

Order Carnivora Carnivores

* Canis latrans Coyote
Canis lupus Gray Wolf
Vulpes vulpes Red Fox
Ursus americanus Black Bear
Ursus arctos Grizzly Bear
Procyon lotor Raccoon
Mustela frenata Long-tailed Weasel
Mephitis mephitis Striped Skunk
Lutra canadensis River Otter
Felis concolor Mountain Lion
Felis rufus Bobcat

Order Artiodactyla Even-toed Ungulates

Odocoileus hemionus Mule Deer
Odocoileus virginianus White-tailed Deer

WOODLAND / GRASSLAND ECOTONE

Order Insectivora

Sorex cinereus Masked Shrew

Sorex monticolus Montane Shrew

Sorex nanus Dwarf Shrew

Sorex merriami Merriams Shrew

Order Chiroptera Bats

Myotis lucifugus Little Brown Bat

Myotis evotis Long-eared Bat

Myotis thysanodes Fringed Myotis

Myotis volans Long-legged Myotis

Lasionycteris noctivagans Silver-haired Bat

Eptesicus fuscus Big Brown Bat

Lasiurus cinereus Hoary Bat

Plecotus townsendii Townsend's Big-eared Bat

Order Lagomorpha Rabbits and Allies

* Sylvilagus nuttallii Nuttall's Cottontail

Lepus townsendii White-tailed Jackrabbit

Lepus californicus Black-tailed Jackrabbit

Order Rodentia Rodents

* Tamias minimus Least Chipmunk

Tamias quadrivittatus Colorado Chipmunk

Marmota flaviventris Yellow-bellied Marmot

Spermophilus elegans Wyoming Ground Squirrel

* Spermophilus variegatus Rock Squirrel

Spermophilus lateralis Golden-mantled Ground Squirrel

Cynomys ludovicianus Black-tailed Prairie Dog

Sciurus aberti Abert's Squirrel

Thomomys talpoides Northern Pocket Gopher

Perognathus fasciatus Olive-back Pocket Mouse

* Peromyscus maniculatus Deer Mouse

Peromyscus difficilis Rock Mouse

Neotoma mexicana Mexican Woodrat

Neotoma cinerea Bushy-tailed Woodrat

* Microtus ochrogaster Prairie Vole

Erethizon dorsatum Porcupine

* Zapus sp.

Order Carnivora Carnivores

* Canis latrans Coyote

Canis lupus Gray Wolf

Vulpes vulpes Red Fox

Urocyon cinereoargenteus Gray Fox

Ursus americanus Black Bear

Ursus arctos Grizzly Bear

Procyon lotor Raccoon

Mustela erminea Short-tailed Weasel or Ermine

Mustela frenata Long-tailed Weasel

Taxidea taxus Badger

Spilogale gracilis Western Spotted Skunk

Mephitis mephitis Striped Skunk

Felis concolor Mountain Lion

Felis rufus Bobcat

Order Artiodactyla Even-toed Ungulates

* Odocoileus hemionus Mule Deer

Bison bison Bison

Ovis canadensis Bighorn Sheep

FOOTHILLS SCRUB

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Sorex nanus Dwarf Shrew

Sorex merriami Merriam's Shrew

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* Neotoma mexicana Mexican Woodrat

Neotoma cinerea Bushy-tailed Woodrat

Erethizon dorsatum Porcupine

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- Vulpes vulpes Red Fox
- Urocyon cinereoargenteus Gray Fox
- Ursus americanus Black Bear
- Ursus arctos Grizzly Bear
- Bassariscus astutus Ringtail
- Mustela frenata Long-tailed Weasel
- Taxidea taxus Badger
- Spilogale gracilis Western Spotted Skunk
- Mephitus mephitus Striped Skunk
- Felis concolor Mountain Lion
- Felis rufus Bobcat

Order Artiodactyla Even-toed Ungulates

- * Odocoileus hemionus Mule Deer
- Odocoileus virginianus
- Ovis canadensis Bighorn Sheep

PONDEROSA PINE

Order Insectivora

- Sorex cinereus Masked Shrew
- Sorex monticolus Montane Shrew
- Sorex nanus Dwarf Shrew
- Sorex merriami Merriam's Shrew

Order Chiroptera Bats

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- Myotis volans Long-legged Myotis
- Lasionycteris noctivagans Silver-haired Bat
- Eptesicus fuscus Big Brown Bat
- Lasiurus cinereus Hoary Bat
- Plecotus townsendii Townsend's Big-eared Bat

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- Spermophilus lateralis Golden-mantled Ground Squirrel
- Sciurus aberti Abert's Squirrel

- * Tamiasciurus hudsonicus Chickaree or Pine Squirrel
- Thomomys talpoides Northern Pocket Gopher
- * Peromyscus maniculatus Deer Mouse
- Peromyscus difficilis Rock Mouse
- Neotoma mexicana Mexican Woodrat
- Microtus montanus Montane Vole
- Microtus longicaudus Long-tailed Vole
- Erethizon dorsatum Porcupine

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- Felis concolor Mountain Lion
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Order Artiodactyla Even-toed Ungulates

- Cervus elaphus Wapiti or American Elk
- * Odocoileus hemionus Mule Deer
- Ovis canadensis Bighorn Sheep

individuals were caught in pitfall traps.

DISCUSSION

The present study partially fulfills the need to provide descriptive baseline data for a portion of the natural resource, the native mammals. These preliminary results for seven habitat types indicate that in most cases a rich and diverse fauna of complex ecological distribution exists on Open Space properties. Species are not widespread and are limited to one or two habitats in most cases. Only one introduced (European) species was encountered during the study period. The complexity of Front Range environmental conditions has provided suitable habitat for species from many faunal elements. The Open Space properties are representative of some of the least abundant habitat types, and those most likely to be developed elsewhere in the region. In particular the foothills scrub habitat type is the principal habitat of most of the Chihuahuan species (Armstrong and Freeman 1984). The uniqueness of Open Space properties makes their stewardship an important responsibility; they are more than just a local resource, they are a distinctive part of our national heritage.

ACKNOWLEDGEMENTS

I would like to thank Dr David Armstrong for his advisory assistance during all phases of this project. Acknowledgements go to Kristina Williams who did all of the live-trapping at Tracy Collins. I would especially like to thank the ranger staff at City Open Space for their help, encouragement, and patience with this project. In particular, special thanks go to Janet George and Richard Smith.

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POTENTIAL NATURAL MAMMALIAN FAUNA

Order Marsupicarnivora 1

Didelphis virginiana Virginia Opossum

Order Insectivora 7

Sorex cinereus Masked Shrew

Sorex hoyi Pygmy Shrew

Sorex monticolus Montane Shrew

Sorex nanus Dwarf Shrew

Sorex palustris Water Shrew

Sorex merriami Merriams Shrew

Cryptotis parva Least Shrew

Order Chiroptera Bats 9

Myotis lucifugus Little Brown Bat

Myotis evotis Long-eared Bat

Myotis thysanodes Fringed Myotis

Myotis volans Long-legged Myotis

Myotis ciliolabrum Small-footed Western Myotis

Lasionycteris noctivagans Silver-haired Bat

Eptesicus fuscus Big Brown Bat

Lasiurus cinereus Hoary Bat

Plecotus townsendii Townsend's Big-eared Bat

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Sylvilagus audubonii Desert Cottontail

Lepus americanus Snowshoe Hare

Lepus townsendii White-tailed Jackrabbit

Lepus californicus Black-tailed Jackrabbit

Ochotona princeps Pika

Order Rodentia Rodents 38

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Tamias quadrivittatus Colorado Chipmunk

Tamias umbrinus Uinta Chipmunk

Marmota flaviventris Yellow-bellied Marmot

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Dipodomys ordii Ord's Kangaroo Rat

Castor canadensis Beaver

Reithrodontomys montanus Plains Harvest Mouse

Reithrodontomys megalotis Western Harvest Mouse
Peromyscus maniculatus Deer Mouse
Peromyscus difficilis Rock Mouse
Onychomys leucogaster Northern Grasshopper Mouse
Neotoma mexicana Mexican Woodrat
Neotoma cinerea Bushy-tailed Woodrat
Clethrionomys gapperi Northern Red-backed Vole
Phenacomys intermedius Heather Vole
Microtus pennsylvanicus Meadow Vole
Microtus montanus Montane Vole
Microtus longicaudus Long-tailed Vole
Microtus ochrogaster Prairie Vole
Onychomys leucogaster Muskrat
Zapus hudsonius Meadow Jumping Mouse
Zapus princeps Western Jumping Mouse
Erethizon dorsatum Porcupine

Order Carnivora Carnivores 16

Canis latrans Coyote
Canis lupus Gray Wolf (na)
Vulpes vulpes Red Fox
Vulpes velox Swift Fox
Urocyon cinereoargenteus Gray Fox
Ursus americanus Black Bear
Ursus arctos Grizzly Bear (na)
Procyon lotor Raccoon
Bassariscus astutus Ringtail

Martes americana Pine Marten \

Mustela erminea Short-tailed Weasel or Ermine

Mustela frenata Long-tailed Weasel

Mustela nigripes Black-footed Ferret (NA)

Mustela vison Mink

Eulo gulo Wolverine (NA)

Taxidea taxus Badger

Spillogale gracilis Western Spotted Skunk

Mephitis mephitis Striped Skunk

Lutra canadensis River Otter (NA)

Felis concolor Mountain Lion

Felis canadensis Lynx (NA)

Felis rufus Bobcat ?

Order Artiodactyla Even-toed Ungulates

Cervus elaphus Wapiti or Elk

Odocoileus hemionus Mule Deer /

Odocoileus virginianus White-tailed Deer

Antilocapra americana Pronghorn

Bison bison Bison

Ovis canadensis Bighorn Sheep

APPENDIX B

SPECIES ACCOUNTS OF OBSERVED ANIMALS

Zapus hudsonius. By John O. Whitaker, Jr.

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Zapus Coues, 1876

Zapus Coues, 1876:253. Type species *Dipus hudsonius* Zimmermann.

CONTEXT AND CONTENT. Order Rodentia, Superfamily Dipodoidea, Family Zapodidae, Subfamily Zapodinae. The genus *Zapus* includes three living species, *Z. hudsonius*, *Z. princeps*, and *Z. trinotatus*.

- | | | |
|---|---|----------------------|
| 1 | First molariform tooth large, about 0.70 mm long and 0.75 wide, with crescentine fold on occlusal surface | <i>Z. trinotatus</i> |
| | First molariform tooth smaller (about 0.55 by 0.50 in <i>princeps</i> and 0.30 by 0.35 in <i>hudsonius</i>) | 2 |
| 2 | Incisive foramina shorter than 4.6 mm; palatal breadth at last molariform tooth less than 4.2; condylobasal length usually less than 20.3; maxillary tooththrow usually 3.7 or less | <i>Z. hudsonius</i> |
| | Incisive foramina longer than 4.6 mm; palatal breadth at last molariform more than 4.4; condylobasal length usually 20.3 or more; maxillary tooththrow usually greater than 3.7 | <i>Z. princeps</i> |

Zapus hudsonius Zimmermann, 1780 Meadow Jumping Mouse

Dipus hudsonius Zimmermann, 1780:358. Type locality Hudson Bay, Canada; restricted by Anderson (1942) to Fort Severn, Ontario.

Dipus labradorius Kerr, 1792:276. Type locality. Preble (1899: 11) states that the type specimen came from Hudson Bay.

Dipus canadensis Davies, 1798:157. Type locality near Quebec City, Province of Quebec, Canada.

Dipus americanus Barton, 1799:115. Type locality near Philadelphia, Pennsylvania.

Meriones microcephalus Harlan, 1839:1. Type locality Becks Farm, a few miles NE Philadelphia, Pennsylvania.

Meriones acadicus Dawson, 1856:2. Type locality Nova Scotia, Canada.

Zapus tenellus Merriam, 1897:103. Type locality Kamloops, British Columbia, Canada.

CONTEXT AND CONTENT. Context noted in generic summary above. The group has been monographed by Preble (1899) and Krutzsch (1954), who recognized the 11 living subspecies listed below.

- Z. h. hudsonius* (Zimmermann, 1780:358), see above (*labradorius* Kerr a synonym).
- Z. h. canadensis* (Davies, 1798:167), see above (*ontarioensis* Anderson a synonym).
- Z. h. americanus* (Barton, 1799:115), see above (*microcephalus* Harlan, *brevipes* Bole and Moulthrop, and *rafinesquei* Bole and Moulthrop are synonyms).
- Z. h. acadicus* (Dawson, 1856:2), see above (*hardyi* Batchelder a synonym).
- Z. h. alascensis* Merriam, 1897:223. Type locality Yakutat Bay, Alaska.
- Z. h. tenellus* Merriam, 1897:103, see above.
- Z. h. campestris* Preble, 1899:20. Type locality Bear Lodge Mountains, Crook Co., Wyoming.
- Z. h. ladas* Preble, 1899:10. Type locality Rigoulette, Hamilton Inlet, Labrador.
- Z. h. pallidus* Cockrum and Baker, 1950:1. Type locality NW corner sec. 4, T. 12 S, R. 20 E, 5½ mi. N, 1¼ mi. E Lawrence, Douglas Co., Kansas.
- Z. h. intermedius* Krutzsch, 1954:447. Type locality Ridgeway, Winneshiek Co., Iowa.



FIGURE 1. Photograph of *Zapus hudsonius* taken at Terre Haute, Vigo Co., Indiana, by Dennis Clark.

Z. h. preblei Krutzsch, 1954:452. Type locality Loveland, Larimer Co., Colorado.

†*Z. h. adamsi* Hibbard, 1955:217. Type locality, XI Ranch Meade County, Kansas, late Sangamon interglacial (Pleistocene, Kingsdown formation, Jinglebob local fauna).

†*Z. h. transitionalis* Klingener, 1963:257. Type locality, base of Mt. Scott, Big Springs Ranch, SE¼, sec. 18, T. 32 S, R. 28 W, Meade Co., Kansas, late Illinoian glacial (Pleistocene, Kingsdown formation, Mt. Scott local fauna).

DIAGNOSIS. *Zapus* is a long-tailed, yellowish mouse with four upper molariform teeth, the first much smaller than the others. *Napaeozapus* differs in having a white-tipped tail and only three molariform teeth; *Eozapus* differs in having a white-tipped tail and a dark longitudinal stripe down the abdomen. *Z. hudsonius* is smaller (187 to 230 mm, 108 to 139, 28 to 31), has a narrower skull in proportion to its length, smaller premolars (0.30 by 0.35), and a shorter tooththrow (usually less than 3.7) than other species of *Zapus*.

GENERAL CHARACTERS. *Zapus* has the hind legs much longer than forelegs; tail attenuate, subcylindrical and longer than body; eyes small and midway between nose and ear; ear dark with narrow pale edge and somewhat longer than surrounding hair; upper lip with median groove; vibrissae conspicuous; teats 8, with 2 pectoral, 4 abdominal, and 2 inguinal; total length of baculum 4.5 to 4.9 mm, width 0.64 to 0.72; general pelage coarse with broad dorsal band of brown or yellowish brown darkened with brownish black hairs; sides paler; underparts white or sometimes suffused with yellowish, but usually separated from sides by band of clear yellowish color; backs of forefeet and hind feet grayish white; tail distinctly bicolor, dark brown above and yellowish white below (Figure 1). Total length is 187 to 255 mm, tail length 108 to 155, and hind foot 28 to 35. Skull with preorbital foramen large and oval; ends of nasals project noticeably beyond incisors; four upper molariform teeth with first reduced in size (illustrated in MAMMALIAN SPECIES No. 14 on *Napaeozapus*); upper incisors strongly grooved; upper and lower incisors deep orange or yellow; enamel pattern complicated, consisting of one re-entrant fold lingually and four labially; three lower molariform teeth, dentition i 1/1, c 0/0, p 1/0, m 3/3.

Specific characters: *Zapus hudsonius* has the back ochraceous to dark brown; sides pale; lateral line ochraceous-buff, indistinct, or absent; belly white or sometimes suffused with ochraceous; additional descriptive data may be found in Krutzsch (1954), Klingener (1963, 1964), and Whitaker (1963, 1966). The skull is illustrated in Figure 2. Whitaker (1963)

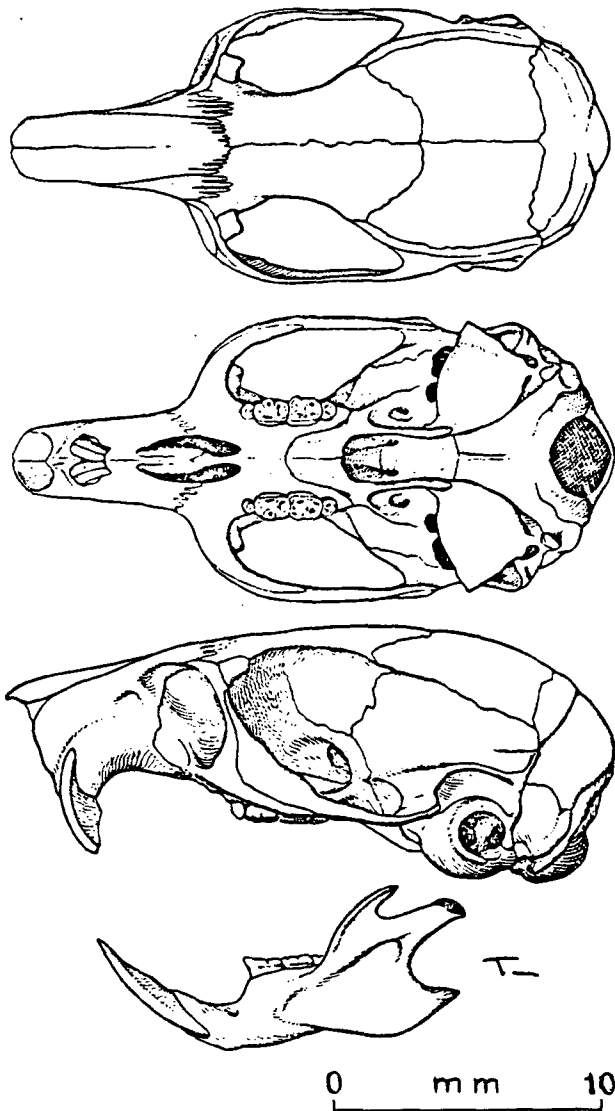


FIGURE 2. Skull and jaw of *Zapus hudsonius*, A. dorsal view, B. ventral view, C. lateral view of cranium and jaw. From Ellerman, 1940:571.

gave information on variability within the species in central New York, including means, ranges, standard errors, and coefficients of variability. Also males and females were compared.

DISTRIBUTION. Eleven living and 2 fossil subspecies of *Zapus hudsonius* have been described (Figure 3). All known extinct taxa of *Zapus* were described from Meade County, Kansas, and *Z. h. transitionalis* has also been taken in Harper County, Oklahoma. These localities are well beyond the present range of *Z. hudsonius* and about 270 miles (450 km) east of the nearest *Z. princeps* localities. *Zapus hudsonius* occurs primarily in abandoned fields, moist abandoned fields, and brushy fields but is sometimes taken in wooded areas when herbaceous ground cover is adequate.

FOSSIL RECORDS. Fossil taxa, *Z. rinker* Hibbard, 1951, *Z. s. sandersi* Hibbard, 1956, *Z. s. rexroadensis* Klingener, 1963, *Z. burti* Hibbard, 1941, and two fossil subspecies of *Z. hudsonius*, listed above, have been described. Klingener (1963) studied 32 *Zapus* fossils from seven localities in Meade County, Kansas, and from one locality in Harper County, Oklahoma. It is not clear where *Z. burti* fits into the phylogeny of *Zapus*, but the Pliocene taxon, *Z. sandersi rexroadensis*, appears to be a logical ancestral stock for *Zapus hudsonius*. *Zapus rinker* appears to have evolved from *Z. s. rexroadensis* by late Pliocene, but then to have died out. *Z. s. rexroadensis* appears to have given rise to *Z. s. sandersi*, *Z. hudsonius transitionalis*, *Z. h. adamsi*, and the living *Z. hudsonius*, in a progressive series.

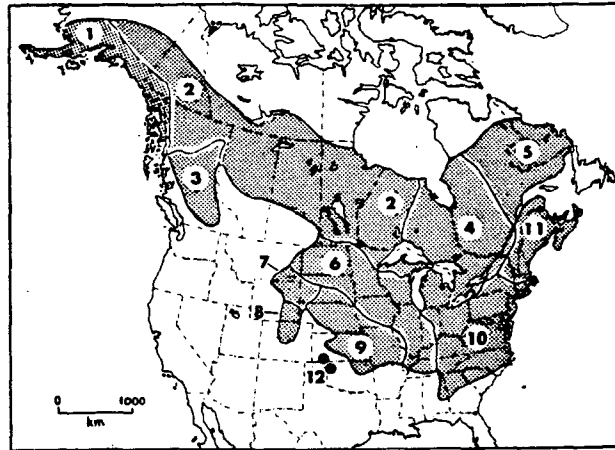


FIGURE 3. Range of *Zapus hudsonius* and its subspecies (Modified from Hall and Kelson, 1959). Subspecies are: 1) *Z. h. acadicus*; 2) *Z. h. alascensis*; 3) *Z. h. americanus*; 4) *Z. h. campestris*; 5) *Z. h. canadensis*; 6) *Z. h. hudsonius*; 7) *Z. h. intermedius*; 8) *Z. h. ladas*; 9) *Z. h. pallidus*; 10) *Z. h. preblei*; 11) *Z. h. tenellus*; 12) fossil sites mentioned in text on distribution.

Guilday *et al.* (1969) found *Zapus hudsonius* in a late Pleistocene cave deposit in Robinson Cave, Overton Co., Tennessee.

FORM. Krutzsch (1954) studied the teeth, baculum, ear ossicles, and hair. In addition to sensory hairs, facial vibrissae, nasal hairs, and carpal vibrissae, three kinds of hairs (guard hairs, overhairs, and underfur) are normally present in *Zapus*. Guard hairs are gray at the base with increased pigmentation (black or brown) at the tips. They are elliptical in cross section, taper at both ends, and range from .096 to .140 mm in diameter (average .115 in *Z. hudsonius*). This is significantly narrower than in *Z. princeps* or *Z. trinitatus*. Individual hairs of the underfur are cylindrical, taper abruptly at each end, are grayish or white proximally, and are yellowish brown distally. The dark dorsal stripe of *Zapus* is caused by the large number of black hairs there. Black hairs are less abundant on the paler sides and essentially absent in the lateral yellow band. Krutzsch (1954) found six individuals with abnormal coloring among 1261 specimens of *Z. hudsonius* examined, four had white spots, one was black, and one lacked any black. Schorger (1951) caught six meadow jumping mice in Dane County, Wisconsin, with white-tipped tails and Whitaker (1963) found five of 1049 that had white tail tips, and one each with a small white spot on the rump and crown, respectively.

Krutzsch (1954) presented data on the length and transverse diameter at the base and tip of the baculum (os penis). Whitaker (1966) figured an os clitoridis bone of *Zapus*, which was 1.7 mm long. Krutzsch (1954) studied geographic variation in *Z. hudsonius*. The subspecies vary mainly in coloration, relative proportions of the tail, hind feet, and body, and size and shape of parts of the skull. Individuals generally have paler backs, brighter sides, and smaller skulls in the southern parts of the range.

Klingener (1964) published on the comparative myology of *Zapus*, *Napaeozapus*, and related taxa, and also (1963) on the evolutionary development of the dentition of *Zapus*. Lyon (1901) compared the osteology of jerboas and jumping mice. Guthrie (1963) studied a specimen of *Napaeozapus* injected with latex and skulls of *Zapus* and *Sicista*, and concluded that the carotid arterial pattern in this group (Zapodidae) is basically the same as in *Microtus*. He discussed the minor differences. Most of the anatomical systems, however, have not been studied at all in *Zapus hudsonius*, even in general terms.

FUNCTION. Most of the work on physiology of *Zapus hudsonius* pertains to hibernation. Waters and Stockley (1965) timed the breathing rate of *Zapus* in hibernation by observing thoracic movements for 25 minutes on 16 January 1963. There were 29 intervals between thoracic movements with long and short intervals interspersed. Sixteen intervals were less than 5 seconds, four were from 6 to 15, and the nine longer than 15 seconds were 63, 70, 95, 95, 100, 107, 109, 115, and 141.

Morrison and Ryser (1962) found the average body temperature for 163 values on nine *Z. hudsonius* to be 37.27° C with a range of 35.1 to 40.1° (s.d. 1.00). They found a rhythmic daily cycle in this species, with highest readings at night (mean of 38.0°C) and lowest readings during the day (mean of 36.9°C), thus reflecting the nocturnal behavior pattern of the species. During exposure to temperatures of 0 to 10°C, body temperature was unstable. Morrison and Ryser concluded that this did not represent an inability to regulate body temperature, because at ambient temperatures below zero, the body temperature again increased to normal nighttime active temperature of about 38°C. This, of course, would be beneficial in keeping the animal from freezing. This response to subzero environmental temperatures has been found in other hibernating mammals and is apparently caused by an increase in metabolic activity (Lyman, 1963).

Waters and Stockley (1965) took rectal temperatures of a *Zapus hudsonius* as it entered, emerged, and finally re-entered hibernation; this sequence occurred from the hour 1920 through noon the next day. Ambient temperatures outside the nest box were below 0°C. The animal remained in hibernation after the probe was inserted until about 2020 whereupon its temperature started to rise. At 2030 it was about 5°C and by 2040 it was about 15° and the animal was emerging from dormancy. By 2050 it had reached 25°, but then fluctuated between 25° and 33° until 2140, when it leveled off at about 33°, and remained there until about midnight. It then became irregular, dropped to around 26°, and between 0200 and 0220 dropped to about 2° and the animal again became dormant. Its temperature rose to about 15° for about 3 hours then dropped to about 7° for several hours. Rectal temperatures exceeded ambient temperatures by at least 3° during nearly all of the observation period. In another mouse in a refrigerator, skin temperatures varied rather directly about 6° to 7° above the refrigerator temperature, until the refrigerator temperature decreased to about -3° to -4°. The skin temperatures of the animal then rose from about 3° to 4° to about 10°.

Morrison and Ryser (1962) studied the relation between temperature and oxygen consumption in nonhibernating animals, although some individuals entered hibernation during the trial. At an ambient temperature of 29°C, oxygen consumption ran slightly more than 2000 mm³/hr/g of body weight in one individual. At 10°, oxygen consumption rose to the vicinity of 5000 and 6000 mm³. After an hour, the metabolic response dropped slightly, and after another half hour, it dropped to 200 mm³, and finally in another 4 hours reached a minimum of 40 mm³. The animal then woke spontaneously and within an hour was utilizing 5000 mm³ necessary for maintenance at 10°C. Pearson (1947) reported a basal level of 3100 mm³ in an 18 g *Z. hudsonius*, and of 3200 mm³ in a 22 g jumping mouse. During 24 hours, oxygen consumption ranged from about 3500 to 5500 mm³/hr/g of body weight, with the maximum occurring at hours 1830, 2230, 0030, and 0730.

Neumann and Cade (1964) found that jumping mice (eight *Napaeozapus* and two *Z. hudsonius*) on short days fattened before hibernation and hibernated for longer periods than did their counterparts on long days (See MAMMALIAN SPECIES No. 14 on *Napaeozapus*). The average weights of the short-day mice decreased rapidly just after the mice entered hibernation, then leveled off, whereas weights of the long-day mice decreased rapidly and continually throughout their sporadic periods of hibernation until death occurred. Quimby (1951) and Hamilton (1935) also noted rapid weight loss in the first days after entrance into hibernation.

Morrison and Ryser (1962) found rapid weight increases up to slightly more than 100% of original body weight. The adult weight before fattening averaged about 19 g, with an increase in one case to 37 g. These workers also found that the rapid and massive increase in weight was not synchronized in the various individuals. One individual began its increase on 18 August, whereas another did not begin until 20 September. This supports the hypothesis of Whitaker (1963) that individuals of this species enter hibernation a few at a time after they have had time to accumulate ample fat and that this occurs over an extended period. The maximum daily increases in weight found by Morrison and Ryser were as high as 1.9 to 2.0 g per day, or 6 to 8% of body weight per day in some individuals over three day periods. The rate was lower over longer periods since the progression in weight is stepwise, with periods of increase interspersed with periods of non-increase. However, there was one average value of 0.94 g per day over 16 days (3.2% per day).

ONTOGENY AND REPRODUCTION.

Whitaker (1963) presented information on 19 newborn young (neonates) *Zapus hudsonius* as follows: total length, mean 34.4, range 30 to 39 mm; tail, mean 9.3, range 7 to 11; hind foot, mean 4.7, range 3 to 6. The average weight of 14 neonates from three litters was 0.8 g (0.7 to 1.0 g). Quimby (1951) found that neonates had minute vibrissae, but otherwise were naked and pink. Their eyes were closed but appeared as dark spots. The ear pinnae were folded over the external ear openings. During the first week, the vibrissae became visible to the naked eye, the tail became bicolor, and pinnae of the ears unfolded and were tipped with black, and the claws appeared. Yellowish hairs appeared about the ninth day dorsally, and spread to include the sides about day 13. By then the vibrissae had become prominent and were about 8 mm long. The eyes were still closed, but a crack down the center was visible by about day 13, when the incisors erupted. They were white. Sparse, pale-colored hairs were visible on the belly back of the feet and on the outer surfaces of the legs. During the third week the hair covering was completed and the external auditory meatus began to open. By this time the young were readily identifiable as jumping mice. During the fourth week the adult pelage replaced the juvenile pelage and the eyes opened. The incisors changed from white to the yellowish orange of the adult and by day 23 all but the third molars had erupted. After the fourth week, growth of the young mice slowed considerably. By this time they were 4.6 times their length at birth, whereas at the end of the 13th week they had increased only to 5.8 times this length. Tail length had increased 10 times in the first four weeks and 12 times in the first 13 weeks. At four weeks the hind foot was 5.6 times longer than at birth and at 13 weeks it was 5.9 times longer. The young weighed about 2 to 4 g at day 10, about 4 to 8 g at day 20, about 8 to 11 g at day 30, and reached a minimum adult weight of about 14 or 15 g at about day 60. By about day 90 they attained a weight of about 20 g.

Quimby (1951) presented information on gestation in four meadow jumping mice. The periods (in days) were 17 or 18, 17 to 19, at least 20 to 21, and 12 to 20. Data for the first two litters were for nonlactating *Z. hudsonius*, the time increased to 20 or 21 days if the female was lactating, as the third was. Quimby concluded that most births take place between 15 June and 30 August in Minnesota, but that three peaks occur, one in late June, a second in mid- and late July and a third in mid-August. Townsend (1935) and Whitaker (1963) reported pregnancies throughout the summer in New York, and Whitaker presented data on estimated birthdates for 78 potential litters. Mice apparently breed soon after emerging from hibernation with dates of emergence influencing breeding dates. Some litters were produced in every 10-day period between 11 May and 20 September. However, only three of the 78 litters would have been produced in May, and only three in September. The greatest numbers of litters were produced in the first 3 weeks in June and the first 3 weeks in August. Quimby (1951) found that many mice have two litters during the year at Minnesota, but that some may have three, and Hamilton (1935) believed two litters per year were produced. Whitaker (1963) found that many mice have at least two litters per year since 67% of the adult females taken in the first major breeding period (21 May to 20 June) were pregnant, or had given birth recently, and 84% of the adult females taken in the period 21 July to 20 August were pregnant or had recently given birth.

Quimby (1951) found an average of 5.7 young per litter in Minnesota (17 litters, range 4 to 7), and Townsend (1935) found a mean of 4.5 in New York (17 litters range 3 to 7). Krutzsch (1954) got a mean of 4.5 by averaging embryo counts from museum labels of 62 individuals; the range was 2 to 8. Whitaker (1963) presented other embryo and litter counts from the literature, and also data concerning numbers of embryos from 78 snap-trapped females taken at Ithaca, New York. The mean number of embryos was 5.5 (range 2 to 9).

Whitaker (1963) studied seasonal changes in the male reproductive tract and found that the length of the seminal vesicles was a more sensitive indicator of breeding behavior than the testis measurements.

ECOLOGY. *Zapus hudsonius* may live in a variety of habitats (Getz, 1961; Quimby, 1951; Whitaker, 1963). The species is widespread in abandoned grassy fields, but is often more abundant in thick vegetation along ponds, streams, and marshes or in rank herbaceous vegetation of wooded areas. Stands of touch-me-not, *Impatiens*, provide particularly good habitat for *Zapus hudsonius*. Ross et al. (1968) found *Zapus*

to be more abundant on low mounds (Mima mounds) of Minnesota than on the surrounding prairie. They hypothesized the mounds might be used as hibernation sites.

Whitaker (1963) concluded that adequate herbaceous ground cover was necessary for maintenance of populations of *Zapus*, but that soil moisture seemed to have little or no direct effect except as it influenced other factors, and that distance to major bodies of water was of little importance. Getz (1961), however, concluded that there was a definite relationship between the species and moisture, but that the species avoided sparse vegetation. Whitaker (1963) found that grassy vegetation favored populations of *Zapus*, but the species of plants present (including food plants) were of little consequence. There appeared to be enough food in most of the habitats studied to support populations of *Zapus*. Other species of mammals, if they competed, did not limit the distribution or abundance of *Zapus*. Bider (1968) found that the activity of zopodids increased with rainfall.

Information concerning predation on *Zapus* has been summarized (Whitaker, 1963). In addition, *Zapus hudsonius* was preyed upon by red tailed hawks in Alberta (Luttich *et al.*, 1970), and by barn and long-eared owls in New York (Eaton and Grzybowski, 1969).

Zapus hudsonius harbors few parasites. (for some, associates might be a better term) in comparison to many other species of small mammals of comparable size (Hamilton, 1935; Whitaker, 1963). Among bacteria, *Escherichia coli*, *Bacillus mycoides*, *Klebsiella* sp., and *Bacteriodes* sp. have been reported from the cecum (Whitaker, 1963). *Bacteriodes* occurs in low numbers in spring but becomes abundant in late summer and autumn. Two species of *Hexamita* and one of *Eimeria* (protozoans), were found in the cecum of *Zapus*, also at Ithaca.

Of the trematodes, *Notocotylus hassali* was reported from Michigan (Erickson, 1938), and *Plagiorchis proximus* and *Quinqueserialis quinqueserialis* were reported from Labrador and Quebec (Schad, 1954). Whitaker (1963) found trematodes in 26 of the 956 mice examined for larger internal parasites. *Plagiorchis* sp. was the most common, being found in 16 mice. Other trematodes found were *Schistosomium douthitti*, *Quinqueserialis* sp., and *Echinostoma* sp. Cestodes reported are *Mesocostoides* sp. (Schad, 1954), larval *Taenia mustelae* (Freeman, 1956), and *Choanotaenia* sp. (Lubinsky, 1957). Only five of the 956 mice examined by Whitaker yielded cestodes, one of which was *Hymenolepis* sp. Reported nematodes are *Subulura unguilatus* and *Spirocerca zapi* (Erickson, 1938), and *Mastophorus muris* in one mouse from Labrador (Schad, 1954). Whitaker (1963) found nematodes in the intestines of only two of 956 examined, these worms were *Citellinoides zapodis* and *Riccularia* sp. Lichtenfels and Haley (1968) found *Longistriata dalrymplei* and *Citellinoides zapodis* in mice from Maryland.

The tick, *Dermacentor variabilis*, was reported from Minnesota (Quimby, 1951) and Nova Scotia (Dodds *et al.*, 1969). Whitaker (1963) found 36 of 864 meadow jumping mice examined for external parasites to harbor *Ixodes muris* in New York, and Martell *et al.* (1969) found the same tick from Nova Scotia. The chigger mites, *Trombicula microti* and *T. subsignata* were taken by Brennan and Wharton (1950), and Farrell (1956) reported *Euschongastia diversa acuta*. Strandmann (1949) reported *Androlaelaps jahrenholzi* (= *Haemolaelaps glasgowi*) and Judd (1950) reported *Haemogamasus hirsutus*.

The most abundant external parasite of the meadow jumping mouse in New York (Whitaker, 1963) and in Indiana (Rupes and Whitaker, 1968) is the hypopus (transport form) of *Dermacarus hypudaei*. This form does not feed on the mouse, and adults of this species have not been found in North America, even though it was found on over half of the specimens examined from New York and Indiana, often in great numbers. No other mites were found with any regularity by Whitaker (1963) or Whitaker and Wilson (1968), but species reported were the chiggers *Neotrombicula subsignata*, *Eutrombicula alfreddugesi*, and *Neoschongastia* sp. Other mites were: *Eulaelaps stabularis*, *Laelaps kochi*, *Haemogamasus alaskensis*, and a few free-living mites considered as accidentals. See remarks at end also.

Flea records summarized by Whitaker (1963) include *Orchopeas leucopus*, *Megabothris asio*, *M. wagneri*, *M. quirini*, *Stenopomia americana*, and *Corrodopsylla curvata*. Only 13 of 864 mice examined by Whitaker harbored fleas (one flea each). Included were *Ctenophthalmus pseudagyrtes*, *Orchopeas leucopus*, and *Megathris asio*. Holland and Benton (1968) re-

cently reported *Ctenophthalmus pseudagyrtes* and *Orchopeas leucopus* from Pennsylvania.

Larval botflies, *Cuterebra*, often have been found on *Zapus hudsonius* (Whitaker, 1963). Hamilton (1935) reported seeing one louse on a *Zapus hudsonius*, and Whitaker (1963) found one, probably *Neohaematopinus* sp., among 864 *Z. hudsonius* examined.

Quimby (1951) found that the home range in *Z. hudsonius* varied from 0.19 to 0.87 acres (0.08 to 0.35 hectares) in females, with a mean of 0.38 (.15 hectares), and male home ranges varied from 0.14 to 1.10 acres, with a mean of 0.43 (.17 hectares) in one area in Minnesota. In another area in Minnesota he found that nine males had significantly larger home ranges (2.70 acres, 1.1 hectares) than did 17 females (average 1.57 ± 0.22 s.d. acres, or 0.63 hectares). Blair (1940) calculated home ranges of 26 males (Michigan) as 0.89 ± 0.11 and of 24 females as 0.92 ± 0.11 acres, the difference not significant.

Quimby (1951) figured some home ranges and suggested that the environment plays a major role in determining the size, and that the shape of home ranges is determined by terrain. Home ranges shift, in one case an adult moved more than a half mile.

Townsend (1935) and Sheldon (1938) suggested that *Z. hudsonius* tends to wander, and Townsend believed that the movement may be associated with the animals seeking moist spots during the dry part of summer. Quimby (1951) found them to have essentially no homing tendencies on the basis of releases of 13 individuals 0.2 to 0.5 miles (0.3 to 0.8 km) from their original home ranges. Only two returned, and both of these appeared to Quimby to have returned by chance wandering. The evidence is not conclusive but suggests that *Zapus* may move about more than is the case with other small mammals.

Quimby (1951) estimated that there were 11.91 mice per acre (48.3/hectare) in one Minnesota study area, and gave monthly averages ranging from 1.81 to 3.57 mice per acre (7.4 to 14.4/hectare) for the second. Quimby (1951) and Blair (1940) agreed that the number of jumping mice in an area may vary considerably from year to year.

FOOD. Quimby (1951) studied food preference in caged *Z. hudsonius*, by making many insects and plants available to them. Of 32 insects tried, all but adult silphid and coccinellid beetles and larval papilionid caterpillars were eaten. Entire plants were made available, but only the fruits and seeds were utilized to any great extent, including several grass seeds and fruits of various shrubs (*Rubus*, *Ribes*, *Cornus*, *Vaccinium*, *Fragaria*, and others). The fruits of 15 plants, including *Typha*, *Cyperus*, *Scirpus*, *Salix*, *Corylus*, *Alnus*, *Chenopodium*, *Trifolium*, *Rhus*, *Cicuta*, *Asclepias*, *Phlox*, *Plantago*, and *Rudbeckia* were not eaten. Hamilton (1935) concluded that seeds are the main food of the species, but that berries, nuts, fruits, and insects are also eaten.

Whitaker (1963) examined the stomach contents of 796 mice of this species. He found that when *Zapus* emerges from hibernation in late April and May it feeds on a variety of foods. Animal material is about half the food and seeds are about 20%. As the season progresses, more seeds and less animal materials are consumed, and the fungus, *Endogone*, becomes important. Seeds, particularly grass seeds, are the basic food in general. The different grasses are used in sequence as they progressively ripen and disappear in the field. Some of the more important seeds eaten were those of *Phleum*, *Anthoxanthum*, *Poa*, *Cerastium*, *Rumex acetosello*, *Dactylus*, *Potentilla*, *Oxalis*, *Echinochloa*, *Ulmus*, and *Asclepias*. The most important of the animal foods were lepidopterous larvae and beetles of the families Carabidae and Curculionidae. It has been suggested that the fungus *Endogone* is taken incidentally with other foods. Whitaker concluded that the fungus is actively sought since the percentages of this food were so high in individual stomachs, since particles of dirt including *Endogone* spores were sometimes found on the cervical and pectoral regions of the animals, and since there was no likely food source with which *Endogone* might be taken incidentally. Available evidence (Quimby, 1951; Whitaker, 1963) indicates that *Zapus hudsonius* does not store food.

BEHAVIOR. The young, at birth, are naked and helpless, but emit a high-pitched squeaking sound, audible for several feet (Quimby, 1951). During the first week of life the young are able to crawl, but are unable to support themselves on their legs. A "suckling note" is made during the first week.

These patterns continue through the second week of life and the young first react to sound about day 20, after the external auditory meatus opens. About this time the young are able to support themselves on their legs, walk, and make short "hops" of an inch or so, although the movements appear awkward because of the hind feet, which appear very large for the size of the animal. The eyes open about day 25, and the behavior patterns then change considerably; the young begin to venture from the nest for the first time, and begin to eat solid food, but nursing does not necessarily end at this time. The young of one litter continued to suckle for the 7 days they were allowed to remain with the female. By the end of the fourth week, the young have the appearance of the adult and are fully able to fend for themselves.

Jumping mice, except when young, are usually silent, but a few sounds have been recorded. York (1945) heard captives utter series of short chirps similar to the sounds of night migrating birds, and another sound which sounded like a cloth being rubbed across damp glass, "cho, cho, cho . . . cho." Quimby (1951) kept many live animals but heard only one vocalization, a clucking noise made when individuals were excited. DeKay (1842) reported a sparrowlike chirping sound. Whitaker (1963) heard the squeaks and suckling notes described by Quimby, and also a drumming noise produced by vibrating the tail rapidly against a surface. This noise was also reported by Sheldon (1938) and Svihla and Svihla (1933).

Meadow jumping mice are docile creatures, seldom attempting to bite even when handled roughly. When startled, they usually take a few jumps of about a meter or so, then a series of shorter hops, or more commonly they may stop abruptly and remain motionless. If one does not know exactly where they have stopped it is difficult to locate them. Quimby (1951) and Sheldon (1934) both felt that this motionless state was their chief means of protection. Whitaker (1963) hypothesized that the dark dorsal stripe might be of benefit in helping to conceal them when motionless, and also that they might produce less odor than other small mammals.

Meadow jumping mice are essentially solitary but when together are generally not antagonistic toward one another. Whitaker (1963) recorded that when a *Zapus* was introduced into a cage in which one was already present, the second usually wandered about the cage, not seeming to smell or notice the first, until the two happened to come face to face. The first mouse would remain motionless and pressed against the floor of the cage in a high state of excitement, with the tail out straight and sometimes quivering slightly. When the second found the first it too would enter this same stance. Quimby recorded that in one case a *Zapus* became imprisoned with a meadow mouse, *Microtus pennsylvanicus*. The *Zapus* attempted to defend itself and inflicted a severe gash on the upper lip of the meadow mouse, but the jumping mouse was killed in the process. These mice would be able to offer little resistance to a predator, and appear to protect themselves by remaining perfectly still. Neither Quimby (1951) nor Whitaker (1963) found any evidence that *Zapus* used burrows or runways extensively, other than the burrow leading directly to nests or hibernacula, although Eadie (1939), Whitaker (1963), and Sheldon (1934) have found *Zapus* occasionally using burrows.

Quimby (1951) and Whitaker (1963) reported that *Zapus* often washed their feet, faces, and especially their long tails. The tail was grasped in the forepaws, and passed completely through the mouth, whereas the hands and feet were washed by means of the forepaws.

Hamilton (1935) reported that the mice can and do dig. Captive mice dig in loose dirt by scooping it back under their bodies. The mice apparently forage mostly on the surface and in the herbaceous vegetation above the ground, but the fungal foods extensively eaten are probably obtained by scratching the ground (Whitaker, 1963).

Quimby (1951) described a caged mouse feeding on grass seeds. It sat on its haunches and fed by means of the front feet. First the fruiting head of the grass was cut off, then all parts were stripped beginning at one end. Only the seeds were eaten, but many of these dropped to the ground, and no effort was made to retrieve them. Similar observations were made by Whitaker (1963). Bailey (1926) found that *Zapus* would reach as high as it could on grass stems, bite them off and pull them to the ground, repeating the procedure until the head was reached and eaten. This process would result in a pile of pieces of grass stem, often with the rachis and glumes on top. Whitaker (1963) found evidence that the same procedure is used in New York at least in the case of timothy,

Phleum pratense, and that in some cases the mouse may climb the stem, cut off the head and bring this to the ground and then consume it.

Mice in captivity regularly drink water, but it is not known whether *Zapus* in the field drink or get their water from green vegetation or from dew, or both.

Zapus hudsonius was often seen during the daytime by Whitaker (1963), who initiated a trapping program during two 5-day periods to determine the daily activity periods of the species. Traps were checked just before and just after dawn and dusk, and at noon. Of 31 *Z. hudsonius*, 27 were taken at night, two at dusk, one in the morning, and one in the afternoon.

Summer nests of *Zapus* have not often been found. Sheldon (1938) described a nest on a hummock of grass and Hamilton (1943) recorded nests of young in open fields under planks. Quimby (1951) found a nest under an overhanging clump of sedge, one in the center of a rotten willow log, and one in a living but hollow red oak under the debris at ground level. Other nests were about 150 mm below ground level. Most of the nests were of grass, but one was a pile of wood pulp and oak and grass leaves in a hollow root, located about 45 mm from the end of a "mouse sized entrance." Quimby (1951) concluded that the "nest is generally located in a protected spot such as a hollow log, hollow tree, under some protecting object, or underground."

The common name of this mouse is a misnomer. Mice of the species do not normally progress by jumping; they more often move slowly through the grass or else take little hops of 1 to 6 inches (Quimby, 1951). They frequently crawl through the grass or under the grass, sometimes flattening their bodies to the ground and proceeding on all fours. When startled, however, a jumping mouse often will take several long leaps of up to a meter, then stop or remain motionless or proceed by means of shorter hops. A jumping mouse in full retreat progresses by means of .3 m hops. Quimby and Whitaker both felt that records of long leaps (over 1 or 1.3 m) are probably errors. Likely these records refer to *Napaeozapus*.

Zapus hudsonius is a good swimmer both on the surface and underwater as has been observed by several workers (Hamilton, 1935; Stone and Cram, 1910; Sheldon, 1938); Jones, 1950; Sutton, 1939; and Quimby, 1951).

Hamilton (1935) and Sheldon (1934) found that *Zapus hudsonius* was able to climb with ease over brush placed in its cage, and Whitaker (1963) found that it was able to climb grass stems.

HIBERNATION. *Zapus hudsonius* is one of the most profound of hibernators, and remains in hibernation as long or longer than most other mammals. Quimby (1951) found that eight of 19 mice entered hibernation between 17 September and 1 October, whereas the remainder had shown no sign of hibernating by this date. The average weight of the hibernating group was 26.44 g, and that of the nonhibernating group was 16.06 g. All of the early hibernating individuals were adults. Seven that had shown no tendency to hibernate by 1 October, had entered hibernation by 16 October. Their average weight was 23.44 just prior to hibernation, whereas the average weight of the four remaining mice was 19.42 g. In both groups of mice the greatest weight gains were during the 2-week period just prior to hibernation. The four remaining mice were removed from the cold room, but they entered hibernation in the heated room.

About 67% of a New York population studied disappeared during the winter, and the average weight of the individuals taken in spring was actually greater than those taken in autumn (Whitaker, 1963). Apparently the smaller animals perished during hibernation. A relatively small proportion of the population had accumulated extensive amounts of fat in the autumn. The animals that reach adult size and have adequate time to accumulate fat are the animals that survive hibernation. Fat production starts in central New York around 1 September, and continues until all animals have disappeared from the active population (by about 20 October). The animals accumulate fat in about 2 weeks, and immediately enter their hibernating quarters. This explains the small number of animals with fat among those caught in traps.

Whitaker (1963) found that nearly all animals had disappeared (presumably entered hibernation) by 20 October, at Ithaca, New York, but there are several later records as follows: 13 and 18 November (New York, Hamilton, 1935); 24 October (Minnesota, Bailey, 1923), and 25 October and 2 November (Washington, D. C.; Bailey, 1929), 26 October, 15 November (Pennsylvania, Richmond and Roslund, 1949);

and 22 October, 1 November (2), and 3 November (Whitaker, 1963).

Kile R. Barbehenn took a specimen of *Z. hudsonius* in an old apple orchard in Montgomery County, Maryland, on 11 February 1960, and Manville (1956) trapped one on 12 February 1955, in Michigan.

Zapus hudsonius apparently emerges from hibernation in the last week in April or the first week in May (Whitaker, 1963; Quimby, 1951; Hamilton, 1935; Bailey, 1929). Males generally precede females.

Several hibernation nests of *Zapus* have been found. Earlier records were summarized by Whitaker (1963). Most reports were of single jumping mice underground or under logs in nests of leaves or grass. Sometimes there was an entrance, sometimes not. Dilger (1948) reported two huddled close together in a layer of compacted wood ash. Linzey and Linzey (1968) found several hibernating individuals in a loose clay bank, each in a separate compartment lined with dry leaves, and approximately 0.5 m below ground level. Another was found 100 to 150 mm below a "clean road fill." Waters and Stockley (1965) found three dormant meadow jumping mice on 11 November 1962 during archaeological excavation on Nantucket Island. The three were in separate nests of bayberry leaves .30, .51, and .56 m below the surface, along with several unoccupied nests in the same area, a sandy knoll.

GENETICS. *Zapus hudsonius* has a diploid number of 72 chromosomes (Meylan, 1968).

REMARKS. The mite referred to as *Dermacarus hypudaei* above and by Whitaker and Mumford (1971) was described as *Dermacarus newyorkensis* by Fain (1969).

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Cryptotis parva. By John O. Whitaker, Jr.

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Cryptotis parva (Say, 1823) Least Shrew

- Sorex parvus* Say, 1823:163. Type locality west bank of Missouri River, approximately 2 mi. E Ft. Calhoun, formerly Engineer Cantonment, Washington Co. Nebraska.
- Sorex cinereus* Bachman, 1837:373. Type locality Goose Creek about 22 miles from Charleston, South Carolina.
- Brachysorex harlani* Duvernoy, 1842:40. Type locality New Harmony, Posey Co., Indiana.
- Blarina berlandieri* Baird, 1858:5. Type locality Matamoros, Tamaulipas, Mexico.
- Blarina exilipes* Baird, 1858:51. Type locality Washington, Mississippi.
- Blarina eximius* Baird, 1858:52. Type locality DeKalb County, Illinois, and St. Louis, Missouri.
- Sorex micrurus* Tomes, 1861:279. Type locality Coban, Alta Verapaz, Guatemala.
- Blarina floridana* Merriam, 1895:19. Type locality Chester Shoal, 11 mi N Cape Canaveral, Brevard Co., Florida.
- Blarina orophila* J. A. Allen, 1895:340. Type locality Volcán Irazú (= Irazu Range), Cartago, Costa Rica (see Goodwin, 1944:2).
- Blarina soricina* Merriam, 1895:22. Tlalpan, 10 mi. S Mexico, Distrito Federal, Mexico.
- Blarina tropicalis* Merriam, 1895:22. A renaming of *micrurus* Tomes, preoccupied.
- Blarina pergracilis* Elliot, 1903:149. Type locality Ocotlán, Jalisco, Mexico.
- Blarina olivaceus* J. A. Allen, 1908:669. Type locality San Rafael del Norte, Jinotega, Nicaragua.
- Cryptotis celatus* Goodwin, 1956:58. Type locality Las Cuevas, Santiago Lachiguiri, District of Tehuantepec, Oaxaca, Mexico.

CONTEXT AND CONTENT. Order Insectivora, Superfamily Soricoidea, Family Soricidae, Subfamily Soricinae. As presently understood, the genus contains about 13 living species. Eight species inhabit Middle America (Choate, 1970), and one of these, *Cryptotis parva*, has a wide range north of Mexico. Most of the species inhabit woodlands, but *Cryptotis parva* is frequently found in open fields. Choate (1970) revised the Middle American taxa and currently is working on the remainder of the genus. Currently nine subspecies are recognized, as listed below.

- C. p. parva* (Say, 1823:163), see above (*cinereus* Bachman, *exilipes* Baird, and *eximius* Baird are synonyms).
- C. p. harlani* (Duvernoy, 1842:40), see above.
- C. p. berlandieri* (Baird, 1858:53), see above (*pergracilis* Elliot a synonym).
- C. p. floridana* (Merriam, 1895:19), see above.
- C. p. orophila* (J. A. Allen, 1895:340), see above (*olivaceus* J. A. Allen a synonym).
- C. p. soricina* (Merriam, 1895:22), see above.
- C. p. tropicalis* (Merriam, 1895:21), see above (*micrurus* Tomes a synonym).
- C. p. pueblensis* Jackson, 1933:79. Type locality Huauchinango, Puebla, Mexico (*celatus* Goodwin a synonym).
- C. p. elasson* Bole and Moulthrop, 1942:97. Type locality Bettsville, Seneca Co., Ohio.

DIAGNOSIS. The genus *Cryptotis* includes small, short-tailed, brownish shrews with four unicuspid teeth on each side of the upper jaw (figures 1 and 2) and a total of 30 teeth. These are the only North American shrews with four unicuspid teeth. *Cryptotis parva*, ranging from 67 to 103 mm total length, 12 to 22 tail, and 9 to 13 hind foot, is small as compared to most other species in the genus. It may be distinguished from other Central American species by its relatively short tail (less than 45% of length of head and body), its lack of bulbous dentition such as occurs in *C. nigrescens*, its small front feet, its condylo-

basal length of 15.3 to 18.4 mm, and other characters given by Choate (1970).

GENERAL CHARACTERS. This small brownish colored shrew has a short tail, inconspicuous ears, minute black eyes, and a long pointed snout. The fur is fine, dense, short and almost velvety. The skull is small but broader and higher than in *Sorex*. The rostrum is short and the zygomatic arches are incomplete. Like most other North American shrews, the teeth have chestnut-colored cusps. There are four unicuspid teeth, but the fourth is tiny and hidden in lateral view (see figure 1).

Some average values for total, tail, hind foot, and condylobasal lengths of *C. parva* from various parts of its range follow: Costa Rica and Panama 84.7, —, 11.6, 16.3 (Choate, 1970); Oaxaca 89.3, —, 12.0, 17.1 (Choate, 1970); Rio Grande area of Texas and Mexico 80.3, —, 11.8, 15.7 (Choate, 1970); Texas 78.2, 17.3, 10.7, —, (Davis, 1941); Maryland 76.3, 15.2, 10, 15.2 (Paradiso, 1969); Indiana 74.3, 15.6, 10.0, —, for males and 77.2, 16.5, 10.5, —, for females (Mumford, 1969) and 77.1, 16.3, 11.2, —, (Lindsay, 1960); North Carolina 75, 16.4, 10.6, — (Hamilton, 1943); North Carolina and Tennessee 74.3, 18.4, 10, — for males and 74.0, 18.0, 10.0, — for females (Komarek and Komarek, 1938); and New Jersey 84.4, 20.4, 11.6, — (Connor, 1953).

DISTRIBUTION. The present distribution is shown in Figure 3 (from Hall and Kelson, 1959; modified using Choate, 1970; Jarrell, 1965; Packard and Judd, 1968; Packard and Garner, 1964). Fossil records indicate (see later) that related species previously occurred much farther west than living species of *Cryptotis*.



FIGURE 1. Lateral view (above) of anterior region of skull of *Cryptotis parva* showing large bicuspid incisor and first three unicuspid teeth (the fourth is hidden), and ventral view (below) showing all four unicuspid teeth. Photos by the author.



FIGURE 2. Dorsal, ventral, and lateral views of skull, and mandible of *Cryptotis parva* (AMNH 163851, a male from Gulf Hammock, Levy Co., Florida). Photographed by Arthur Singer, Department of Photography, American Museum of Natural History.

FOSSIL RECORD. Three extinct species of *Cryptotis* have been described. One is *C. adamsi* (Hibbard, 1953), from the late Pliocene of Meade County, Kansas, Rexroad formation, Rexroad fauna. This species also was reported from the mid-Pliocene Christmas Valley local fauna of Lack County, Oregon (Repenning, 1967), but Choate (1970) questioned this record. The others are *Cryptotis meadensis* Hibbard, 1953, same data; and *C. kansasensis* Hibbard, 1958, from the early Pleistocene of Kingman County, Kansas. *C. adamsi* has five unicuspid, which indicates close relationship with and probable origin from *Blarina* (Choate, 1970).

A closely related fossil genus, *Paracryptotis*, contains two species, *P. rex* Hibbard, 1950, from the late Pliocene of Meade County, Kansas, Rexroad formation, Rexroad fauna; and *P. gidleyi* (Gazin, 1933) from the late Pliocene, Hagerman Lake beds, near Hagerman, Idaho. *P. rex* was also recorded from the mid-Pliocene Rome fauna of Oregon (Repenning, 1967); *P. gidleyi* is known only from the type locality.

Cryptotis parva has been reported from Pleistocene deposits of Robinson Cave, Overton Co., Tennessee (Guilday *et al.*, 1969), from Crankshaft Cave, Jefferson Co., Missouri (Parmalee *et al.*, 1969), and from Nichol's Hammock, 0.7 mi N Princeton, Dade Co., Florida (Hirschfeld, 1968). All these localities are within the present range of *C. parva*.

FORM. The homologies of the "unicuspid" of shrews are quite uncertain. Choate (1970) reviewed the literature and elected to retain the descriptive term unicuspid for the small teeth behind the large incisor. The tooth formula for Recent *Cryptotis* is thus (Choate, 1970): i 1/1, u 4/1, p 1/1, m 3/3, total 30. The milk teeth are shed in *Cryptotis* prior to birth. Choate found no evidence of secondary sexual differences.

The male reproductive tract and penis of *Cryptotis parva*

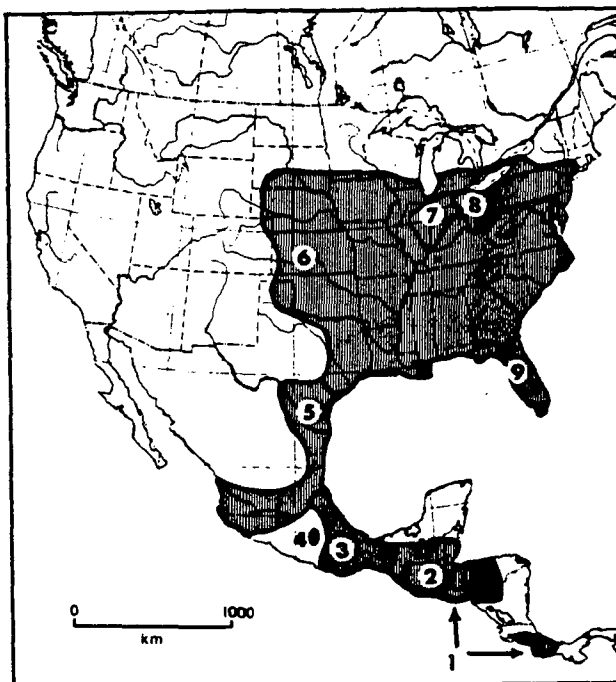


FIGURE 3. Geographic distribution of *Cryptotis parva* and its subspecies, as follows: 1, *C. p. orophila*; 2, *C. p. tropicalis*; 3, *C. p. pueblensis*; 4, *C. p. soricina*; 5, *C. p. berlandiera*; 6, *C. p. parva*; 7, *C. p. harlani*; 8, *C. p. elasson*; 9, *C. p. floridana*.

were figured by Martin (1967). The glans penis of *Cryptotis* "is rather bulbous, short and heavily sulcated," compared to *Blarina*. The prostate glands are round, flattened structures surrounding the anterior portion of the urinary vesicle, whereas the bulbo-urethral glands are attached to the penile crura. The testes are posterior and dorsal to the penis, and in breeding males occupy "pouchlike extensions of the caudal end of the abdominal cavity" at the base of the tail.

Dryden and Conaway (1970) found "anal tonsils," two pairs of lateral lymphoid masses (but none ventrally) in 10 adult *Cryptotis* examined. These masses "were associated with lateral folds of the anal canal, but some masses were not deeply indented by folds. When the fold did extend into the lymphoid area, the anal epithelium was unmodified." The tonsils vary structurally between groups of insectivores, and some lack them entirely.

Hamilton (1944) discussed molting in a captive individual; it commenced on 17 September, starting on the face and progressing rapidly over the head and shoulders. The summer pelage was being replaced by the winter pelage, which is darker because it lacks the sepia-tipped hairs. Concurrently, pea-sized areas on the rump and mid-belly began shedding. These areas remained well defined for several days, then the lines of demarcation were "lost in the general renewal of fur." Hamilton further reported that he took individuals in southern Georgia and Florida that were molting, but that there was little seasonal color change, at least in south Florida. *Cryptotis* apparently molts irrespective of season although molt is more common in late spring and late autumn (Hamilton, 1944; Pfeiffer and Gass, 1963a). Choate (1970) stated that the molt from juvenal or adult summer pelage to adult winter pelage begins on the rump or venter, and that it usually progresses more rapidly below than above, often forming a saddle across the back. The molt progresses anteriorly, the head being the last area to molt. Molt from juvenal to summer pelage may start on the head and progress posteriorly, or in reverse. Spring molting usually begins anteriorly and progresses posteriorly. Old adults however, may molt at any time of year and may cease molt abruptly, forming patterns including old and new hair.

Elder (1960) reported a white specimen with pink eyes taken on 24 January 1953 in Missouri, and Choate (1970) reported an individual from Texas (U.S. National Museum 347435) that "lacks pigment in the hairs except in the basal gray region, which appears normal." Other morphological abnormalities found by Choate in three specimens were the

absence of one unicuspid, the absence of a pair of upper unicuspids, and "enormously robust parastyles on both second upper molars, causing those teeth to be markedly distorted."

FUNCTION. Sealander (1964) obtained blood values for two adult females from Arkansas: one, a pregnant female weighing 4.3 g, yielded hemoglobin concentration 1.27 mg/10 mm³ of blood, corpuscles made up 43.9% of blood volume, mean concentration of hemoglobin in the corpuscles was 29.0%; in another female, nonpregnant and weighing 2.6 g, corresponding values were 1.90, 57.4, and 33.1. In the second individual the oxygen capacity of the blood was 26% by volume. The erythrocyte diameter in the two averaged 6.3 μ m (5.8 to 6.4).

Digestion is rapid. Pieces of chiton and hair traversed the entire digestive tract in periods of 95 to 114 minutes (Hamilton, 1944). The consistency of fecal material changed within 2 hours of a change in diet (Davis and Joeris, 1945).

Other shrews have high metabolic rates and the smallest species appear to be near the theoretically lowest limit of mammalian size (Redmond and Layne, 1958). Data from seven shrews of both sexes, weighing from 4.1 to 5.0 g, were compared with the same data from white mice, white rats, and rabbits, and decreased metabolic rates (as measured by volume of oxygen consumed per unit of dry weight of tissue per hour) were obtained with increased size of the animal. However, the rate for liver was lower for *Cryptotis* than for the mouse or rat, and higher than for the rabbit. The rate for the kidney, was much higher in the shrew than in the other species. For lung the rate was approximately equal for shrew, rabbit, and rat, but slightly higher for mouse; for diaphragm it was about equal for shrew and mouse, but lower in rat. Because of its small size, one would expect the values for the shrew to be above those for the other species in each case. The authors stated that the striking difference "would seem to indicate that the high respiratory rates exhibited by shrews must be due to 'extrinsic' factors such as nervous stimulation, hormone levels, or concentrations of metabolites in blood or tissue fluids rather than to generally higher 'inherent' rates of tissue metabolism." The authors suggested two alternative explanations, both admittedly speculative: 1) the observed low rates for the tissues may reflect the relatively primitive status of insectivores among mammals, with the high rate being maintained through evolutionary development of controlling mechanisms to compensate for heat loss or other physiological factors; 2) the low rates in the three tissues could themselves be an energy conserving measure, through lowered metabolic rates during inactive periods. This is supported by observations that shrews sleep soundly (Christian, 1950) and awake slowly and sluggishly, with trembling or convulsive movements suggestive of an animal waking from hibernation (Layne and Redmond, 1959). Determinations of respiratory rates of sleeping shrews would be desirable. Moore (1943) timed the breathing of a *Cryptotis* at rest at about 70 breaths per minute.

The mean of 32 rectal temperatures, taken between the hours of 0900 and 2400 from four adult shrews, two females and two males weighing 5.1 to 6.4 g, over an 8-day period was 35.0 \pm 0.3 $^{\circ}$ C, with a range of 31.9 to 39.1 $^{\circ}$ C (Layne and Redmond, 1959). Temperatures of individual shrews were relatively constant from day to day. One which was docile and easily captured averaged 33.6 $^{\circ}$ C, while the other three, which were highly excitable and struggled to avoid capture, averaged 35.6, 35.4, and 35.5. The mean of 16 measurements taken between 1600 and 2400 was 35.5 $^{\circ}$ C, while the mean of 16 taken between 0900 and 1230 was 34.6 $^{\circ}$ C. This difference was associated with slightly more activity in the evening than during the morning. Layne and Redmond (1959) recorded skin temperatures for sleeping shrews on four occasions. They held a rapidly equilibrating thermometer firmly against the shrew's abdomen in such a way that the bulb was practically surrounded by tissue. Ambient temperatures averaged about 26.0 $^{\circ}$ C. The recorded temperatures were 34.5, 34.8, 35.4, and 35.5 $^{\circ}$ C. From these measurements the authors conclude that "the possibility that a pronounced depression of temperature occurs during sleep . . . does seem unlikely." Three oral temperatures were obtained on recently born *Cryptotis* weighing 0.33 and 0.37 g the day of, and the day following, their births. The readings were 31.4, 31.7, and 31.9 $^{\circ}$ C, or about 3 degrees below the mean body temperatures of adults. The temperature data support Pearson's (1948) contention that shrews do not have significantly higher body temperatures than mice, even though they have much higher metabolic rates. Layne and Redmond (*op. cit.*) suggested that shrews may have greater metabolic lability than do other nonhibernating small mammals.

The fact that near normal temperatures are maintained by shrews while asleep may be indicative of "internal heat-regulating mechanisms to control heat lost to a point at which a substantial reduction of metabolism is possible. Behavioral phenomena such as communal nesting and huddling may also play a role in this connection."

Barrett (1969) used a metabolic cage to measure food intake and fecal and urine production in an adult female. There was approximately 2660 cc of space in the cage, and water supply was unrestricted. The shrew showed no change in weight throughout the study period of 7 weeks; it averaged 3.6 \pm 0.2 g. The shrew was fed only baby mice. Caloric values per gram of dry weight were: shrew feces 3.35 kcal; urine 1.88 kcal; baby mice 6.20 kcal (or 1.24 kcal/g of live weight). The mice were 20.26% of their total weight when dry. 6.61% of dry weight was fat; one value of 9.01 kcal/g of fat was obtained. The mean ingestion was 4.57 \pm 1.62 st. dev. kcal/day, or 3.83 \pm 1.31 g wet weight of food per day. Hence, the shrew consumed an average amount of food per day of slightly more than its own body weight. Springer (1937) had found a 5.0-g shrew to ingest 5.5 g wet weight of food per day, and Hamilton (1944) found a 4.7-g shrew to use 3.6 g per day; ingestion coefficients of these two were thus 1.1 and 0.8, respectively. Barrett found the energy lost as feces was 0.47 kcal/day and as urine 0.11 kcal/day. Respiration was estimated from these values to be 4.17 kcal/day or 1.16 kcal/g/day. The assimilation efficiency [(ingested energy minus fecal energy) \cdot 100/ingested energy] was 90.1.

Pfeiffer and Gass (1963b) found that oxygen consumption in a 6.36-g adult male nearly doubled from a basal rate of 7.0 cc/g/hr to 13.2 cc/g/hr during vigorous activity.

ONTOGENY AND REPRODUCTION. Hamilton (1944) described a newborn young. Its weight was 0.32 g, total length 22 mm, tail 3 mm, and hind foot 2.5 mm. Vibrissae were present, but small. Claws were small but distinct. Even when stained with alizarin no developing teeth could be seen in either jaw. The skull was 7.4 mm long and the dentary was 4 mm long. The forelimbs were better developed than the hind limbs. Conaway (1958) gave the following details concerning development: there was little change in appearance during the first 2 days, but by day 3 the dorsum began to darken and crawling movements occurred; on day 4 pigmentation was seen in the nose and chin, and the dorsum had become dark by day 5; hair was visible on day 6 and had become prominent on the side glands by day 7; by day 14 the eyes had opened, the young were fully haired and appeared as adults except for the small size and the silvery immature pelage. The weight increase through 30 days was figured. The birthweight was about 0.3 g (two individuals) and on days 1 to 5, respectively, weights were about 0.5 (two), 0.6 (three), 0.7 to 0.9 (three), 0.9 to 1.6 (four), and 1.0 to 1.8 (six). Corresponding values on days 10, 15, 20, and 25 were 2.3 to 2.7 (three), 3.1 (one), 3.7 (one), and 3.7 to 4.6 (five). By about 30 days the weight had leveled off presumably at the adult level. Hamilton (1943) stated that weaning did not occur until nearly day 21, and Conaway (1958) found that nursing continued until day 21 or 22. Young *Cryptotis* followed close behind the mother until day 20 to 23, but without attaching to her (Gould, 1969). Gould also stated that the ears opened on days 10 or 11.

Relatively little is known about reproduction in this species. Hamilton (1944) stated that breeding probably is from March to November in the northern parts of its range, but that in Florida breeding may extend throughout the year. Choate (1970) indicated that breeding may occur throughout the year in Middle America, at least at certain elevations and altitudes, but stated that "the peak of reproduction occurs between the vernal equinox and autumnal equinox." He found young in every month but March and May. Published records and personal observations of embryo counts range from two to seven, with a mean of 4.9, and the numbers of young in 16 litters vary from three to seven, with a mean of 4.5 (Brimley, 1923; Broadbooks, 1952; Choate, 1970; Conaway, 1958; Connor, 1953; Davis and Joeris, 1945; Hamilton, 1934, 1944; Kilham, 1954; Pournelle, 1950; and Welter and Sollberger, 1959). In addition, I examined one female shrew taken in Indiana on 27 June 1965, which appeared to have three placentae but no embryos in each uterine horn, indicating recent partus. Histological examination by R. A. Smith confirmed this interpretation. In addition, in Indiana, no embryos or placental scars were found in 56 females taken between October 18 and March 14. Numbers each month were 10, 24, six, 11, one, and four. Gottschang (1965) found one nursing female in Ohio on 4 November, and a male in breeding condition was taken

on 20 March, but none of 37 others examined from November 1962 through March 1963 showed evidence of breeding. Layne (1958a) took one female on October 30 that had enlarged mammary glands, indicating a recent litter, but she was no longer lactating. Davis and Joeris (1945) observed no evidence of reproduction in individuals taken from November to February in Texas.

Conaway's (1958) observations of copulation on seven occasions were similar to Pearson's (1944) for *Blarina*. Copulation occurred on 2 days in two instances, and on 1 day in the remainder. Gestation, counting from the last mating, lasted 21 to 23 days for each of five litters produced in captivity. Birth was never observed, but occurred in late afternoon. Postpartum estrus occurred in one female of three that were caged with males after partus. In one female, partus (five young) occurred on 3 March, copulation occurred on 3 March, and a litter of four was produced on 24 March. One litter was in a cage with six adults including both sexes and all young died of starvation in 5 days. Conaway concluded that disturbance caused by the excess adults prevented the young from nursing. The nest and young of another litter produced in a cage with four adults were intentionally scattered. All four adults immediately ran about carrying young from place to place in the cage. Sometimes two adults picked up the same individual, then tugging occurred until finally possession was gained by one of the adults. Finally all young were moved to the site of the old nest, and the adults reassembled the nest. The litter survived. Cooper (1960) also reported that after a female *Cryptotis parva* had been separated from her young, she "picked one after another up in her mouth and carried them frantically around the box for as long as 20 to 25 seconds each." Before long she had gathered them together, under a section of limb.

ECOLOGY. In general, *Cryptotis parva* inhabits grassy, weedy, and brushy fields, at least in the northern parts of its range. (Hamilton, 1934; Lindsay, 1960; Gottschang, 1965; Howell, 1954; Davis and Joeris, 1945; Choate, 1970; Layne, 1958a; Mumford, 1969; Paradiso, 1969; Komarek and Komarek, 1938). Lyon (1925), however, took one individual in oak-maple woods near a clearing in Porter County, Indiana. Mumford (1969) stated that woods are evidently unsuitable. He reported that one was found dead at the bottom of a ravine in deciduous woods in Indiana, but that a predator could have dropped it there. I have taken approximately 150 *Cryptotis* from Indiana, all from field areas, none from woods. Perhaps in the south *Cryptotis* is more apt to use woodland habitats, for Smith (1938) found a nest in a cabbage palm forest with an understory of waxmyrtle (*Myrica cerifera*), and Layne (1968) took ten, one in pine-oak woodland, six in level pine-lands, one in wetlands, and two in oldfields. Davis and Joeris (1945) took one from woodland in Texas. Choate (1970) reported them as sometimes occurring in "scrubby live oak, pine-oak, dense humid tropical forests, and in cloud forests" of Mexico and Central America. Komarek and Komarek (1938) took some from *Synaptomys* runways in an open grassy patch at the forest margin in the Smoky Mountains. Some authors have mentioned that the species uses runways of other small mammals (such as *Microtus*, *Sigmodon*, or *Oryzomys*) or makes tiny runways of its own (Lindsay, 1960; Gottschang, 1965; Davis and Joeris, 1945; Layne, 1958a; Hamilton, 1944). Many authors mentioned the dryness of fields where *Cryptotis* are taken, but Connor (1953) took five adults and a nest of four young in a brackish tidal meadow in New Jersey under the side of a shack that had fallen over. Choate (1970) stated that *Cryptotis*, primarily a grassland animal, may also occur in mesquite, yucca, agave, or grass covered llanos. However, in Middle America it is most often taken in numbers in "restricted damp or mesic areas, such as at the borders of streams or lakes, within otherwise relatively arid habitats." He reported them from many elevations, varying from 10 m along the Rio Grande and on the coastal plain, to 2950 m on the Sierra de Coalcoman in Michoacan. In the United States, 905 m is the highest elevation at which the species has been reported (Komarek and Komarek, 1938). Peterson (1936) reported one individual from a basement and one from a garage in New York.

Davis and Joeris (1945) felt that soil type was not important in determining whether *Cryptotis* was present or absent. They felt that the presence of dense herbaceous ground cover, especially of grasses (particularly *Andropogon*, *Cynodon* and *Sorghum halepense*), was important. Paradiso (1969) and Hamilton (1944) reported *C. parva* from the coastal marshes of Maryland and Virginia, respectively, and Paradiso reported that on the coastal island of Assateague it is found in all

habitats except the beach dunes and is one of the two most common small mammals (with *Microtus pennsylvanicus*).

There is a surprising amount of information concerning predation on this species, especially by owls, considering the relatively small number of individuals usually taken by mouse-trapping. This indicates that *Cryptotis* is often rather common but is less susceptible to trapping than are many other species of small mammals. Latham (1950) found 138 *Cryptotis parva* among items in 834 long-eared owl pellets from Pennsylvania. 108 among an unspecified number of barn owl pellets from Delaware and Pennsylvania, and one among prey items in 22 stomachs of housecats from Pennsylvania. Among the prey of barn owls in Ohio, Stupka (1931) and Phillips (1951) respectively, found 126 *Cryptotis* (among 8151 skulls) and 12 *Cryptotis* (or 1.41%). Davis (1938, 1940) found 171 (41% of the prey items, from an unknown number of pellets) and 102 of 152 prey in 25 barn owl pellets from Texas, only nine pellets lacked *Cryptotis* and one contained 20. Kirkpatrick and Conaway (1947) found 47 *Cryptotis* skulls in 145 barn owl pellets from Tippecanoe County, Indiana. Linsdale (1928) reported two *Cryptotis* were caught, but that the lower jaws of 99 individuals were found in short-eared owl pellets from one Missouri locality. Pearson and Pearson (1947) found 3 *Cryptotis* among 1152 mammals taken by Pennsylvania barn owls. Stickle and Stickle (1948) found *Cryptotis* remains in 3 of 118 pellets and Dalquest (1968) found a few *Cryptotis* in barn owl pellets from Texas. Linzey and Linzey (1971) reported a *Cryptotis* in the stomach of a screech owl from The Great Smoky Mountains. Mumford and Handley (1956) found the remains of 11 in owl pellets, and Wolfe and Rogers (1969) found 6 *Cryptotis* among 42 small mammals in owl pellets from Alabama. As of 1961 (Jackson, 1961), there were only three specimens of *Cryptotis* from Wisconsin, all from predators, two from the great horned owl (Nelson, 1934) and one from a red fox (Hanson, 1944). Cope (1949) found 27 *Cryptotis* in the digestive tract of one rough-legged hawk from Indiana; Crabb (1941) found *Cryptotis* remains in 11 of 330 spring scats of the spotted skunk, *Spilogale putorius*, from Iowa, but none in 75, 254, or 185 scats of this species collected in winter, summer, and autumn. McMurry (1945) found three least shrews in the stomach of a feral house cat from Oklahoma, the only remains of *C. parva* in 223 stomachs of this predator examined. Kilgore (1969) reported one *Cryptotis* among 488 scats and seven stomachs of swift foxes, *Vulpes velox*, from Oklahoma. Welter and Solleberger (1939) found a *Cryptotis* in the stomach of a hognose snake, *Heterodon platyrhinos*. Snyder (1929) found three young to have been regurgitated by a milksnake, *Lampropeltis dolia triangularis*. He concluded they had been recently swallowed, because one survived. Hunt (1951) found a young *Cryptotis* in the stomach of *Lampropeltis calligastor*, and Hamilton (1934) reported a dog digging one from an underground nest in New York. Cooper (1960) reported that a coastal plain milksnake, *Lampropeltis dolia temporalis*, would not eat a *Cryptotis*, although it would eat young mice the same size.

Layne (1968) looked for the nematode, *Capillaria hepatica*, in 10 *Cryptotis* from Florida but found none, and Solomon and Warner (1969) found a *Cryptotis parva* from Virginia negative for *Trichinella spiralis*. The following species of mites have been reported from *C. parva*; *Orycteropus soricis* (Rupes and Whitaker, 1968; Whitaker and Wilson, 1968; Whitaker and Mumford, 1972); *Dermacarus hypudaei* (Whitaker and Mumford, 1972); *Androlaelaps jahrenholzi* (Strandtmann, 1949; Whitaker and Wilson, 1968; Whitaker and Mumford, 1972); *Eulaelaps stabularis* (Jameson, 1947); *Haemogamasus harperi* (Keegan, 1951); *H. liponyssoides* (Whitaker and Wilson, 1968; Whitaker and Mumford, 1972); *Hirstionyssus talpae* (Drummond, 1957; Herrin, 1970; Jameson, 1947; Whitaker and Mumford, 1972); *Myonyssus jamesoni* (Whitaker and Wilson, 1968; Whitaker and Mumford, 1972). *Blarinobia cryptotis* (McDaniel, 1967; Whitaker and Mumford, 1972), and *Protomyobia claparedei* (Ewing, 1938; McDaniel, 1967; Whitaker and Wilson, 1968; Whitaker and Mumford, 1972). Whitaker and Corthum (1967) and Whitaker and Mumford (1972) reported four species of fleas from the least shrew, *Corrodopsylla hamiltoni*, *Ctenophthalmus pseudagyrtis*, *Peromyscopsylla scotti*, and *Epitedia wenmanni*, with only the first two being of regular occurrence. Traub (1944) and Jameson (1947) reported *Corrodopsylla hamiltoni* from *Cryptotis* from New York and Kansas. Wilson (1961) reported *Ctenophthalmus pseudagyrtis* on *C. parva* from Indiana. Layne (1958b) reported *Corrodopsylla curvata* on *Cryptotis parva* from Illinois, and Hamilton reported *Doratopsylla blarinae* on this species from New York. The chigger, *Neotrombicula sylvilagi* (Brennan

and Wharton) was found on *Cryptotis parva* from Kansas by Kardos (1954). Loomis (1956) reported the following species of chiggers from *C. parva*; *Eutrombicula alfreddugesi*, *E. lipovskiyana*, *Neotrombicula sylvilagi*, *Euschongastia jonesi*, and *Pseudochongastia janneri*.

The most regularly occurring parasites seem to be: *Orycterxenus soricis* (actually a hypopial or transport form), *Androlaelaps jahrenholzi*, *Protomyobia claparedi*, *Hirstionyssus talpac*, *Blarinobia cryptotis*, *Ctenophthalmus pseudagyrtis*, and *Corrodopsylla hamiltoni*.

Verts and Barr (1960) found six individuals of this shrew from Illinois negative for rabies.

Hamilton (1944) examined the stomach contents of 12 least shrews and reported fragments of insects, earthworms, centipedes, molluscs, and a small amount of vegetation. Included among the insects were Scarabaeidae, Carabidae, and beetle larvae. He reported that on Chincoteague Island, Virginia, *Cryptotis* was apparently eating snails, *Melampus lineatus* Say. Evermann and Butler (1894) reported that the species was referred to by an Indiana native as the "bee mole" because of its habit of entering bee hives and feeding on the brood. Mohr (1935) examining the stomach of one *Cryptotis* from Illinois found it had eaten 50% chinch bugs (five individuals) and 50% spider (one individual). Hatt (1938) found that when a medium sized *Rana pipiens* was put in with a captive shrew, the shrew attacked the knees of the frog, immobilized it by finally severing the patellar tendons, and then ate it. Hatt also saw attempts at this behavior when three *Cryptotis* in a window well were chasing a frog. A baby housemouse, *Mus musculus*, was not touched. The shrew would also bite the joints of the largest legs of grasshoppers and crickets before eating them. Welter and Sollberger (1959) reported that *Cryptotis* ate crickets in captivity by giving several bites to the head; six were killed this way and used later. Chamberlain (1929) stated that when a captive shrew was offered a large grub, the shrew pounced on it, bit its head in several places, then commenced feeding at the head.

Springer (1937) kept two captive *Cryptotis* from Florida. Each consumed between 3.5 and 8.1 g of food per 24-hour period (average of 5.5 g). In captivity they ate many kinds of invertebrates and also frogs and lizards. They drank frequently. *Blatta orientalis*, *Spirobolus* sp., and snails (*Planorbis* sp. and *Euglandina* sp.) were refused. The shrews would make a preliminary bite, then a series of scattered bites over the body of the prey, then would start feeding when movement became feeble. Lizards were seized by the tail until it came off; it was then eaten. Presumably the lizard could then escape. Moore (1943) observed *Cryptotis* kill grasshoppers by biting them in the head after creeping up to them, but in contrast, shrews would run up to crickets "like a football player after a fumbled ball" and bite them also in the head. They attacked a preying mantis in the same way, but otherwise attacked by running in and nipping at prey. Small and softer individuals of grasshoppers as well as crickets and softer arthropods were eaten in their entirety, whereas only the insides of larger grasshoppers were eaten. Shrews preferred crickets over grasshoppers and ate grasshoppers only after the crickets were gone. When excess insects were provided, they were taken into the burrow and stored there. Insects were carried in the jaws, or, in the case of larger individuals, the shrew would enter the burrow and afterwards pull in the prey. Hamilton (1934) recorded that a captive *Cryptotis*, which averaged 4.7 g in weight, consumed about 3.6 g of food per day. Stomachs of three shrews of this species from New York examined by him contained fragments of earthworms, adult beetles, and centipedes along with much finely chewed insect material. Layne (1958a) found earthworms, insects, and unidentified arthropods in three stomachs from shrews of this species from Illinois.

Whitaker and Mumford (1972) examined the stomachs of 109 least shrews from Indiana. The top five foods, listed in percentages of volume (percent frequencies in parentheses) were lepidopterous larvae 17.9 (29.4), earthworms 11.2 (15.6), spider 6.8 (11.0), internal organs of crickets and grasshoppers 6.6 (7.3), and coleopterous larvae 4.7 (7.3). Other foods found were unidentified insect (5.8% volume), Aphididae (3.8), Chilopoda (3.6), mast (3.5), snails and slugs (3.3), Gryllidae (3.2), unidentified Coleoptera (3.0), internal organs of coleopterous larvae (2.8), dipterous larvae (2.4), unidentified Hemiptera (2.2), Miridae (2.2), sowbug (1.9), unidentified Hymenoptera (1.8), Carabidae (1.7), unidentified Diptera (1.6), Scarabaeidae (1.2), unidentified seeds (1.2), Acrididae (1.1), Cicadellidae (1.0), *Endogone* (0.9), Membracidae (0.9), Formicidae (0.8), unidentified fungal spores (0.8), vegetation (0.5), *Setaria* seeds (0.4), Cantharidae (0.4), Vespidae (0.3),

scarabaeid larvae (0.2), muscoid fly (0.1), mites (0.1), and Enchytraeidae (trace). It appeared that under field conditions (as also seen in the laboratory by Moore, 1943) least shrews must often open the abdomens of larger crickets and grasshoppers and eat out the internal organs.

Practically nothing exists in the literature concerning populations or population dynamics of *C. parva*, presumably because the species is so difficult to trap in numbers using conventional techniques. Davis (1938, 1940) reported heavy concentrations on the basis of large numbers in barn owl pellets in Texas, as noted above. Kirkpatrick and Conaway (1947) took 22 shrews of this species in 92 trap-nights in Tippecanoe County, Indiana, along with 47 skulls in 145 barn owl pellets. These figures also suggest a high local population. Howell (1954) used a circular study area to determine populations of several species. He stated that the home range for *Cryptotis* was difficult to determine, but estimated it for one female at 0.57 acre (2800 m²), and for one male at 0.41 acre (1700 m²). He trapped individuals indicating a density of at least 1.73 per hectare, but estimated that about 4.95 per hectare actually were present. One indication of longevity is available. Pfeiffer and Gass (1963a) stated that one captive individual they kept from a nestling died at 21 months apparently of "old age."

BEHAVIOR. Several authors report this species to be somewhat colonial or at least social, inasmuch as they exhibit the unlikely characteristic for shrews of being able to exist together in numbers in the same nest. Jackson (1961) reported about 25 shrews of this species found in a single leaf nest under a log in April in Virginia. Connor (1953) found two females huddled together in plant remains under a horizontal section of wall in a brackish tidal meadow in New Jersey (an adult and four young were found in the same spot 2 weeks later), and he and Springer (1937) reported that captives huddled together in the laboratory. Hamilton (1934) reported five in a nest of rootlets and grass under a heavy rock slab, all huddled in a ball, and another instance of three in a nest of dry grass about 100 mm below the surface of the ground. Davis and Joeris (1945) found a nest in December in Texas occupied by 12 individuals, and also reported that captive individuals ate and slept together. McCarley (1959) found a *Cryptotis* nest under a log on a hillside in an open field with sparse vegetation on 7 January 1958, in Nacogdoches, Texas. The log was in contact with the ground throughout its length and the nest, in a 50 mm depression, was of leaves and grass. It measured about 100 by 150 mm, with no extensive runways leading from it, but adjacent to the nest was a pile of fecal droppings about 100 by 150 mm in diameter and 12 mm high, indicating that the nest probably had been in use for some time. The nest contained at least 31 individuals, and the next day contained six. McCarley hypothesized that this behavior functioned as a heat conservation measure. Smith (1938) found a nest with two individuals under a prostrate cabbage palm (*Sabal palmetto*) in a forest of cabbage palms with an understory of wax myrtle and scrubby live oaks. A tunnel ran the length of the log, a lateral tunnel led to the nest and another ran to the main tunnel about 0.6 m from the nest. The nest was loosely constructed of panic grass (*Panicum mutabile*) and was about 125 mm in diameter. The leaves were loosely piled in a globular mass that also included shed snake skin. Runways opened to the surface and became paths, or lead to shallow runways under humus. Snyder (1929) found two individuals in a nest of leaves and dried grass under driftwood on an open sandy beach. The nest had entrances at top and bottom, and a short tunnel led to the bottom entrance. Lindsay (1960) found two shrews in a nest under a board. The nest was in a depression, was about 100 mm in diameter and 70 mm deep, was of dry grasses, and had entrances at the top and bottom. A short tunnel in the soil led to the bottom entrance. Broadbooks (1952) found a nest containing three young and both parents in Texas under a large piece of sheet metal. The nest was a loose pile of willow leaves, 180 mm in diameter and 50 mm high in a shallow depression. Two runways connected with the nest, one from the bottom and one from the side. There was a toilet area about 75 mm in diameter at the edge of the nest.

Gottschang (1965) reported runways about the "diameter of a lead pencil." Paradiso (1969) stated that *Cryptotis* will use the burrows of other mammals but may also make its own, which are difficult to identify because of similarity to those of certain insects. *Cryptotis* digs by rooting about with its snout, and using the forefeet and sometimes the hind feet for dirt removal (Chamberlain, 1929); Davis and Joeris (1945) stated that the front feet are used for digging, and recorded

two shrews cooperating in building a burrow. One did most of the digging, the other removed dirt and packed the tunnel walls with most of it, although a little was scattered near the entrance. In about 2 hours of continuous work the two formed a burrow 0.6 m long and with four openings. These captive shrews burrowed through the surface soil in the manner of moles, pushing up a tiny ridge of soil as they went. Moore (1943) measured the burrow produced by a captive as 13 mm high and 18 mm wide.

A female *Cryptotis* (Conaway, 1958) was aggressive in that she attempted to bite whenever her young were handled. She carried them back to the nest if placed outside until after they were 18 days old, when they were first permitted to leave the nest. A litter born to a captive female was killed by the female (Broadbooks, 1952).

Davis and Joeris (1945) found *Cryptotis* to be cleanly, "washing and combing" its fur with the front feet. Special parts of the cage were used for defecation, and the nest was kept clean. Moore (1943) stated that feces and urine were extruded at the same time, taking but an instant, but accompanied by a contortion, seemingly a peristalsis of the whole body.

Hamilton (1934, 1944) and Davis and Joeris (1945) stated that *Cryptotis* is active at all hours, but more active at night. Broadbooks (1952) found a captive female to scurry about rapidly, often holding her nose in the air, sniffing and quivering her vibrissae. Hamilton (1944) and Jackson (1961) stated that individual *Cryptotis* will sleep for a considerable period when well fed, with "head, feet, and tail curled under its belly." Broadbooks found the species to be a good swimmer. In water its body was so high that it nearly seemed to be running on the surface.

Hamilton (1944) did not think sight and smell were of great importance to this species, nor that hearing was acute, unless for supersonic sounds. Moore (1943) felt that *Cryptotis* depended little on sight, more on hearing, yet mostly on smell. Springer (1937) found the species to produce odor detectable to 3 m, only at times. Cooper (1960) also stated that a female "exuded a characteristic musky smell." Springer (1937) found the species to make "flicker-like" calls, which were not excessively high and thin, and could be heard to about 0.5 m, and Moore (1943) reported that individuals often emitted tiny "bird-like chirpings."

Gould (1969) studied sound production and communication in *Cryptotis*. Baby *Cryptotis* emitted clicks when removed from their mothers at 9 days of age and "twittered" when a dispersed group was put back into the nest with the mother. Gould described several calls in adult *Cryptotis* including low intensity "clicks," "puts," and "twitters," but the clicks were the prominent calls. These calls often are used when shrews are alone and exploring unfamiliar surroundings. Sometimes forward and upward body extensions are associated with the calls. The "put" rate is similar to the "sniffing" rate, hence Gould suggested that this call is simply an accoustical result of intense sniffing. Single chirps are sometimes given during excretion. Twittering had developed by 10 days of age, and possibly earlier. The clicks apparently are identical to those of infant shrews and are produced by males during courtship as well as during exploration. When the response of the female has begun to shift from aggressive to slightly receptive, the male may sit close to her with his snout alongside hers and their vibrissae in contact. One male in this situation emitted 13 clicks in five seconds. Clicks are also emitted when the forefeet are used to wash the mouth, when investigation of a small object is occurring, or when the snout is extended over the edge of an object. Females emit single and repeated clicks of medium intensity when receptive, and a medium intensity ultrasonic train of pulses (50 to 420 ms, mean of 12 pulses 162 ms) was produced by shrews of either sex during intense exploration. Gould felt it was probably used for echolocation. High intensity sounds consisted of buzzes and usually were produced during close encounters between two individuals, especially by unreceptive females encountering males.

No fights were observed during the many encounters studied by Gould between two shrews of this species. Springer (1937) likewise found no fighting, even when two shrews were feeding from the same piece of food. They occupied the same nest in apparent harmony.

For information on nests of *Cryptotis* containing two or more adults see above. Many of those nests were in relatively sparsely vegetated situations under some flat object such as rocks, boards, or sheet metal. In two cases there was a fecal pile near the nest. Reports of other nests are as follows: nest

of dried grass under a flat rock in Kentucky (Welter and Sillberger, 1939); nest and runway system in dense *Berimuda* grass, under a piece of tin about 0.6 m square—the nest about 13 mm deeper than the burrows and 75 mm in diameter, and its sides and bottom lined with grass (Hunt, 1951); nest under a plank in a cow pasture in dry earth and sparse vegetation, in a damp depression, and containing pieces of grass and leaves. Another nest 50 mm in diameter and of the same material was under a fence post in a closely cropped field (Kilham, 1954). A nest of shredded grass, smaller than a baseball, flattened above (Hamilton, 1944), and thought to be that of *Cryptotis* was under a marsh elder (*Iva frutescens*). A nest under a log in Texas was of shredded corn husks (Jackson, 1961). Another nest was in a leaf filled hollow under a board on an earthen bank (Cooper, 1960).

Davis and Joeris (1945) found three burrows occupied by *Cryptotis*. One appeared to be essentially a crack in clay soil, but extended about 200 mm below the surface and ended in a nest; one, slightly less than 25 mm in diameter and 250 mm long, was in sandy loam and apparently was dug by the shrew. It reached 200 mm below the surface and terminated in a nest. The third was at least 1.5 m long, reached to 200 mm below the surface, and had a short side branch leading to a nest chamber. Davis (1944) dug a *Cryptotis* out of a sand bank.

GENETICS. No information was found on genetics of this species.

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Sylvilagus nuttallii. By Joseph A. Chapman

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Sylvilagus nuttallii (Bachman, 1837)
Nuttall's or Mountain Cottontail

Lepus nuttallii Bachman, 1837:345. Type locality west of the Rocky Mountains in the Columbia and Shoshonee River drainages (later fixed as the mouth of the Malheur River, eastern Oregon, by Nelson, 1909).

Lepus artemesia Bachman, 1839:94. Type locality Fort Walla-Walla, Washington.

Sylvilagus (*Sylvilagus*) *nuttallii* Lyon, 1904:336. First use of name combination.

CONTEXT AND CONTENT. Order Lagomorpha, Family Leporidae, Genus *Sylvilagus*, Subgenus *Sylvilagus*. There are about 14 recognized living species of *Sylvilagus* and three recognized subspecies of *S. nuttallii* (Hall, 1951:161-162; Hall and Kelson, 1959:264-265) as follows:

- S. n. nuttallii* (Bachman, 1837:345). See above (*artemesia* Bachman, and *grangeri* Lyon are synonyms).
- S. n. pinetis* (J. A. Allen, 1894:348). Type locality White Mountains south of Mount Ord, Apache Co., Arizona (Warren, 1942:270).
- S. n. grangeri* (J. A. Allen, 1895:264). Type locality Hill City, Black Hills, Custer Co., South Dakota (*perplicatus* Elliot, 1903, a synonym).

DIAGNOSIS. Size is relatively large for the genus. Hind legs are long; the feet are densely covered with long hair. Ears are rounded at tips and relatively short; inner surfaces are noticeably haired; tympanic bulla are medium in size. Vibrissae are never all black, some are white or partly white. Tail is large, grizzled and dark above, white beneath. Rostrum is quite long. Supraorbital processes are small and have abruptly pointed anterior projections. Postorbital processes are long and slender. Brain case is quite rounded. Palatal bridge is of medium length and usually without a posterior median spine. Molariform teeth are quite large; the first upper molariform tooth possesses three re-entrant angles, and the posterior halves of the second through fourth lower molariform teeth possess lateral diameters rarely equal to more than half the lateral diameters of the anterior halves. The enamel ridge separating the molariform teeth into anterior and posterior sections is strongly crenulated along the median two-thirds (modified from Orr, 1940; Hall, 1951). The skull is illustrated in Figure 1.

GENERAL CHARACTERISTICS. Descriptions are in Nelson (1909:199-211), Orr (1940:98-103), Hall (1951:161), and Hall and Kelson (1959:264). Females are slightly less than 4% larger than males (Orr, 1940). The dental formula is $i\ 2/1, p\ 3/2, m\ 3/3$, a total of 28.

Some external measurements (in mm) for *S. n. nuttallii* males are: total length, 352.4, 338 to 371; length of tail, 43.7, 30 to 54; length of hind foot, 94.6, 87 to 110. Corresponding measurements for females are: 372.0, 345 to 390; 49.6, 36 to 54; 94.3, 90 to 101 (Orr, 1940). Weight of adult males averaged 719.9g, 628.5 to 830, and adult females averaged 790.3g, 690 to 871 (Orr, 1940).

Cranial measurements (in mm) of adult *S. n. nuttallii* males are: basilar length, 49.6, 48.2 to 50.7; zygomatic breadth, 32.8, 30.7 to 33.5; postorbital constriction, 11.1, 10.3 to 11.8; length of nasals, 28.9, 24.7 to 29.7; width of nasals, 13.6, 12.1 to 15.0; length of molariform series, 12.4, 12.0 to 12.9; diameter of external auditory meatus, 4.9, 4.7 to 5.4; breadth of braincase, 22.0, 20.9 to 22.6; length of palatal bridge, 5.6, 5.1 to 5.9. Corresponding measurements for females are: 49.5, 48.1 to 51.7; 33.0, 32.1 to 33.6; 11.4, 10.8 to 11.8; 28.7, 27.7 to 30.9; 13.6, 12.8 to 14.5; 12.5, 12.2 to 12.6; 4.8, 4.1 to 5.4; 22.3, 21.8 to 22.9; 5.6, 5.3 to 6.0 (Orr, 1940). Additional data on measurements may be found in Nelson

(1909), Orr (1940), Hall (1951), Hall and Kelson (1959), and Long (1965).

DISTRIBUTION. The species is confined to the intermountain area of North America. It ranges from just above the Canadian border south to Arizona and New Mexico, and from the foothills of the eastern slopes of the Rocky Mountains west to the eastern slopes of the Cascade-Sierra Nevada Range (figure 2). According to Hall (1951:161): "In the northern part of its range *S. nuttallii* occurs principally in the sagebrush areas but it occurs also in the timbered areas in the southern part of its range." Cowan and Hatter (1940) noted a northward extension of the species into southern British Columbia. In California, the species is found from 4500 feet (1372 m) to at least 10,500 feet (3200 m) (Orr, 1940). Genoways and Jones (1972) noted that *S. nuttallii* evidently has been replaced by *S. floridanus* "over much, if not all," of southwestern North Dakota in recent years.

FOSSIL RECORD. There are no fossil records of *S. nuttallii*. Dr. W. W. Dalquest (personal communication) reported that the earliest appearance of the genus known to him was the Broadwater local fauna, early Pleistocene, of Nebraska. He further pointed out that identification of Pleistocene *Sylvilagus* to species is difficult unless unusually good material is available.

FORM AND FUNCTION. There are four or five pairs of mammae: one pair pectoral, two or three pairs abdominal, and one pair inguinal (Dice, 1926). "An adult female taken May 24, 1929, is in very worn pelage, and the new coat is well started beneath the old worn hair. Two adults collected October 23 and 24, 1929, are in full winter pelage" (Borell and Ellis, 1934). Thus, a single annual molt is apparent in this species.

ONTOGENY AND REPRODUCTION. The nest of *S. nuttallii* is reported to be a cuplike cavity lined with fur and dried grass. The top of the nest is covered with fur, grass, and small sticks, probably placed there by the female (Orr, 1940). Cowan and Guiquet (1956) believed the nest is constructed in a burrow. Orr (1940) reported young that were able to move about at a weight of as little as 40.1 grams, but further pointed out that these young may have been scared from the nest prematurely. Young weighing about 75 grams apparently do move at least short distances from the nest because Orr (1940) reported small trails from a nest that probably were made by the young rabbits.

In Oregon, a fetal sex ratio of 1 male to 1.05 females was found; the adult sex ratio was 1 male to 1.18 females (Powers and Verts, 1971).

In northeastern California, Orr (1940) believed that the breeding season began about April and ended in July. A female rabbit collected in Nevada on 24 May 1924 was suckling young (Borell and Ellis, 1934). The breeding season in Oregon lasted from 22 February to 30 July (Powers and Verts, 1971); most females there produce four litters per year but some produce five. However, Orr (1940) believed that in California the number of litters produced per year did not exceed two. The gestation period is 28 to 30 days (Cowan and Guiquet, 1956).

In California and Nevada, Orr (1940) reported the mean litter size to be 6.1 (range 4 to 8). Hall (1946) and Borell and Ellis (1934) reported a mean litter size of 5.0 (range 4 to 6) for Nevada. Davis (1939) reported a rabbit that contained six embryos. Dice (1926) reported a mean litter size of 4.7 (range 4 to 5) for three rabbits collected in Washington and Oregon. Cowan and Guiquet (1956) reported a mean litter size of 2.0 for British Columbia. An average of 4.3 (range 1 to 6) viable embryos per pregnant female examined in Oregon was reported by Powers and Verts (1971). Turner (1974) recorded

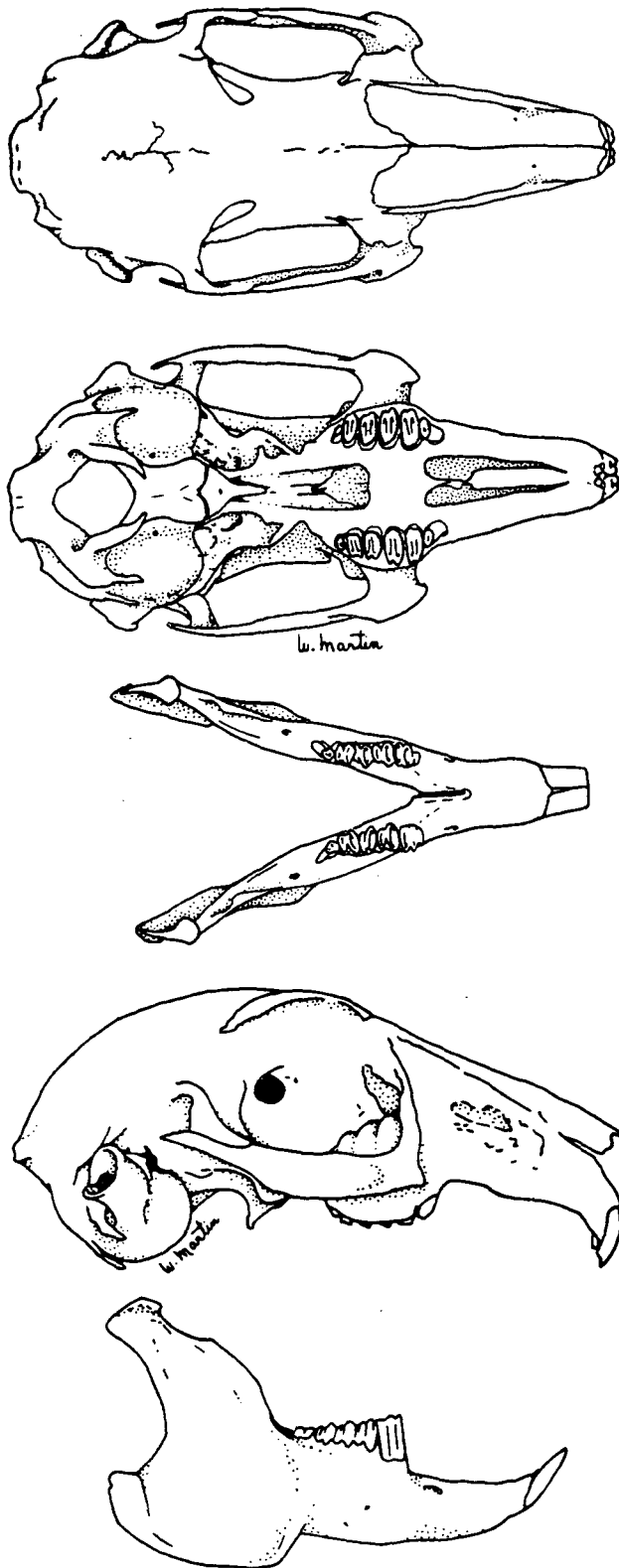


FIGURE 1. Skull and mandible of *Sylvilagus nuttallii nuttallii*. From top down: dorsal view, ventral views of cranium and mandible, and lateral views of cranium and mandible. Drawn by Wilma Martin from a female (USNM 212428) taken at Herrett Ranch, Vale, Oregon, on 1 June 1916.

females pregnant with three, four, and five embryos from the Black Hills of South Dakota.

Powers and Verts (1971) found a mean ovulation rate of 5.0, a mean implantation rate of 4.6, and a mean of 0.3 embryos resorbed. They reported one instance of a juvenile

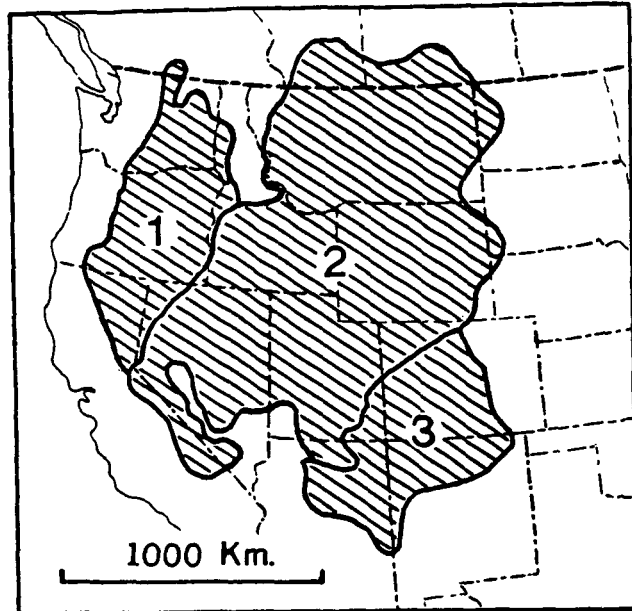


FIGURE 2. Distribution of *Sylvilagus nuttallii* and its subspecies in western North America: 1, *S. n. nuttallii*; 2, *S. n. grangeri*; 3, *S. n. pinetis* (adapted from Orr, 1940; Hall, 1951; Hall and Kelson, 1959; Hoffmeister and Lee, 1963).

female about 90 days old breeding, but felt that such occurrences were rare. They calculated that an adult female breeding throughout the reproductive season would produce about 22 young in five litters, or if she stopped breeding in late June, about 17 young in four litters. They noted that the species seems more fecund than previously believed.

ECOLOGY. The species inhabits rocky, wooded, or brushy areas (Dice, 1926; Orr, 1940; Hall, 1951; Dalquest, 1941). In Washington, *S. nuttallii* "was common in late June in the rocky ravines of the sagebrush-covered hills, and several were secured from about old houses in the wide sagebrush-covered valley, but none were seen in the general sagebrush apart from these situations" (Dice, 1926:17). Dice also noted this rabbit in the willows along the Walla Walla River, in cultivated fields, and among the rocks and ravines on the lower slopes of steep, bunchgrass-covered hills. In California, the species occupies rocky, sage-covered hills and canyons (Orr, 1940). In Nevada, the species prefers higher, rocky, sage-grown regions, whereas the Audubon's cottontail (*S. audubonii*) occupies the adjacent desert valleys (Orr, 1940).

The species uses burrows and forms, the extent depending on the nature of the environment (Orr, 1940). Rabbits living in dense sagebrush or riparian growth probably spend most of their time above ground. Those inhabiting less dense vegetation frequently resort to crevices in rocks or burrows for protection. Orr (1940) excavated a burrow of *S. nuttallii* in a small ravine at the base of a large clump of sagebrush. The burrow had two entrances which extended at right angles to each other for a distance of 1 m before they joined in a small pocket containing dried grass. The greatest depth of the burrow system was 0.6 m. Feces of both young and adult cottontails indicated that young may have been reared in the burrow. Orr (1940) did not know if the species digs its own burrows or utilizes those excavated by other animals. However, Walker *et al.* (1964) reported that, so far as is known, only the pygmy rabbit (*S. idahoensis*) constructs its own burrows.

The fact that *S. nuttallii* unfailingly took refuge beneath the abundant rocks in Petes Valley, California, led Grinnell *et al.* (1930) to conclude that a shortage of food, rather than of shelter, was the main delimiting factor in that area.

Mammalian predators include bobcats, *Lynx rufus*, and coyotes, *Canis latrans* (Orr, 1940). Avian predators include: great horned owls, *Bubo virginianus*; long-eared owls, *Asio wilsonianus*; marsh hawks, *Circus hudsonius*; Swainson hawks, *Buteo swainsoni*; red-tailed hawks, *B. borealis* (Borell and Ellis, 1934); and golden eagles, *Aquila chrysaetos* (Hall, 1946). One possible reptilian predator, the rattlesnake, *Crotalus oreganus*, also has been noted (Grinnell *et al.*, 1930).

Known helminth parasites of *S. nuttallii* include: cestodes, *Cittotaenia pectinata*, *C. perplexa*, *C. variabilis*, *Railletina retractilis*, and *Taenia pisiformis*; and nematodes, *Dermatoxys veligera*, *Nematodirus neomexicanus*, *Protostrongylus pulmonalis*, and *Trichostrongylus colubriiformis* (Erickson, 1947; Honess, 1935; Hall, 1908; Dikmans, 1937; Scott, 1943). Coccidia also have been reported from this species (Honess, 1939).

The most important food item of *S. nuttallii* in eastern Lassen County, California, during most of the year is believed to be sagebrush (Orr, 1940). Western juniper (*Juniperus occidentalis*) also is eaten; Orr pointed out that after the first snowfall, little else is available in the region. In spring and summer, grass is selected in preference to all other vegetation (Orr, 1940).

BEHAVIOR. The mountain cottontail appears to be more solitary than some other members of the genus. Orr (1940) attributed this to the environment in which these rabbits live, which is mostly in habitats of uniform sagebrush. In areas where patches of green grass or other desirable habitats are found, *S. nuttallii* may concentrate in the same manner as does *S. bachmani* or *S. audubonii* within their respective ranges.

When disturbed, mountain cottontails usually run anywhere from 5 to 15 m away from the point of danger. Then the rabbit will pause, facing directly away from, or at an angle to, the source of danger. The rabbit, with its ears held erect, usually remains motionless and well screened from observation by intervening brush. If any further disturbance is detected by the rabbit, it will hop away in a semicircular path to "fool" the pursuer and draw attention from the actual direction of retreat (Orr, 1940).

S. nuttallii usually feeds in the shelter of brush, or in clearings a few meters from cover. Clearings near cover seem to be preferred along streams and near springs (Orr, 1940). Feeding usually occurs in the early morning and evening. In Lassen County, California, Orr (1940) reported that mountain cottontails feed from dawn until 0930 and again as early as 1430, whereas in Lincoln County, Nevada, most were seen along the margin of a creek between 1745 and dark. Orr (1940) reported that heavy rain and wind apparently reduced open ground feeding, but that cold did not appear to interfere with predawn activities.

GENETICS. The nuttall cottontail has a diploid chromosome number of 42 (Worthington and Sutton, 1966).

Johnson (1968) electrophoretically examined the blood of 23 *S. nuttallii* and reported that it was similar to that of other species of *Sylvilagus* he studied. Johnson and Wicks (1964) showed an electropherogram of both the proteins and hemoglobins of *S. nuttallii* and compared them with those of *S. floridanus*, *S. bachmani*, and *Brachylagus idahoensis*.

REMARKS. Some early mammalogists believed that intergradation occurred between *Sylvilagus floridanus similis* and *S. n. grangeri* along the eastern base of the Rocky Mountains. However, Hall and Kelson (1951) concluded that the two species do not intergrade.

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Canis latrans. By Marc Bekoff

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Canis latrans Say, 1823

Coyote

- Canis latrans* Say, in James, 1823:168. Type locality Engineer Cantonment, about 19.2 km SE present town of Blair, Washington Co., Nebraska.
- Canis ochropus* Eschscholtz (1829:1). Type locality Sacramento River Valley near Sacramento, California.
- Lyciscus cagottis* Hamilton Smith (1839:164). Type locality Río Frio, west slope of Mount Iztaccihuatl, México.
- Canis frustror* Woodhouse (1850-51:147). Type locality Red fork of the Arkansas River, probably near 97° west longitude, near Perkins, Payne Co. (now Cimarron River), Oklahoma.
- Canis lestes* Merriam (1897:25). Type locality Toyabe Mountains near Cloverdale, Nye Co., Nevada.
- Canis mearnsi* Merriam (1897:29). Type locality Quitobaquito, Pima Co., Arizona.
- Canis microdon* Merriam (1897:29). Type locality Mier, on Río Grade, Tamaulipas.
- Canis peninsulae* Merriam (1897:28). Type locality Santa Anita, Cape Saint Lucas, Baja California.
- Canis estor* Merriam (1897:31). Type locality Noland's Ranch, San Juan River Valley, San Juan Co., Utah.
- Canis vigilis* Merriam (1897:33). Type locality near Manzanilla, Colima.
- Canis clepticus* Elliot (1903:225). Type locality San Pedro Martir Mountains, 2,590 m, Baja California.
- Canis impavidus* Allen (1903:609). Type locality Río de las Bocas, 2153 m, northwestern-Durango.
- Canis goldmani* Merriam (1904:157). Type locality San Vicente, Chiapas.
- Canis jamesi* Townsend (1912:130). Type locality Tiburon Island, Sonora.
- Canis hondurensis* Goldman (1936:33). Type locality Cerro Guinote, NE of Archaga, on the Talanga road north of Tegucigalpa, Honduras.

CONTEXT AND CONTENT. Order Carnivora, Family Canidae, Genus *Canis*, in which there are eight recognized species. There are 19 recognized subspecies of *C. latrans*, which is considered to be a close relative of the jackals (*C. aureus*, *C. mesomelas*, and *C. adustus*)—see Kurtén, 1974, and Remarks. For more details on subspecies see Nelson (1932), Jackson (1951), and Hall and Kelson (1959).

- C. l. latrans* Say (in James, 1823:168), see above (*pallidus* Merriam and *nebracensis* Merriam are synonyms).
- C. l. ochropus* Eschscholtz (1829:1), see above.
- C. l. cagottis* (Hamilton-Smith, 1839:164), see above.
- C. l. frustror* Woodhouse (1850-51:147), see above.
- C. l. lestes* Merriam (1897:25), see above.
- C. l. mearnsi* Merriam (1897:29), see above (*estor* Merriam a synonym).
- C. l. microdon* Merriam (1897:29), see above.
- C. l. peninsulae* Merriam (1897:28), see above.
- C. l. vigilis* Merriam (1897:33), see above.
- C. l. clepticus* Elliot (1903:225), see above.
- C. l. impavidus* Allen (1903:609), see above.
- C. l. goldmani* Merriam (1904:157), see above.
- C. l. texensis* Bailey (1905:175). Type locality Santa Gertrudis, Kleberg Co., Texas.
- C. l. jamesi* Townsend (1912:130), see above.
- C. l. dickeyi* Nelson (1932:224). Type locality near Cerro Mogote, 3.2 km W Río Goascoran, La Unión (13°30' north latitude), Salvador.
- C. l. colatus* Hall (1934:369). Type locality Isaacs Lake, Bowron Lake Region, British Columbia.
- C. l. hondurensis* Goldman (1936:33), see above.
- C. l. thamnus* Jackson (1949:31). Type locality Basswood Island, Apostle Islands, Ashland Co., Wisconsin.
- C. l. umquensis* Jackson (1949:31). Type locality 5 mi. SE Drew, Douglas Co., Oregon.

DIAGNOSIS. The coyote can be differentiated from other *Canis* in the Western Hemisphere (gray wolf, *C. lupus*; red wolf,

C. rufus; and domestic dog, *C. familiaris*) using a number of criteria. The coyote is typically smaller than the gray wolf (see General Characters and also Mech, 1974), but there is overlap when comparing the coyote with the red wolf and the domestic dog. Also, depending on geographic locale, there may be slight overlap with *C. lupus* (Lawrence and Bossert, 1967). The nose pad of the coyote (approximately 25 mm in diameter) is smaller than that of the wolf as is the diameter of the pad on the hind foot (less than 32 mm as opposed to greater than 38 mm, respectively). The ears of the coyote are longer than those of the gray wolf. The track of the coyote (approximately 70 mm by 60 mm—O. J. Murie, 1954) is more elongated than that of the domestic dog, but shorter than that of both the gray wolf and the red wolf. Riley and McBride (1975) presented mean values of 66 mm (57 to 72 mm) and 102 mm (89 to 127 mm) for the track length (from the back of the heel to the end of the longest claw) for the coyote and red wolf, respectively. The stride of the coyote is less than that of the gray wolf or red wolf. The mean length of the stride of the coyote is approximately 414 mm (324 to 483 mm), whereas that of *C. rufus* is approximately 658 mm (552 to 762 mm; Riley and McBride, 1975).

Dental characters also have been used to distinguish *latrans*, *lupus*, and *rufus*, but Jackson (1951) stressed that such measurements may not be especially reliable. In the coyote, the tips of the upper canine teeth usually extend below a line drawn through the anterior mental foramina of the mandible when the mandible is articulated and the jaws closed. Howard (1949) suggested a way for differentiating *latrans* from *familiaris* that is about 95% reliable, depending on subspecies. A ratio of palatal width (between the inner margins of the alveoli of the upper first molars) to length of the upper molar toothrow (from the anterior margin of the alveolus of the first premolar to the posterior margin of the last molar alveolus) is calculated. If the tooth row is 3.1 times the palatal width, the specimen is a coyote; if the ratio is less than 2.7, the specimen is a dog.

Various cranial measurements have been used to differentiate species of *Canis* (Lawrence and Bossert, 1967, 1969, 1975; Paradiso, 1968; Paradiso and Nowak, 1971; Wortmann, 1971; Gipson *et al.* 1974). The coyote has a relatively larger braincase than does *C. lupus* (Mech, 1974). Paradiso and Nowak did extensive analyses on skulls of *latrans*, *lupus*, and *rufus*, and demonstrated the usefulness of indices. They found no overlap when comparing the largest coyote to the smallest wolf (*lupus*) in zygomatic breadth (greatest distance across zygomata), greatest length of the skull (see figure 1), or bite ratio (the ratio of the width across the outer edges of the alveoli of the anterior lobes of the upper carnassials to the length of the upper molar toothrow, as defined above). *C. rufus* resembles *C. latrans* more than *C. lupus*, but Paradiso and Nowak (1971) regarded *latrans* and *rufus* as sufficiently distinct to warrant specific recognition. The differences between the red wolf and the coyote are far greater than those between recognized subspecies of *C. latrans*. The most reliable feature separating *latrans* from *rufus* is lesser size; there is almost no overlap in greatest length of the skull (figure 1). Also, *rufus* has heavier bone structure, a relatively broader skull, and generally a more pronounced sagittal crest. Lawrence and Bossert (1967), using multiple character analyses and linear discrimination techniques, found nine cranial and six dental measurements (see Lawrence and Bossert, 1967, table 1 and appendix A, for particulars) that could be used reliably to differentiate *latrans* from *lupus* and *familiaris*, but no single character was found without overlap between a pair of species. *C. latrans* differed more from *lupus* and *familiaris* than *lupus* differed from *familiaris*.

The coyote brain differs from that of *C. lupus* (Radinsky, 1973) in that the wolf has a dimple in the middle of the coronal gyrus, whereas the coyote does not. Using gross cerebellar morphology, Atkins and Dillon (1971) distinguished *latrans* from both *lupus* and *rufus* (see Remarks). The coyote differs from *C. lupus* and *C. familiaris* serologically (Leone and Wiens, 1956; but see also Seal, 1975).

Behaviorally, the coyote can be differentiated from *C. lupus* and *C. familiaris*. The coyote shows higher levels of aggression earlier in life than does the wolf or beagle (and probably most

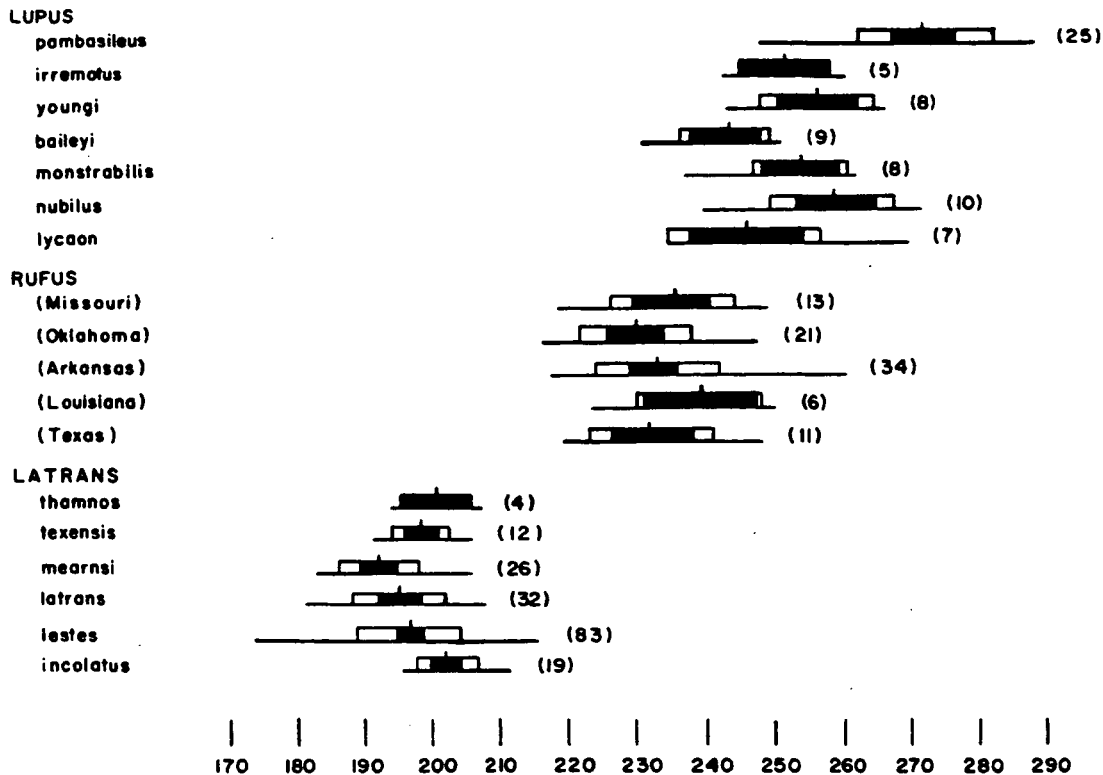


FIGURE 1. The greatest length of skull (mm) in male gray wolves (*lupus*), red wolves (*rufus*), and coyotes (*latrans*). A similar trend also is evident in females (slender line = range; black bar = 2 standard errors of the mean; vertical line on top of black bar = mean; black bar plus white portion on either side indicate one standard deviation on either side of the mean). After Paradiso and Nowak, 1971, with permission.

other domestic dogs as well) and also performs a "species-typical" behavior called the "inguinal response" which consists of rotating a hind-leg outwards or lifting it off the ground in response to light inguinal contact (see figure 2, and Bekoff, 1972a, 1973, 1974a).

GENERAL CHARACTERS. The size of the coyote varies with subspecies and geographic locale (Jackson, 1951; Hall and Kelson, 1959). Adult males usually are heavier and larger than adult females (approximately 8 to 20 kg as opposed to 7 to 18 kg, respectively). In Sagehen Creek Basin (northeastern California), Hawthorne (1971) found that males averaged 11.12 kg (8.17 to 12.49 kg) and females averaged 9.76 kg (7.72 to 12.03 kg), whereas in Texas Daniel (1973a) found that 71 males averaged 16.75 kg (11.35 to 20.43 kg) and 70 females averaged 13.62 kg (10.90 to 17.25 kg). Gier (1975) reported that northern subspecies are larger (approximately 18 kg) than more southern subspecies on the Mexican deserts (11.5 kg). Body length varies from 1.0 to 1.35 m and the tail is about 400 mm long. Females are shorter than males in both length and height. The largest coyote on record was taken in Wyoming. It weighed 33.94 kg and measured 1.60 m from tip of nose to tip of tail (Young, 1951).

Color and texture of the fur vary geographically. The hair is longer and coarser in northern subspecies (see Form). The banded nature of the hair presents blended colors—gray mixed with a reddish tint. Those coyotes at higher altitudes tend toward more gray and black, whereas those in the desert are more fulvous (Jackson, 1951). Black patches may be found on the front of the forefeet and near the base and tip of the tail (Gier, 1968). The belly and throat are paler than the rest of the body. Melanistic coyotes are rare (Young, 1951; van Wormer, 1964; Gipson, 1976).

DISTRIBUTION. Coyotes are Nearctic canids originally inhabiting open country and grasslands (Young, 1951; Gier, 1975). Within historic time, they have occupied many diverse habitats. They now can be found between 10° north latitude (Costa Rica) and 70° north latitude (northern Alaska) and throughout the continental United States and Canada (fig. 3). The range of the coyote is expanding. When considering the expanding range of *C. latrans* it is important to know whether this reflects true movement of coyotes or whether some recently discovered populations (in some cases a few dens) are the result of animals being transplanted into the region by man. Transplanta-

tion appears to have occurred into Florida (Cunningham and Dufford, 1970) and Georgia (Fisher, 1975). Paradiso (1968) considered the expansion of the coyote into Arkansas, Mississippi, and Louisiana to have been unassisted by humans.

FOSSIL RECORD. Fossils resembling *C. latrans* were found in Pleistocene deposits in Cumberland Cave, Maryland (Gidley, 1913; Matthew, 1930). Differentiation of modern canids occurred in the Pleistocene and in Recent times (see Giles, 1960; Colbert, 1969; Todd, 1970).



FIGURE 2. A "species-typical" action, the inguinal response, performed by the coyote on the left. The leg is not being pushed up but is lifted due to light stimulation in the inguinal region.

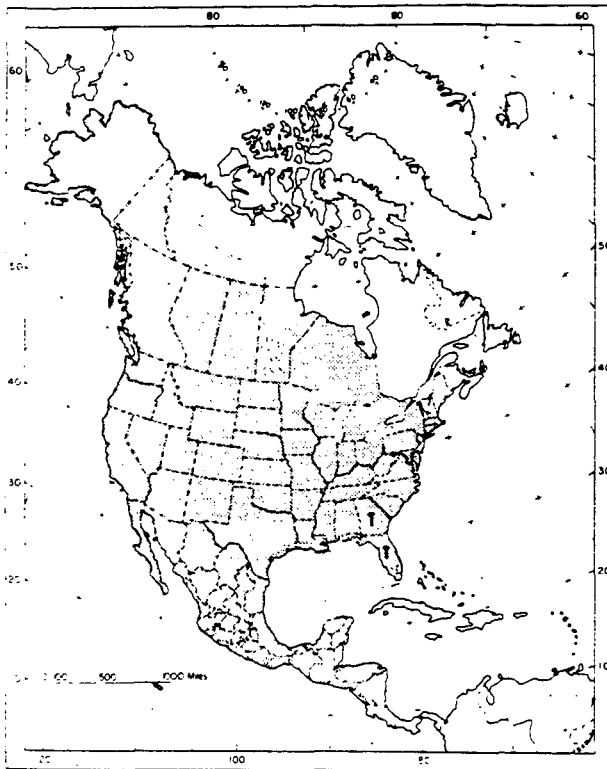


FIGURE 3. Current distribution of coyote (T, probable transplants by man—see text).

FORM. Coarse guard hairs are about 50 to 90 mm long (in the mane, 80 to 110 mm) with imbricate scales that are acuminate in the proximal region, crenate medially, and flattened distally. The fine underfur has coronal scales and may be as long as 50 mm (see Adorjan and Kolenosky, 1969; Ogle and Farris, 1973). There usually is one main molt between late spring and autumn, the summer coat (both guard hairs and underfur) is shorter than the winter coat. About 50 mm down from the base of the tail there is an oval tail gland (10 by 3 mm; Hildebrand, 1952). Normally there are eight mammae. The front foot has five toes and the hindfoot four. On the front foot there is a dew claw proximal from the other four toes. P. S. Gipson (personal communication) observed a specimen with a well-developed dew claw on each hindfoot. The toes are non-retractile and the stance digitigrade. There are 42 teeth (i 3/3, c 1/1, p 4/4, m 2/3; for further details on dentition see Slaughter *et al.*, 1974, and Bekoff and Jamieson, 1975). The skull of a mature male weighs between 170 and 210 g and is 180 to 205 mm long (figures 4 and 5) from the tip of the premaxilla to the posterior rim of the coronal crest (Gier, 1968). Males show greater development of the sagittal ridge than do the females.

The structure and evolution of the coyote's brain have been described by Radinsky (1969, 1973), Atkins and Dillon (1971), and Elias and Schwartz (1971).

Mossman and Duke (1973) described the ovaries of various canids. The adrenals of canids were studied by Ogle (1971) and Heinrich (1972). Ogle (1971) reported that the left adrenal is heavier than the right in both males and females and that the adrenals of females tend to be heavier than those of males (1.14 ± 0.01 as opposed to 1.08 ± 0.03 g, respectively).

FUNCTION. The coyote's fur is similar in insulative value to that of the gray wolf (Ogle and Farris, 1973). The critical temperature of *latrans* is -10°C (O₂ consumption = 7.35 mm³/g/min; Shield, 1972). The longer winter fur coat conserves heat considerably better than the shorter summer coat, there being a decrease of about 87% in thermal conductivity and an increase in insulative value by a factor of five (for details, see Ogle and Farris, 1973). The coyote can run as fast as 48 km/hr (Sooter, 1943) but usually trots at less than 32 km/hr. Coyotes, like other canids (Kleiman, 1966; Mech, 1974) appear to use olfactory cues during their activities and deposit "marks" (urine, feces, and possibly glandular secretions) on conspicuous objects, possibly for territory demarcation (as yet an unsubstantiated assumption). Ozoga and Harger (1966) reported that the coyotes

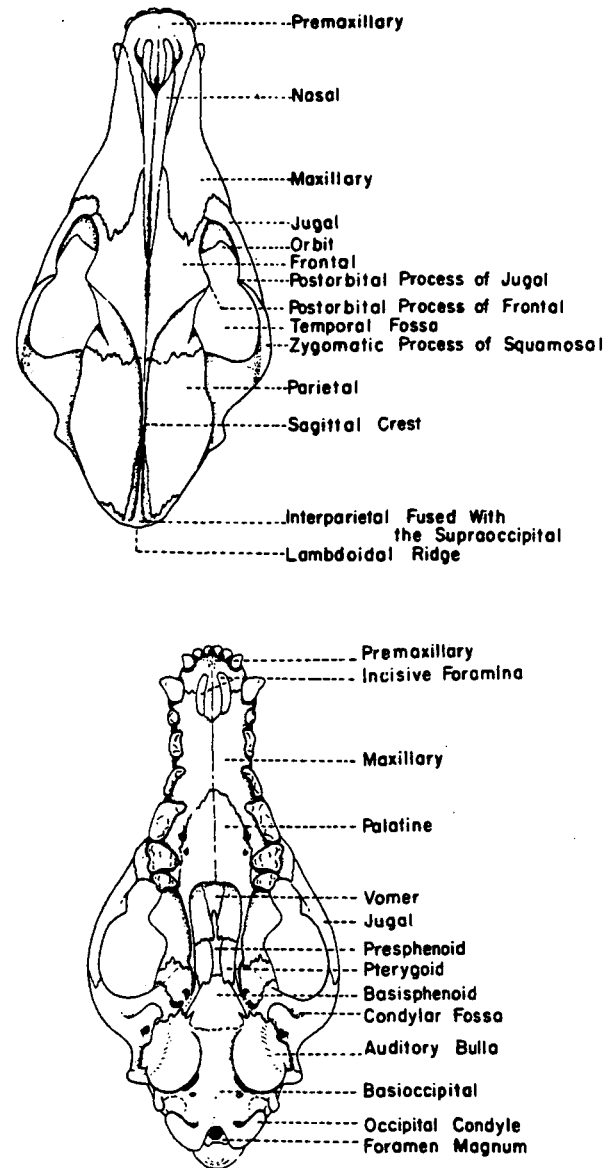


FIGURE 4. Skull of coyote: upper left, dorsal view; lower left, ventral view (from Lechleitner, 1969, with permission of the publisher).

they observed urinated an average of once per 4.0 km and defecated every 10.4 km. Gipson and Sealander (1972) reported urination and defecation occurring three times per 1.6 km and one time per 3.2 to 4.8 km, respectively. Scratching of the ground is also a common component of the eliminative process in canids and it is possible that scent from interdigital glands is thus deposited.

The coyote has an elaborate vocal repertoire (Tembrock, 1963; Lehner, 1975). The region of maximal sensitivity to auditory stimuli is 100 Hz to 30 kHz with a top limit of 80 kHz (Petersen *et al.*, 1969). The retina is duplex and has a preponderance of rods. The absolute scotopic (rod) threshold is approximately 1.4 foot-candles. The adaptation curve shows distinct rod-cone breaks (Horn and Lehner, 1975). The electrocardiograph of the coyote based on the ventricular activation process is the same as of other carnivores (Szabuniewicz, 1970).

REPRODUCTION AND ONTOGENY. Field data on courtship in coyotes and other species of *Canis* are scanty. Data on captive animals (Bekoff and Diamond, 1976) indicate that courtship may begin as long as 2 to 3 months before there are attempts at copulation. The female is monoestrous, showing one period of "heat" per year. This usually occurs between January and March, and both males and females show seasonal changes and cycles in reproductive anatomy and physiology (Hamlett, 1938; Gier, 1968; Kennelly, 1972; Dunbar, 1973).

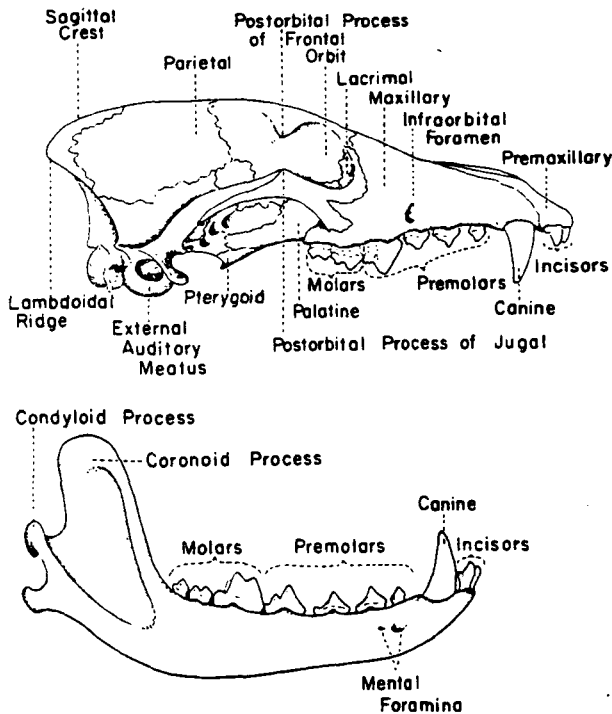


FIGURE 5. Skull and jaw of coyote in lateral view (from Lechleitner, 1969, with permission of publisher).

Proestrous lasts between 2 and 3 months (Whiteman, 1949; Kennelly and Roberts, 1969; Bekoff and Diamond, 1976), estrus lasts about 2 to 5 days (Kleiman, 1968; personal observations), and ovulation occurs about 2 to 3 days before the end of the female receptivity. The times of, and durations of, proestrous and estrous differ in various locales and the relationship is not clear-cut (Hamlett, 1938). The same is true for the spermatogenic cycle of the male. Behavioral changes that occur during courtship parallel those reported by Golani and Mendelsohn (1971) for the golden jackal (*C. aureus*). Courtship "rituals" are not so highly specific that hybridization cannot occur. Coyotes can successfully mate with domestic dogs, gray wolves, red wolves, and jackals. Copulation ends with the typical "copulatory tie," during which the male's penis is locked in the female's vagina (Dewsbury, 1972; Grandage, 1972; Fox and Bekoff, 1975). The tie can last 15 to 25 minutes (Kleiman, 1968; Bekoff and Diamond, 1976). It is generally accepted that the same individuals will mate from year to year, but not necessarily for life.

The percentage of females that breed during a given year may vary from 33% to 90% depending on local conditions (Gier, 1968; Knowlton, 1972; Gipson *et al.*, 1975). Both yearling males and females are capable of reproducing, yearling females usually breeding later than older females (Gier, 1968) and thus contributing minimally to the population (Knowlton, 1972). Gipson *et al.* (1975) found that no yearling females bred. However, (Gier, 1968) reported that in good rodent years, 75% of yearling females may breed. Nellis and Keith (1976) reported pregnancy rates of 94% for adult females and 14% for yearlings, with adults showing more (6.0) placental scars than yearlings (5.2)—not a significant difference. Asdell (1964), summarizing the literature, reported the mean number of embryos in 1370 cases to be 6.23 and the number of den young in 1582 cases to be 5.70. Hamlett (1938) reported that the number of young per litter was about 85% of the number of embryos per female. Gier (1975) estimated that the number of young born was equal to about 80% of the ovulated ova depending on whether or not it was a good rodent year. Gipson *et al.* (1975) reported the mean number of ova per breeding female to be 6.2, with 4.5 becoming implanted.

Gestation lasts approximately 63 days (58 to 65). Coyotes and dogs appear to develop similarly *in utero* (Gier, 1968). Average litter size is six with a sex ratio of females to males of about 1:1. Nellis and Keith (1976) reported a mean litter size of 5.3 for 26 litters. Litter size is known to be accepted by population density (Knowlton, 1972) and rodent populations (Gier, 1968). Litter size averaged 4.3 at high densities and 6.9 at low densities. In good rodent years mean litter size was 5.8 to 6.2 and in poorer rodent years average litter size was 4.4 to 5.1.

TABLE 1. Mortality in coyote populations. (After Mathwig, 1973: 184; mean percentage values based on seven studies).

Age (years)	Percent of population
1	41.1
2	19.1
3	11.0
4	6.6
5	6.6
7	3.7
8	2.7
9	2.1
10	1.3
11	0.3
12	0.9

Young are born blind and helpless, usually in an excavated den. Favorable den sites include brush covered slopes, steep banks, thickets, hollow logs, rock ledges, often on south-facing slopes (Gier, 1968). Dens of other animals may be used. Dens are usually about 0.3 m in diameter and may be from 1.5 to 7.5 m long (van Wormer, 1964). More than one entrance may facilitate the movement of young when the den site is disturbed. The same den may be used from year to year, and dens may be shared. Nellis and Keith (1976) found that 3 of 29 dens had two litters.

Young are nursed by their mother (see Ewer, 1973:331, for data on the composition of coyote milk) and are weaned at about week 5 to 7 (Snow, 1967; unpublished data). They begin to eat solid food at about week 3, and the female (and possibly the male) begins regurgitating semi-solid food at this time. The male apparently plays some role in rearing the young by bringing food to the lactating bitch and the pups. Pregnant and lactating females require about 900 g, or 1.5 times the "normal" amount, of food per day (Gier, 1975). Weight at birth is about 250 to 275 g and length of the body (tip of head to base of tail) is about 160 mm (Gier, 1968; Bekoff and Jamieson, 1975). Between birth and week 8 the average weight increase is about 0.31 kg/week (Bekoff and Jamieson, 1975), and the pups reach adult weight at about month 9. Eyes open at about day 14. Teeth erupt as follows (on the average): upper canines (day 14), lower canines and upper incisors (day 15) and lower incisors (day 16) (Bekoff and Jamieson, 1975). The young are able to urinate and defecate without maternal assistance by week 2 or 3. Jackson (1951) described the sequence of the closing of cranial sutures.

Young emerge from the den in week 2 or 3 and may disperse in months 6 to 9. Not all young disperse. Although there are no field data, consistent reports on the development of social behavior in captive coyotes (Fox and Clark, 1971; Bekoff, 1972a, 1974a, 1975a) indicate that young coyotes form dominance relationships via severe, unritualized fights between 25 and 35 days of age.

Coyotes in captivity may live as long as 18 years (Young, 1951) but in wild populations few individuals live more than 6 to 8 years (Gier, 1968; Mathwig, 1973). Maximum ages known in the wild are 13.5 (Nellis and Keith, 1976) and 14.5 years (Knowlton, 1972). In an unexploited population, Knowlton (1972) found 70% of individuals in spring (pre-whelping) to be less than 3 years old and less than 5% to be more than 9 years old. In autumn, more than 80% of the individuals were less than 3 years old. Knowlton reported a 40% annual mortality rate for coyotes more than a year of age, with relatively high survival between years 4 and 8. Estimated mortality rates in central Alberta (Nellis and Keith, 1976) were 71% through year 1 and 36% to 42% for animals more than a year old (see table 1). In Iowa, Mathwig (1973) found greatest life expectancy at 1½ years and least at 5½. To maintain stability, a net survival of 33% was needed in the populations that Knowlton (1972) studied, whereas Nellis and Keith calculated that 38% survival was necessary. Gier (1968) felt that there were three basic limits on reproduction: 1) climatic factors, 2) parasites and disease, and 3) food. Losses due to predation, accidents, and man are also important.

ECOLOGY. More is known about the ecology of the coyote than perhaps any other carnivore (see Bekoff, 1974b). Many data have been collected because of the economic interests of control and management programs. The coyote is an opportunistic predator and includes a wide variety of food in its diet, the percentage by volume and weight varying individually and also with season and locality. Korschgen (1957) listed 56 animal, 28 plant, and six miscellaneous food items in Missouri and A. Murie (1940) and Mathwig (1973) and others have included large numbers of plant species. Individuals in captivity (Gier, 1975) require about 600 g of meat per day.



FIGURE 6. Aggressive displays by two 23-day-old coyotes.

Because of the varied diet, it is impossible to list all food items that have been found in scats and stomachs or observed being taken in actual kills. Deer, elk, sheep, rabbits, various rodents, ground-nesting birds such as the ferruginous hawk (Angell, 1969), bobwhite quail (Lehmann, 1946), and Canada geese (Vermeer, 1971), amphibians (Minckley, 1966), lizards, snails, fish, crustaceans, and insects comprise the "meat" items. Various berries, peaches, pears, apples, persimmons, watermelons, cantaloupes, and carrots are included in the vegetables, and leather boots, tin cans and the like are included in the miscellaneous list. Overall, about 90% of their diet is mammalian flesh.

In the winter, much of the coyote's diet is made up of the carrion of large game animals such as deer (see Sperry, 1933, who reviewed data for 10 western states; O. J. Murie, 1935; A. Murie, 1940; Ozoga and Harger, 1966; Gier, 1968; Ogle, 1971; Mathwig, 1973; Nellis and Keith, 1976) and little vegetable food is eaten. In the spring, summer, and autumn there is an increase in the percentage (by volume and weight) of various rodents (A. Murie, 1940; Nellis and Keith, 1976). Fichter *et al.* (1955) noted that a striking seasonal trend in Nebraska was an autumnal increase in the utilization of fruit. Gipson (1974) summarized five studies on the food habits of coyotes in their original range and the compiled percentage data were as follows: rabbits, 41.1; rodents, 36.2; carrion, 25.5; livestock, 21.9; wild birds, 15.0; deer, 7.9; fruits, 6.7; and poultry, 4.8. Most analyses of coyote predation on both large game mammals and domestic livestock indicate that young, old, and sick animals constitute the bulk of this portion of their diet (A. Murie, 1944; Ozoga and Harger, 1966; Knowlton, 1968; Cook, White, Trainer, and Glazener, 1971; Ogle, 1971; Hawthorne, 1972; Davenport, Bowns, and Workman, 1973), and that coyote predation was not a primary limiting factor on game and livestock. A. Murie (1935) found that 70.29% of the coyote's diet in Jackson Hole, Wyoming, was "beneficial" to the prey, 18.22% was "neutral," and only 11.49% was "harmful." Similarly, Mathwig (1973) found that 85% of the coyote's diet in Iowa was not "harmful," whereas 15% was "detrimental." Ozoga and Harger (1966) reported that healthy deer could escape from coyotes and bighorn sheep are able to chase off coyotes (Weaver and Mensch, 1970). Davenport *et al.* (1973) indicated that most lambs lost during spring died from causes other than predation, such as starvation, disease, abandonment, docking, and infection. Daniel (1973b) wrote "... although fawn survival rates most probably are closely related to coyote numbers and predation, there are other factors of perhaps more importance [my emphasis] exhibiting strong influence upon the growth and stability of deer herds. . . ." There is little evidence that coyote predation is a primary limiting factor on populations of big game or domestic livestock.

Ozoga and Harger (1966) wrote that the average chase of a deer by a coyote was about 55 m and they observed two long futile attempts of 4.32 and 4.64 km by single coyotes. Coyotes will hunt in pairs or in larger groups (Cahalane, 1947; Dobie, 1961; Young, 1951; Ozoga and Harger, 1966; Gier, 1968) and will form hunting relationships with other predators such as golden eagles (Engel, 1966), ravens (A. Murie, 1940), and badgers (Dobie, 1951). Actual coyote attacks are rarely observed and little is known about their predatory habits (White, 1973). A presumed "coyote kill" often has been killed by some other predator, sometimes a domestic dog (Davenport *et al.*, 1973). Ogle (1971) listed five criteria that can be used to distinguish deer killed by coyotes from those fed on as carrion. Coyote kills may be characterized by: 1) large patches of hide leading to the carcass; 2) separation of vertebral column in the thoracolumbar

TABLE 2. Data on coyote movements from eight representative studies (distances in km).

Study	Adult		Juvenile		Both sexes
	Males	Females	Males	Females	
Carlough, 1940					42.9
Robinson and Cummings, 1951	12.6	17.8			16.8
Young, 1951	36.2				
Young, 1951	45.3	40.0			
Robinson and Grand, 1958	45.6	34.2			40.6
Hawthorne, 1971	6.4	7.6	5.2	6.4	
Chesness, 1972	10.1		6.4	6.6	
Gipson and Sealander, 1972	20.5	8.16		7.4	
Nellis, 1975	6	7	6	26	

region of adults and at the atlas of fawns; 3) nasal and maxillary bones chewed away; 4) ribs, vertebrae, and scapulae chewed; and 5) limbs widely scattered. For adult deer, the first criterion is considered to be the most reliable. Attacks on the head and neck frequently are used on deer (Ozoga and Harger, 1966; White, 1973) as are belly and rump attacks (Ogle, 1971). A shearing bite is used (Young, 1951), and a bite-and-tear sequence is common. For smaller mammals a stalk-and-pounce approach is common. Coyotes generally eat the contents of the stomach and intestines of young but not of adults (Davenport *et al.*, 1973; White, 1973). See Bekoff (1975a, 1975b) for information on the development of predatory behavior in coyote pups.

Coyotes carry a wide variety of parasites (Young, 1951; Gier, 1968; Thornton, Bell, and Reardon, 1974). Fleas are the most common external parasite—e.g. *Pulex similan*, *Hoploxyllas affinis* and *Cediopsylla simplex* (rabbit flea), *Chaelyopsylla lotoris* (raccoon flea), and *Juxtapsylla porcinus* (javelina flea). Other external parasites include various ticks (*Ixodes simulans*, *I. kingi*, and *Dermacentor variabilis*) and lice (*Demidectes*). Internal parasites include the cestodes *Taenia pisiformis* (common according to Gier, 1968) and *Mesocestoides corti*; roundworms, *Physaloptera rara* and *Filaroides osteri* (in the trachea, bronchi, and rarely in the lungs); intestinal worms such as *Toxascaris leonina*; dog hookworms, *Ancylostoma caninum*, that can pass through the placenta; whipworms, *Trichuris vulpis*; heartworms, *Dirofilaria immitis*; pinworms, Oxyuridae; thorny-headed worms, *Uncincola canis* and *Spricocerca lupi*, in the esophagus, stomach, and aorta; and coccidia fungus, *Isospora riohata*. Coyotes also have been found to carry tularemia (Kunkel, 1930; Lundgren *et al.*, 1957), distemper (Harispe and Wainer, 1941), rabies (Swick, 1972; Behymer *et al.*, 1974; and others), and bubonic plague (A. M. Barnes, personal communication). In addition, coyotes suffer from dental anomalies (Nellis, 1972), mange (A. Murie, 1944; Holmes and Podesta, 1968), cancer (Trainer *et al.*, 1968; Dietrich and van Pelt, 1972), Q fever (Enright *et al.*, 1971), aortic aneurysms (Thornton *et al.*, 1974), various cardiovascular disorders (Ross and Suzuki, 1973), and serious wounds (for example, bullet wounds), missing limbs, and broken bones.

Coyotes and other carnivores can live in the same area, but coyotes, like other smaller predators, do not compete well with the wolf (Mech, 1966, 1974). Coyotes generally do not tolerate foxes or bobcats (Young, 1951) and puma will kill and eat coyotes (Young, 1946).

Coyotes spend a good deal of time on the move. They are active primarily in early evening, especially in winter (Ozoga and Harger, 1966; Chesness, 1972), but do show sporadic activity in the daylight hours. Gipson and Sealander (1972) showed a principal activity peak at sunset with a minor peak at day-break in Arkansas. In summer, they found animals to be more active by day, with pups more active by day than adults. Coyote movement patterns have been studied in various places and like the movement patterns of wolves (Mech, 1974), they can be classified as travels within a "territory" or home range, as dispersals, or as long migrations. Males tend to have larger home ranges than do females. In Minnesota, Chesness and Bremicker (1974) found home ranges of males to average 41.92 km², whereas those of females averaged 10.08 km². Furthermore, the home ranges of the males overlapped considerably but those of the females did not (an implication, but not proof, of ter-

territoriality). In Arkansas, Gipson and Sealander (1972) reported male home ranges from 20.8 to 41.6 km² and female home ranges from 8 to 9.6 km². Other studies have reported home ranges of 20.8 to 32 km² (Nellis and Keith, 1976), 57.6 to 80 km² (Ozoga and Harger, 1966) and 9.6 to 12.8 km² (Camenzind, 1974). In Minnesota, home ranges were elongate with mean length about 1.8 times mean width.

Many data have been collected concerning length of movements of marked individuals in various locales (table 2). No consistent differences between sexes have been seen. Coyote movements of over 160 km are not uncommon. Ozoga and Harger (1966) found average daily travel to be about 4.0 km.

Movements of young coyotes also have been studied (table 2). Dispersal usually occurs in autumn and winter (October to February), some pups not dispersing during their first year. Dispersal occurs randomly in all directions. Pups will move upwards of 80 to 160 km. Unfortunately, few pups marked at dens are relocated by investigators (22% by Nellis and Keith, 1976).

The density of coyote populations varies with local conditions. Knowlton (1972) suggested that a density of 0.2 to 0.4/km² (0.5 to 1.0/mi²) would be a realistic educated guess for densities over a large portion of the range, and his suggestion fits well with data collected by others (Young, 1951; Ozoga and Harger, 1966; Gier, 1968; Mathwig, 1973; and Nellis and Keith, 1976).

Coyotes are usually observed as lone individuals (Ozoga, 1963; Ozoga and Harger, 1966; Chesness, 1972) or as pairs (especially during the breeding season). Larger groups of coyotes are probably parent(s) and young. "Packs" of coyotes have been described in the literature (Dobie, 1961; Camenzind, 1974), but whether or not they operate as do wolf packs is as yet unknown.

The relationship of the coyote with early man was one of harmony and mutual respect (Dobie, 1961; Gill, 1970). Within the last 150 years this relationship has changed considerably, particularly because of the coyote's predatory habits. In fact, in a recent paper by Shelton (1973), the coyote was referred to as being a "dispensable animal." Indeed, the coyote has been responsible for large economic losses to the domestic livestock industry (Young, 1951; Gier, 1968; Cummings, 1972; Neese, 1973). One of the first bounties on coyotes was established in Missouri in 1825 (Young, 1951). In the 1860's, when beaver decreased in value, the value of coyote rose to about \$.75 to \$1.50 per animal (for more detail on prices see Young, 1951, and van Wormer, 1964). Coyote fur is not in great demand (Frye and Lay, 1942, ranked it sixth out of seven skins) and Young (1951:118) felt that the use of coyote skins and the success of the bounty system depended on the "fickle dictates of fashion." The bounty system has not been effective (Howard, 1973) and has been supplemented by use of various other control methods such as shooting from snowmobiles (Wetmore *et al.*, 1970) and airplanes, trapping (see Casto and Presnall, 1944, for a comparison of various trapping methods), coyote-getters (M-44 cyanide gun, a selective method—see Beason, 1974), aversive conditioning (Gustavson *et al.*, 1974; Bekoff, 1975c), and the use of various chemicals such as strychnine, 1080 (sodium monofluoroacetate, considered by some to be the "best poison"—Howard, 1973), and antifertility agents (diethylstilbestrol—Balsler, 1964; Kennelly, 1969). Dose regulation and distribution have been problems. Linhart and Kennelly (1967), developed a "marker" (demethylchlorotetracycline) to "label" animals taking various baits. The efficiency of removing animals that have actually preyed on the items reported damaged is also an important consideration (Gipson, 1975). Knowlton (1972) suggested that control programs should consider the removal of particular individuals from populations. Another control method that has worked to reduce loss of domestic livestock simply involved the removal of carrion by farmers in central Alberta, because coyotes do depend heavily on carrion as part of their winter diet (Todd and Keith, undated). Gier (1968:23) wrote that "coyotes may be encouraged or even taught to kill poultry and other farm animals by farmers discarding dead animals where coyotes can find them." Hunter-trapper programs appear to be the most successful (Howard, 1973; Gier, 1975). However, it is important to realize that few control programs have been effective.

The lack of success of coyote control programs basically is due to the lack of objective studies on the biology of the coyote and other predators (see Hornocker, 1972, and Howard, 1973). Little is known about population dynamics and predatory methods. In addition, ranchers and environmentalists appear equally reluctant to discuss issues (Buys, undated). Howard (1973:3) summed up the problem well: "The ecological role of predators, that of the coyote for example, seldom gets rational consideration, and unproven concepts are often perpetuated rather than challenged scientifically." The lack of patience by those persons suffering economic losses is understandable, however, it might prove beneficial in the end to stop using ineffective methods and harness both time and energy to more efficient, scientifically based programs (Pringle, 1975). Otherwise, indis-

criminate attempts at population suppression may once again be resorted to.

Wild coyotes have been studied primarily using radiotelemetry and capture-recapture methods. Both these techniques provide information on movements. Food habits are inferred from scat and stomach analyses and infrequently studied by direct observation. The use of trapping along with other methods provides information on age, sex, weight, size, and breeding condition, and allows blood samples to be drawn. Intramuscular injections of 25 mg of phenacyclidine hydrochloride + 25 mg of promazine hydrochloride have been used to immobilize trapped animals (Chesness, 1972). Censusing is frequently done by "siren inventories and trapping." Ages of coyotes may be estimated by counting dental cementum annuli (Linhart and Knowlton, 1967). Utsler (1974) recently suggested alternate methods (eye lens, weight of the baculum, and thermal contraction of tail tendons) that appear to be as accurate as the counting of cementum annuli, and less expensive and less elaborate.

BEHAVIOR. Because of the elusive nature of the coyote, there have been few direct observations of social behavior(s). Detailed studies of behavior other than those dealing with territorial or home range movements have been done on captive animals (Fox, 1970; Fox and Clark, 1971; Bekoff, 1972a, 1972b, 1974a, 1975a; Brown, 1973). Field observations indicate that the coyote is less social than either the gray wolf of the red wolf (Riley and McBride, 1975), although large "packs" of coyotes have been observed. Gier (1975) wrote that there is no known social structure other than the family. Young coyotes form dominance relations via severe fights between 25 and 35 days of age (figure 6; Fox and Clark, 1971; Bekoff, 1972a, 1974a). The relationship between early fighting and later social organization is not clear, but there are rank-related behaviors that may play some role. For example, higher ranking animals are less successful at getting littermates to play with them and spend less time interacting with them (Bekoff, 1977a). These animals also tend to remain at a greater distance from littermates and frequently are asynchronous in activity with the rest of the group. Such higher ranking individuals may be those who later leave the group. In addition, it has also been found (unpublished data) that the lowest ranking member of a litter interacts infrequently with littermates and perhaps such individual(s) would also leave the group. Field testing of these hypotheses is underway. During agonistic interactions, dominant pups and adults approach one another with a stiff-legged gait, ears forward and erect, fur on the back erect (piloerection), the tail at about a 45° angle from the vertical, and frequently snarling and exposing the teeth by vertically retracting the lips. Submission may take the form of flight, active avoidance, or passive or active submission (see Schenkel, 1967, for detailed descriptions). During passive submission the animal rolls over on its back, flattens its ears against its head, usually retracts the lips horizontally into a "submissive grin," and may urinate and whine. During active submission the animal approaches its "partner" in a low crouch-walk with the tail either tucked or held low, and may perform face-licking and face-pawing. Active submission probably develops from food-begging and passive submission appears to have developed from the posture that the pups assume when they are stimulated to excrete by their mother or other adults (Schenkel, 1967). There are large increases in aggression at the time that the female comes into heat. Detailed studies of social play behavior have been reported by Bekoff (1974a, 1975d).

During early stages of courtship, the male becomes increasingly attracted to the female's urine or feces, or both (Bekoff and Diamond, 1976). See Reproduction and Ontogeny for more detail. When the female is ready to copulate she will tolerate mounting attempts by the male and will flag her tail to one side. After "tying" the male steps over the back of the female and the couple remain locked at 180° for periods of 5 to 25 minutes.

Coyotes use visual, auditory, olfactory, and probably tactile signals for communication purposes. Alcorn (1946) recognized three distinct calls (squeak, howl call, and distress call). Lehner (1975), through extensive analyses of coyote vocalizations, detailed 11 graded signals. Vocally, the coyote is much like the jackal (Tembrock, 1963). Visual signals such as postures, gestures, and facial expressions have also been described (Fox, 1970, 1975a; Bekoff, 1972a, 1972b, 1974a). The coyote appears to have a more elaborate repertoire of visual signals than do more solitary canids such as the red fox, *Vulpes vulpes*, but a less elaborate repertoire than does the wolf (Fox, 1975a). Coyotes do deposit scent but the use of this for territorial demarcation and identification has not been proven (see Kleiman, 1966, for alternative hypotheses). During social investigation there is considerable sniffing of various regions of the body. Whether or not scent is deposited from interdigital glands is not known.

GENETICS. The coyote has 39 pairs of chromosomes (Wurster and Benirschke, 1960). The autosomes are acrocentric or telocentric and the sex chromosomes are submetacentric (Hsu and Benirschke, 1967, cited by Mech, 1974). Fertile hybrids have been produced by crossing coyotes with domestic dogs (Young, 1951; Kennelly and Roberts, 1969; Silver and Silver, 1969; Mengel, 1971), with wolves (*Canis lupus*)—Young, 1951; Kolenosky, 1971; Paradise and Nowak, 1971; Riley and McBride, 1975), and with the jackal (Seitz, 1965). Coyote-dog hybrids show decreased fecundity (Mengel, 1971; Gipson *et al.*, 1976). See Riley and McBride, 1975, for detailed comparisons of external characteristics of red wolves, coyotes, and hybrids.

There has been considerable controversy about the "New England canid" (see Lawrence and Bossert, 1969, 1975; Silver and Silver, 1969; Richens and Huggie, 1974). This canid differs from known coyote-dog hybrids and has incorrectly been referred to as a coy-dog. The general consensus is that the New England canid is an extreme expression of a trend already present in *C. l. thomsoni* and cranial evidence (Lawrence and Bossert, 1969) and data from behavioral development (Bekoff *et al.*, 1975) suggests that New England canids predominantly are coyotes with some introgression of dog and wolf genes.

REMARKS. The word "coyote" means "barking dog" and is taken from the Aztec word "Coyotl."

The coyote resembles jackals in many respects and Atkins and Dillon (1971) have grouped *C. latrans* with *C. mesomelas* (black-backed jackal) and *C. aureus* (golden jackal) based on cerebellar morphology.

During its movements, the coyote may function as a seed-carrier (Young, 1951). Kleiman and Eisenberg (1973) made detailed comparisons of canids and felids and Fox (1975b) edited a volume dealing with wild canids. A fairly comprehensive bibliography has been compiled (Bekoff, 1974b) and Knowlton (1974) also assembled a useful list of references. Volume 3 of the *Coyote Research Newsletter* contains abstracts of papers presented at a National Coyote Workshop (Denver, Colorado, November 1974). Many aspects of coyote biology will be dealt with in a forthcoming volume (Bekoff, 1977b).

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Spermophilus tridecemlineatus. By Donald P. Streubel and James P. Fitzgerald

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Spermophilus tridecemlineatus
Mitchill, 1821

Thirteen-lined Ground Squirrel

Sciurus tridecemlineatus Mitchill, 1821:248. Holotype not designated; type locality fixed in "central Minnesota" by J. A. Allen, 1895:338.

Arctomys hoodii Sabine, 1822:590. Type locality Carlton House, Saskatchewan.

Spermophilus tridecemlineatus Audubon and Bachman, 1849:294. first use of current name.

CONTEXT AND CONTENT. Order Rodentia, Family Sciuridae, Genus *Spermophilus*, Subgenus *Ictidomys*. *Spermophilus tridecemlineatus* is divided into nine Recent subspecies (Howell, 1938; Armstrong, 1971) as follows:

- S. t. tridecemlineatus* Mitchill, 1821:248, see above (*hoodii* Sabine a synonym).
- S. t. pallidus* J. A. Allen, 1877:872. Holotype not designated; lectotype and type locality, "mouth of the Yellowstone River, Montana," designated by Howell 1938:112 (*olivaceus* J. A. Allen a synonym).
- S. t. parvus* J. A. Allen, 1895:337. Type locality Kennedy's Hole, Uncompahgre Indian Reservation, 20 mi NE Ouray, Uintah Co., Utah.
- S. t. texensis* Merriam, 1898:71. Type locality Gainesville, Cooke Co., Texas (*badius* Bangs a synonym).
- S. t. alleni* Merriam, 1898:71. Type locality near head of Canyon Creek, 8000 ft., W slope Bighorn Mtns., Wyoming.
- S. t. hollisteri* V. Bailey, 1913:131. Type locality Elk Valley, 8000 ft., Mescalero Indian Reservation, Sacramento Mtns., New Mexico.
- S. t. monticola* A. H. Howell, 1928:214. Type locality Marsh Lake, 9000 ft., White Mtns., Arizona.
- S. t. arenicola* A. H. Howell, 1928:213. Type locality Pendennis, Lane Co., Kansas.
- S. t. blanca* Armstrong, 1971:533. Type locality near Blanca, San Luis Valley, Colorado.

DIAGNOSIS. The dorsal area of *S. tridecemlineatus* is striped, which separates it from other species in the subgenus *Ictidomys*; the metaloph of P4 is not continuous, which separates the species from ground squirrels of other subgenera.

GENERAL CHARACTERS. Hall and Kelson (1959) described *S. tridecemlineatus* as follows: "Upper parts marked with a series of alternating dark (brownish or blackish) and light longitudinal stripes; a row of nearly square white spots in each of the dark dorsal stripes; lowermost stripes on sides less well defined than on back; in some subspecies some of the light dorsal stripes are broken into spots. Skull long, narrow, and lightly built in comparison with that of *S. townsendii*; molariform tooth rows only slightly convergent posteriorly." A more detailed description may be found in Howell (1938).

Spermophilus tridecemlineatus, the thirteen-lined ground squirrel, is a small- to medium-sized member of the genus similar in size to *S. spilosoma*. External measurements (millimeters) range as follows: total length, 170 to 297; length of tail, 60 to 132; length of hind foot, 27 to 41.

Average cranial measurements (millimeters) taken from nine subspecies listed by Howell (1938) and Armstrong (1972) are: greatest length of skull, 38.0; palatilar length, 17.6; zygomatic breadth, 21.9; cranial breadth, 16.8; interorbital breadth, 7.6; postorbital constriction, 11.5; length of nasals, 13.2; and maxillary toothrow, 6.7. For more detailed morphological comparison of the subspecies of *S. tridecemlineatus* see Howell (1938) and Armstrong (1971, 1972). The skull is illustrated in Figure 1.

DISTRIBUTION. The thirteen-lined ground squirrel has a wide distribution from south-central Canada to Texas and gen-

erally east of the Rocky Mountains to the northern Lake States; the eastern extent of its range is east-central Ohio. Figure 2 shows the approximate distribution of the nine currently recognized subspecies of *S. tridecemlineatus*.

Spermophilus tridecemlineatus is found in habitats ranging from the well drained grasslands of the Lake States to high (2740 m) mountain grasslands in eastern Arizona (Howell, 1938; Hall and Kelson, 1959; Armstrong, 1971). Evans (1951), attesting to the preference of this species for grasslands, noted that from about 1900 to 1950 it expanded its range northward in Michigan and Wisconsin, and eastward in Ohio as the land was cleared. The species also adapts to grassy roadsides and fencerows in intensively farmed areas.

FOSSIL RECORD. Hibbard (1940) found a number of lower jaws, maxillaries, and other skeletal elements of *S. tridecemlineatus* in a Pleistocene deposit in Meade County, Kansas, that appeared identical to those of the modern populations. In Texas, Dalquest (1965) collected about 20 cheekteeth of this species from an outcrop of the Seymour Formation of the Kansan (mid-Pleistocene) age.

FORM AND FUNCTION. The species has two distinct pelages and molts per year. Adults emerge from hibernation in winter pelage; the summer pelage is attained in May in Colorado. The physiology of *S. tridecemlineatus* has been studied more

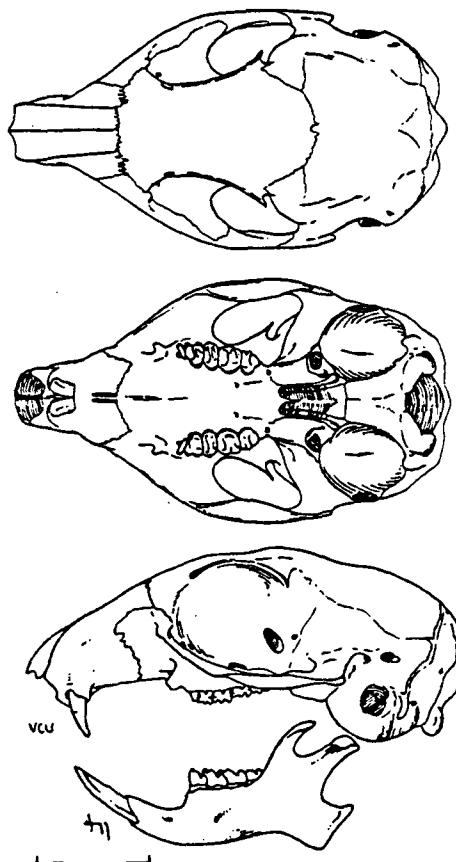


FIGURE 1. Views of skull of *Spermophilus tridecemlineatus* from 6 mi W Bird City, Cheyenne Co., Kansas, KU 12079 (from Hall, 1955). The scale shown at lower left represents 10 mm.

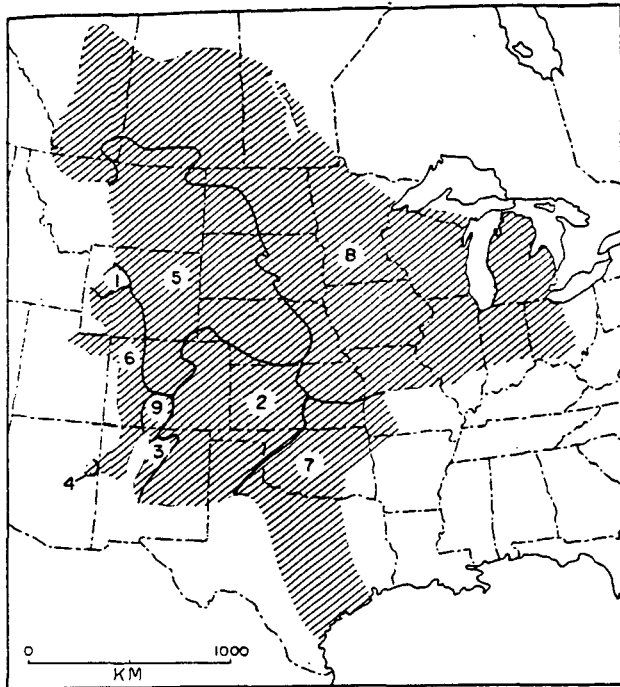


FIGURE 2. Distribution of *Spermophilus tridecemlineatus*, modified from Hall and Kelson (1959) and Armstrong (1971). 1. *S. t. alleni*; 2. *S. t. arenicola*; 3. *S. t. hollisteri*; 4. *S. t. monticola*; 5. *S. t. pallidus*; 6. *S. t. parvus*; 7. *S. t. texensis*; 8. *S. t. tridecemlineatus*; 9. *S. t. blanca*.

extensively than that of most ground squirrels, primarily in relation to hibernation (Johnson, 1930; Wells, 1935; Fisher and Mrosovsky, 1970; and others).

The ultrastructure of the pineal gland was studied by Matsushima and Reiter (1975), and by Povlishock *et al.* (1975). West and Dowling (1975) studied the structure of the eye and found that 4 to 5% of the light receptors were rodlike. Forman (1974) studied the microscopic structure of the accessory reproductive glands. The baculum of *S. tridecemlineatus* was described in detail by Wade and Gilbert (1940) and compared with that of certain other members of the genus.

Hudson and Deavers (1973) studied the physiological adaptations of eight species of ground squirrels and found *S. tridecemlineatus* to be unusually well insulated as compared to desert species such as *S. spilosoma*.

Thirteen-lined ground squirrels gain weight rapidly prior to hibernation. For example, Hohn (1966) observed two adult females in Minnesota that gained 85 g in 22 days and 48 g in 13 days, respectively. He also reported that an adult male gained 59 g in 13 days and another weighed 246 g prior to hibernation, a 38% weight increase during its season of activity.

ONTOGENY AND REPRODUCTION. Bridgewater (1966), in laboratory studies, documented four matings and a gestation period of 27 to 28 days for *S. tridecemlineatus*; Asdell (1964) also reported a 28-day gestation period for the species.

Males are capable of reproduction when they emerge from hibernation. Wells (1935) and Asdell (1964) reported spermatozoa in testes as early as December, more than a month before the testes had reached maximum size and nearly three months before breeding.

Wade (1927), Wells (1935), Hohn (1966), McCarley (1966), and Flake (1974) all reported on the sexual condition of males, based on testes size. However, because of the advanced testicular activity necessary for spermatogenesis, testes size may not be a good indicator of the breeding period (Wells, 1935; Tomich, 1962). Two-year-old (or older) males reach breeding condition earlier than do one-year-old males (Wade, 1927; Wells, 1935; McCarley, 1966).

In females, ovaries begin to enlarge as early as the first of January (Asdell, 1964) and females are in "full heat" approximately five days after emergence (Foster, 1934). Asdell (1964) and McCarley (1966) reported that older females emerge in a more advanced sexual state than do young animals. Johnson *et al.* (1933) observed that females exhibit the usual stages of the es-

trous cycle and that they are induced ovulators. Foster (1934) noted that ovulation occurred within 48 hours after copulation and implantation probably occurred on the fifth day.

Litter sizes (means and standard deviations) have been reported for *S. tridecemlineatus* as follows: 8.1 ± 0.1 in Manitoba (Cridde, 1939), 8.7 ± 0.3 in Wisconsin (Rongstad, 1965), 9.0 ± 0.4 in Kansas (Johnson, 1931), and in Colorado 8.7 ± 1.1 (Flake, 1974) and 6.2 ± 1.4 (Streubel, 1975). In Texas, McCarley (1966) noted differences between litter sizes of old and young females; old females had a mean litter size of 7.0 ± 0.3 and younger females an average of 4.9 ± 0.6 . McCarley found in one year of his study that five of 22 females produced second litters; all five females were older than one year, and all conceived their first litter in April. McCarley's observations refuted statements by Wade (1927) and Asdell (1964) that *S. tridecemlineatus* is monestrous. However, the thirteen-lined ground squirrel could be monestrous in the northern part of its range and diestrous in the south.

Emergence dates of litters have been reported as 20 to 23 June in Wisconsin (Rongstad, 1965), 23 June to 5 July in Minnesota (Hohn, 1966), 16 June in Oklahoma (Bridgewater, 1966), and 8 June to 19 August in Texas (McCarley, 1966).

Conception dates, usually estimated from the time of litter emergence, have been reported as follows: 13 April to 4 May in Wisconsin (Rongstad, 1965), 25 April to 7 May in Minnesota (Hohn, 1966), 18 April in Oklahoma (Bridgewater, 1966), and 10 April to 22 June (second litter) in Texas (McCarley, 1966). The breeding period may be prolonged if, during the breeding period, a week or more of warm weather is followed by a period of cold weather (Foster, 1934). Apparently, cold weather suppresses estrus in the female.

Bridgewater (1966) observed the following ontogenic chronology of *S. tridecemlineatus*: light coat of hair beginning to emerge at postnatal day four, eyes opened during a two-day period from day 21 to 31, lower incisors appeared by day 17, upper incisors appeared two days later, molars appeared from day 24 on. The young acquired adult coloration from day 21 to 25, weaning began when the upper and lower incisors erupted and was essentially completed by day 28. In the field, weaning of young occurred along with emergence from burrows (Rongstad, 1965). Most adult modes of behavior are acquired by the young prior to emergence from the nest burrow (Bridgewater, 1966). Average weight increments of 1.3 g per day were noted through week 11 by Bridgewater (1966). The weight then (about 100 g) was well below average adult weight. Adult body length was attained by week 11.

ECOLOGY. *Spermophilus tridecemlineatus* is typically a grassland inhabitant. In Michigan and Wisconsin, the species extended its range after land was cleared for farming (Evans, 1951). Throughout its range, it is found predominantly on relatively high prairies and knolls; wet ground is avoided (Johnson, 1917). In Nebraska, Jones (1964) noted that the species preferred areas of short grass such as heavily grazed pastures, golf courses, and mowed borders of highways. In Kansas, it is generally considered a species of the native prairies and closely mown grasslands (Hall, 1955).

Johnson (1917) reported that *S. tridecemlineatus* preferred black or clay soil to sand. However, Whitaker (1972) trapped the species on a strip of sandy soil along the Wabash River, Indiana, and none were trapped in the river bottom or in upland silt-loam soils. In southeastern Wyoming, Maxwell and Brown (1968) found *S. tridecemlineatus* primarily in a grass community (*Bouteloua* sp., *Stipa* sp., *Aristida* sp.) where the vegetation was less than 250 mm tall and the soil a sandy loam.

Fitzpatrick (1925) related the habitat of *S. tridecemlineatus* to food supply and stated that the species was partly dependent on insects for food. He noted that the squirrels left areas where grazing was discontinued and moved into newly mown fields where insects were readily available. According to Weaver and Flory (1934), grazing causes an increase in thirteen-lined ground squirrels, but Phillips (1936) noted a reduction in burrow density on normally grazed and moderately overgrazed conditions.

Grant (1972) estimated population density on four experimental environmental control areas on the Pawnee National Grasslands in northeastern Colorado. He found populations lowest on sites receiving irrigation and fertilizer treatment where vegetation had the greatest density, and highest on the "natural" short-grass prairie where the vegetation had the lowest density. Johnson (1917) reported that the species was sometimes found in "thin woods or shrubbery." Population estimates by Rongstad (1965) were 2.5 to 5.0 per ha in the spring and 24.6 per ha follow-

ing emergence of young. Mitchell (1972) estimated 18 per ha on grazed prairie and Grant (1972) estimated 4.5 per ha on ungrazed pasture, both in Colorado.

McCarley (1966) found that in one year of his study the mortality rates of juvenile males was 96% and that of juvenile females was 74%. The following year, the mortality rates for juvenile males and females were 89 and 88%, respectively, but the following spring the male population appeared sharply reduced. Rongstad (1965) estimated the annual mortality to be 81% and found that the adult population declined slightly during the early part of the summer but then remained stationary. Most mortality among juveniles occurred prior to hibernation. Differential mortality of males and females probably is due to greater predation on juvenile males because of their greater tendency to disperse, especially into marginal habitats.

Both Rongstad (1965) and McCarley (1966) found initially even juvenile sex ratios. McCarley reported the overall sex ratios of one male to 2.8 females and one male to 2.1 females in two years of his study. Rongstad reported that the juvenile sex ratio remained even until early August and decreased progressively to one male to 1.7 females by the end of September.

McCarley (1966) observed that the cohesiveness of family units began breaking down 12 to 14 days after emergence of juveniles, and he speculated that the mock fighting prevalent in juvenile behavior may have contributed to dispersal. McCarley observed that juvenile males dispersed an average of 267 m from their nest burrows, whereas juvenile females dispersed an average of 189 m. Rongstad (1965) noted that juveniles began dispersing eight days after emergence, and he reported that 46 juvenile females dispersed a mean distance of 53 ± 4.7 m, whereas 45 juvenile males dispersed a mean distance of 80 ± 8.4 m.

The structure of burrows and burrow systems and their use has been studied by Johnson (1917), Fitzpatrick (1925), Evans (1951), and Rongstad (1965). Desha (1966) found that of 65 burrows (with a total of 100 entrances), 78% were shallow burrows in which squirrels simply sought retreat and 22% were below the average frost depth of the study area and contained nests.

The mean home range size of the males is 4.74 ± 0.85 ha (greatest, 12.7 ha) and for females 1.42 ± 0.20 ha (greatest, 5.7 ha) according to McCarley (1966). Males remain close to their nest burrows shortly after emergence from hibernation, then expand their home ranges to maximum size during the breeding season, and again restrict their movements in late June prior to entrance into estivation (McCarley, 1966; Streubel, 1975). Females restrict their movements after emergence; their primary period of home range expansion evidently occurs during pregnancy and lactation when litters are within the nest burrows. Once litters emerge, females again restrict home ranges until after young are weaned. Females tend to use the same home range area year after year (Evans, 1951; Rongstad, 1965).

Few direct observations of predation on the species are available in the literature. Streubel (1975) observed a bull snake (*Pituophis melanoleucus*) attempt to prey on a large male *S. tridecemlineatus*. The snake had already constricted around the ground squirrel, but released it when the observer approached too closely. McCarley (1966) observed predation on the species by roadrunners (*Geococcyx californicus*) in Texas.

Spermophilus tridecemlineatus has been observed preying on the following animals: house sparrows, *Passer domesticus* (Grubitz, 1963); small chickens (Bailey, 1923; Green, 1925); young cottontails, *Sylvilagus floridanus*, a six-lined racerunner, *Cnemidophorus sexlineatus* (Bridgewater and Penny 1966); and a blue racer, *Coluber constrictor* (Wistrand, 1974). Fitzpatrick (1925) and Streubel (1975) observed the species preying on grasshoppers and lepidopterous larvae.

Jones (1964) suggested that *S. tridecemlineatus* occurs sympatrically with *S. spilosoma* in Nebraska, but did not mention possible competition. In Colorado, Streubel (1975) found that competition between the two species was minimized because seasonal events of the annual cycle of *S. tridecemlineatus* occurred from two to four weeks before these events for *S. spilosoma*. Thus, despite their coexistence in the same habitat, competition was minimal. In about 150 hours of observation of the two species, only 20 interspecific encounters were observed.

Johnson (1917) reported that the stomach contents of *S. tridecemlineatus* consisted of nearly 50% animal matter. Fitzpatrick (1925) examined 82 stomachs of the species from Iowa; insects comprised about 70% of the diet in May, 30% in June and July, and increased to about 50% in August and September. Grass and seeds comprised the remainder of the stomach contents. Fitzpatrick noted that insect larvae were important in the spring, but that grasshoppers were the preferred food. He suggested that the

thirteen-lined ground squirrel acted as an important natural check on the increase of grasshoppers.

Whitaker (1972) examined 135 stomachs in Indiana and found lepidopterous larvae to be the most important food item, followed by clover leaves (*Trifolium* sp.). Seeds collectively amounted to 39.4% and animal matter 38.8% of the total volume. In Colorado, Streubel (1975) observed that the species fed heavily on lepidopterous larvae in May, but that flowers and fruit heads of *Festuca octoflora* and *Distichlis stricta* became important food sources in late May and June. Adult males appeared to feed almost entirely on fruit heads of *Festuca octoflora* prior to hibernation.

Bridgewater (1966) described laboratory breeding of the species in detail; he observed 12 litters born in captivity. Zimmerman (1974) also reported on laboratory breeding and observed nursing behavior. Zimny (1965) reported that capture of pregnant females does not prevent successful birth and rearing of young while in captivity; 32 of 35 females captured in one year bore litters in captivity, and of the 220 young born, 180 survived and grew to adulthood.

Internal parasites of *S. tridecemlineatus* include *Fasciola hepatica* (Ford and Lang, 1967), *Nippostrongylus brasiliensis* (Cross et al., 1964), and *Riticularia cielli* and ascarid larvae (Fritz et al., 1968). Whitaker (1972) studied the external parasites of *S. tridecemlineatus* and presented an extensive literature review.

Many ground squirrels have been subjected to control measures by man. Fitzpatrick (1925) reviewed the economic status of *S. tridecemlineatus* in Iowa. He concluded that the species is beneficial in that it consumes many insects that are injurious to crops, but that it can be detrimental by destroying newly planted grain. He reviewed the analyses of other workers, all of whom seemed to rate the species as neutral relative to economic impact on man. Burnett (1924) reached a similar conclusion.

BEHAVIOR. *Spermophilus tridecemlineatus* generally is considered to be nonterritorial (Hohn, 1966; Wistrand, 1974; Streubel, 1975), but individuals do defend specific areas; violation by another squirrel of such a defended area stimulates intraspecific agonistic behavior (Wistrand, 1974; Streubel, 1975). Streubel reported that individual squirrels concentrated their activities in relatively confined areas within what appeared to be larger home ranges, a form of social organization defined as "core monopolization" by Fisler (1969).

Agonism is not a major component of the behavioral repertoire of this species: Wistrand (1974) observed only 19 intraspecific interactions in approximately 150 hours of observation, and Streubel (1975) observed 45 intraspecific encounters during 61 hours of observation. He noted that the majority of agonistic encounters occurred during the breeding season.

Wistrand (1974) and Streubel (1975) described in detail the sexual behavior of *S. tridecemlineatus*. Streubel (1975) observed copulation on three occasions; one continued without interruption for 14.66 minutes, whereas the other two copulations both were interrupted by intruding males and lasted only 3.16 and 5.0 minutes, respectively. Wistrand (1974) speculated that copulation may occur in burrows.

In Colorado, sexual behavior occurred most frequently the first two weeks after emergence from hibernation, and thereafter was insignificant.

Bailey (1893) and McCarley (1966) described the call of *S. tridecemlineatus*. Bailey referred to the communicative function of the call and McCarley observed several behavior patterns in the auditory communication between females and their young. He found that the female alarm call was given only after the young emerged from their nest burrows, but that young did not respond to the alarm call for one to three days after emergence. After three to four days, the young responded by diving for a burrow entrance. A female did not give the call later than four weeks after her litter emerged.

McCarley (1966) also observed a distress call given by the young when they wandered from their nest burrow and apparently got lost. He described it as a "peep" call and observed that a female would retrieve her young when she heard the call.

Wistrand (1974) noted that the primary means of locomotion by *S. tridecemlineatus* was walking, which occurred while the animal was in three different positions, and that individuals ran in a quadrupedal ricochet fashion as described by Eisenberg (1968). Wistrand (1974) and Streubel (1975) described the various postures assumed while feeding and while alert, which were similar to those observed in *S. armatus* (Balph and Stokes, 1963) and *S. spilosoma* (Streubel, 1975).

According to Streubel (1975), foraging and feeding comprises about 70% of the aboveground time of a thirteen-lined ground squirrel, alert behavior 12%, maintenance behavior (including sunning, grooming, eliminating, resting in the shade, sandbathing) 8%, nesting activities 6%, and investigative (nonforaging) behavior about 3%. Sexual and agonistic behavior made up only a small percentage of the total behavior budget.

Bridgewater (1966) studied the development of behavior in young and observed that the attainment of characteristic adult behavior patterns appeared to coincide with weaning.

McCarley (1966) noted that activity in March and April was represented by a unimodal curve with a peak between noon and 1400. In May and early June, the curve lengthened out and activity was greatest from 0900 to 1700. From late June through early September, the activity curve was bimodal with peaks in mid-morning and late afternoon. Activity was inhibited when the temperature was less than 10°C and surface winds were more than 25 km/hr. Individuals were not consistent in their daily activity patterns, and changeable weather made generalizations difficult.

The annual activity cycle includes a long period of hibernation. In Texas, McCarley (1966) recorded the mean hibernation time of six males as 237 days and that for 28 females as 240 days. He noted that the onset of hibernation coincided with decreasing photoperiod length, increased temperatures, and accumulation of fat deposits. In Colorado the species emerged from hibernation generally between 1 and 15 April, and more males than females seemed to be present during the first week after emergence (Streubel, 1975). Males entered hibernation in July, females in late July and early August, and most young in early September (Streubel, 1975). Streubel estimated the seasonal periods of activity to be 100 to 120 days for females.

Spermophilus tridecemlineatus has been used for the study of hibernation by many investigators. Fitzpatrick (1925) suggested that cold weather in the autumn reduced activity of the species. He further observed that only one individual existed per hibernation burrow, hibernation burrows had plugged entrances, the pulse rate of hibernating animals was reduced from 200 to four per minute, and respiration was reduced to "practically zero." Johnson (1928) found the body temperature of hibernating *S. tridecemlineatus* to be about 1 to 3°C above the environmental temperature.

Behavior changes prior to hibernation: individuals become more aggressive and intolerant of others (Wade, 1930), their home range is reduced, and they become relatively inactive (Streubel, 1975). Mrosovsky (1971) suggested that the intolerance may tend to limit one squirrel to a nest burrow. The greatest pre-hibernation weight gain occurs during this period of inactivity (Hohn, 1966), but the intake of food does not increase significantly (Richter, 1967). Johnson (1930) observed that fat animals enter hibernation more readily and sooner than do thin animals.

Hibernation is interrupted by periodic arousal. Intervals between arousals vary from 10 to 26 days (Johnson, 1931; Fisher, 1964; Folk, 1957). The stimulus for arousal has been studied by Fisher and Mrosovsky (1970), who found that potassium may cause arousal. Johnson (1929) found that a decrease in environmental temperature acted as an arousal stimulus, but he noted that if the environmental temperature approached 0°C, death might occur rather than arousal.

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Sylvilagus audubonii. By Joseph A. Chapman and Gale R. Willner

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Sylvilagus audubonii (Baird, 1857)

Desert or Audubon's Cottontail

- Lepus audubonii* Baird, 1858:608. Type locality San Francisco, California.
Lepus baileyi Merriam, 1897:148. Type locality Spring Creek, E side of Big Horn Basin, Wyoming.
Lepus laticinctus Elliot, 1903:254. Type locality Oro Grande, Mohave Desert, San Bernardino Co., California.
Sylvilagus audubonii Nelson, 1909:214. First use of name combination.

CONTEXT AND CONTENT. Order Lagomorpha, Family Leporidae, Genus *Sylvilagus*, Subgenus *Sylvilagus*. There are about 14 recognized species of the genus *Sylvilagus*. There are 12 recognized living subspecies of *S. audubonii* (Hall, 1951:164-166; Hall and Kelson, 1959:265-268) as follows:

- S. a. audubonii* (Baird, 1858:608), see above.
S. a. arizonae (J. A. Allen, 1877:332). Type locality Beals Spring, 50 mi. W Fort Whipple, Arizona (*laticinctus* Elliot, *major* Mearns, and *rufipes* Elliot are synonyms).
S. a. minor (Mearns, 1896:557). Type locality El Paso, Texas.
S. a. baileyi (Merriam, 1897:148), see above.
S. a. confinis (J. A. Allen, 1898:146). Type locality Playa María, Baja, California.
S. a. sanctidiegi (Miller, 1899:387). Type locality, Mexican Boundary Monument no. 258, (Pacific Ocean) San Diego Co., California.
S. a. goldmani (Nelson, 1904:107). Type locality Culiacán, Sinaloa.
S. a. parvulus (J. A. Allen, 1904:34). Type locality Apam, Hidalgo.
S. a. cedrophilus Nelson, 1907:83. Type locality Cactus Flat, 20 mi. N Cliff, New Mexico.
S. a. neomexicanus Nelson, 1907:83. Type locality Fort Sumner, New Mexico.
S. a. vallicola Nelson, 1907:82. Type locality San Emigdio Ranch, Kern Co., California.
S. a. warreni Nelson, 1907:83. Type locality Coventry, Colorado.

DIAGNOSIS. Size is relatively large for the genus. Hind legs are long; the feet are slender and do not possess the dense, long pelage of some other members of the genus. Ears are long, pointed, and sparsely haired on the inner concave surface. Vibrissae are generally black. The tail is large, dark above and white underneath. Cranial features are: long rostrum; prominent and upturned supraorbital processes; broad postorbital extensions of the supraorbital processes; general palatine foramina may be constricted posteriorly; palatal bridge medium in length; auditory bullae much inflated. Dental features are: molariform teeth relatively large; anterior surface of first upper molariform tooth having three re-entrant angles; lateral diameters of posterior halves of the second to the fourth lower molariform teeth about 80% of the lateral diameters of the anterior halves; ridge of enamel separating the molariform teeth into anterior and posterior sections strongly crenulated along the median two-thirds (modified from Orr, 1940; Hall, 1951). The skull is illustrated in Figure 1.

GENERAL CHARACTERISTICS. Descriptions are in Nelson (1909:214-237), Orr (1940:110-126), and Hall and Kelson (1959:265). Females are about 2% larger than males (Orr, 1940:20). The dental formula is $i\ 2/1, p\ 3/2, m\ 3/3$, total 28.

Some average external measurements (in mm) for *S. a. audubonii* adult males are: total length, 385.4 (372 to 397); length of tail, 56.0 (45 to 60); length of hind foot, 88.6 (83 to 94); length of ear from notch, 70.5 (70 to 71). Corresponding measurements in females are: 385.4 (375 to 400); 51.3 (39 to 56); 90.1 (81 to 93); 72.8 (72 to 75). Weight of adult males averaged 841.0 (755.7 to 907.5) g and adult females averaged 988.5 (883 to 1250) g (Orr, 1940).

Cranial measurements in millimeters of adult males of *S. a. audubonii* are: basilar length 53.0 (52.0 to 54.1); zygomatic breadth, 34.7 (33.9 to 35.2); postorbital constriction, 11.8 (11.0 to 12.6); length of nasal, 29.4 (28.2 to 30.4); width of nasals, 14.0 (13.2 to 15.4); length of molar series, 13.1 (12.1 to 12.6); diameter of external auditory meatus, 4.4 (4.2 to 4.5); breadth of braincase, 22.6 (21.6 to 23.6); length of palatal bridge, 5.5 (5.1 to 5.9). Corresponding measurements in females are: 53.2 (51.9 to 54.5); 35.2 (34.0 to 36.7); 12.2 (11.2 to 12.8); 29.4 (27.7 to 31.0); 14.1 (12.7 to 15.9); 13.1 (12.2 to 14.3); 4.4 (3.9 to 4.7); 22.4 (21.6 to 23.2); 5.6 (5.0 to 6.1). See Orr, 1940.

DISTRIBUTION. The species ranges from near the Canadian border in Montana south to central México and as far west as the Pacific coast (figure 2). The species is typically an inhabitant of arid regions. *S. audubonii* ranges in elevation (Orr, 1940) from below sea level in Death Valley, California, to at least 1829 m (6000 ft.). According to Findley (1969), this cottontail occurs in woodlands, grasslands, and deserts at all lower elevations in the Southwest.

FOSSIL RECORDS. The fossil history of *S. audubonii* is well documented from Pleistocene deposits. Hay (1927) and Dice (1925) referred specimens from the Rancho La Brea deposits to the subspecies *S. audubonii pix*, which is now extinct. Specimens of *Sylvilagus* from the Pleistocene Slaton local fauna of Texas also are believed to be *S. audubonii* (Dalquest, 1967).

FORM AND FUNCTION. There are four pairs of mammae: one pair pectoral, two pairs abdominal, and one pair inguinal (Dice, 1926).

Seasonal physiological responses of *S. audubonii* were studied by Hinds (1973) near Tucson, Arizona. A shift upward of the thermoneutral zone occurs from winter to summer and basal metabolism decreases by 18% during the same period. There is no relationship between the percent of metabolic heat production dissipated by evaporative heat loss and season of the year; it equals 100% at an ambient temperature of 41.4° C. Body temperature is 38.3° C when ambient temperatures are below 30° C and is not affected by season of the year. Body temperature equals ambient temperature of 41.9° C in summer and a predicted 42.9° C during the winter. According to Hinds (1973:708) "*Sylvilagus audubonii* survives in the desert by taking advantage of every possibility to minimize the heat load and water expenditure." A relatively high evaporative cooling capacity and high lethal body temperature of 44.8° C provide a safety factor for desert cottontails if avoidance is not possible.

ONTOGENY AND REPRODUCTION. The breeding season in California extends for seven months from December through June (Orr, 1940); however, Ingles (1941) found breeding the year around. The breeding season in Arizona lasts eight to nine months from January until August or September (Sowls, 1957; Stout, 1970). In Texas, the breeding season does not begin until late February or early March (Chapman and Morgan, 1974).

Ingles (1941) found the nests of five female *S. audubonii*, three of which contained young. The nests were pear-shaped excavations in the ground, 150 to 250 mm deep, with a 150 mm diameter near the bottom. In all the nests, the axis of the excavation was inclined to the north. The cavity was first lined with a thick layer of fine grass and weeds, then filled with rabbit fur, within which the young were found. The type of site selected for a nest or burrow may vary with habitat (Fitch, 1947).

Ingles (1941) gave the following approximate measurements for neonates: total length, 90 mm; tail, 10 mm; hind foot, 18 mm; and ear, 15 mm. Hair is sparse on the young and they lack the white spot on the forehead present in the eastern cottontail (*S. floridanus*). When the hair in the nest is touched, the young rabbit lunges upward and utters a "gupp" sound, which may be a call response prior to nursing. Ingles (1941) found that the female nurses the young by crouching over the nest. On one occasion,

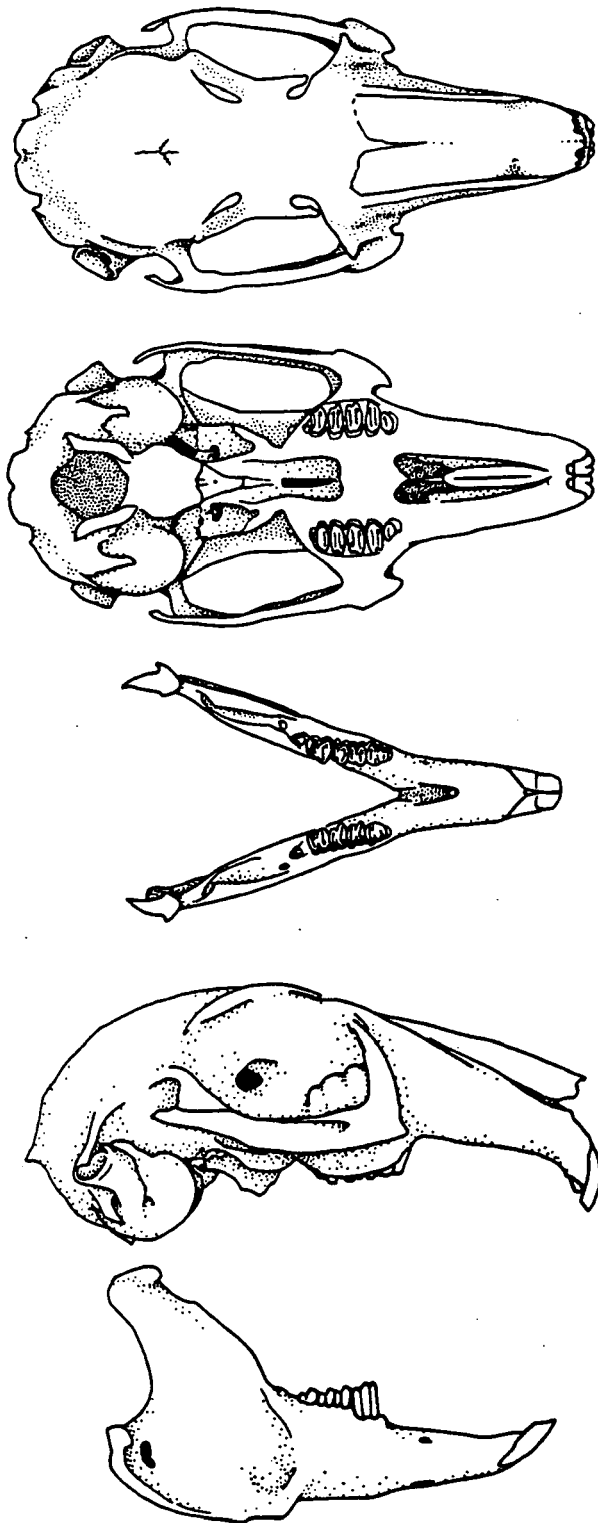


FIGURE 1. Skull of *Sylvilagus audubonii cedrophilus*. From top to bottom, dorsal and ventral view of cranium, dorsal view of dentary bone, lateral view of cranium, and lateral view of dentary. Drawn from an adult female (USNM 160741) collected at Socorro, New Mexico, on 20 August 1909.

the young cottontails were fed between the hours 1300 and 1400 after 31.5 hours had elapsed since the previous feeding. Later, the young were fed at hour 2000 following 30 hours without a feeding.

✓ By postnatal day 10 the young have both eyes open (Ingles, 1941). They leave the nest between days 10 and 14 and remain near the nest for up to three weeks.

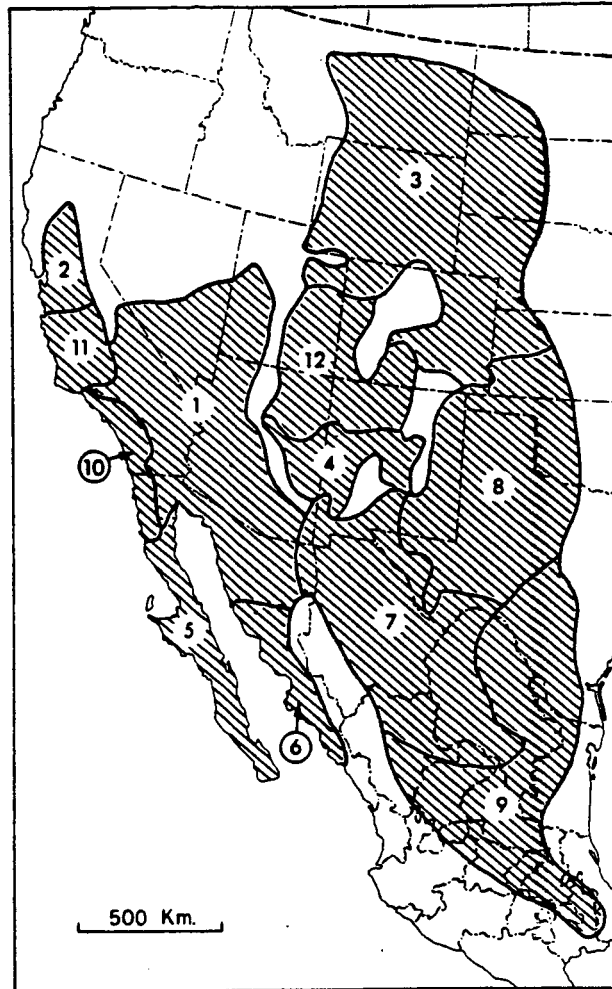


FIGURE 2. Distribution of *Sylvilagus audubonii* and its subspecies in North America: 1, *S. a. arizonae*; 2, *S. a. audubonii*; 3, *S. a. baileyi*; 4, *S. a. cedrophilus*; 5, *S. a. confinis*; 6, *S. a. goldmani*; 7, *S. a. minor*; 8, *S. a. neomexicanus*; 9, *S. a. parvulus*; 10, *S. a. sanctidiegi*; 11, *S. a. vallicola*; 12, *S. a. warreni* (adapted from Hall and Kelson, 1959).

The desert cottontail appears to be less fecund than some other members of the genus. Mean litter sizes reported for Arizona are 2.9 (Sowls, 1957) and 2.7 (Stout, 1970). The mean size for first litters in Texas is 2.6 (Chapman and Morgan, 1974). In California, Orr (1940) reported a mean litter size of 3.6.

In Texas, the mean ovulation rate for rabbits pregnant with their first litters was 3.30, indicating that 6% of the ova failed to implant; 16% of the embryos were resorbed (Chapman and Morgan, 1974). Stout (1970) found that 40% of the *S. audubonii* examined from Arizona contained visibly resorbing embryos.

Apparently, sexual maturity is attained as early as day 80 (Stout, 1970). The gestation period is 28 days (Dice, 1929).

Assuming that *S. audubonii* is a post-partum breeder, as are other members of the genus, these rabbits could produce a large number of litters each year. However, Sowls (1957) estimated that five was a reasonable average for litters actually produced in Arizona.

ECOLOGY. The species is found throughout lower elevations and deserts of the Southwest and the intermountain region, hence its vernacular name "desert cottontail." In California, the species occurs in heavy brush and willows along rivers where Dice (1926) noted some burrows of this cottontail. Dice further reported *S. audubonii* living under old buildings, around lumber piles and brush piles, and in fields where weeds made a thick mat a meter or so high. In winter, these rabbits remain hidden in thickets during the day, but in late spring they may be seen moving about at any time (Ingles, 1941).

In pinyon-juniper woodlands, shrubs are the primary cover for desert cottontails (Kundacli and Reynolds, 1972); 170 to 220

downed trees or shrubs per hectare provided the best habitat. Uprooting, piling, and burning all the pinyon-juniper trees in an area of New Mexico was found to depress the population of cottontails (Kundaeli and Reynolds, 1972).

The species mostly inhabits the Lower Sonoran Life-Zone in California (Orr, 1940). Plant species associated with this rabbit in Butte County, California, were willow (*Salix* sp.), buttonwillow (*Cephalanthus occidentalis*), and wild grape (*Vitis californica*). In the Berkeley Hills, the species was most often associated with arroyo willow (*S. lasiolepis*). In Fresno County, it was seen at the edges of brushland (*Adenostoma fasciculatum*) and on hillsides interspersed with *Eriodictyon* and *Eriogonum* sp. Occasionally, the species is found where there is little or no vegetative cover (Orr, 1940). In southern Nevada, these cottontails were commonly associated with arrow-weed (*Pluchea sericea*), screw-bean mesquite (*Prosopis pubescens*), and catclaw (*Acacia greggii*) (Orr, 1940).

Cattle grazing affects the abundance of desert cottontails, which are most common in pastures under moderate-summer and moderate-winter grazing pressures (Flinders and Hansen, 1975).

Home range size of desert cottontails in California was found to be equal to the size of the blackberry clumps they inhabited (Ingles, 1941). This finding was also reported for the brush rabbit, *S. bachmani*, in western Oregon (Chapman, 1971). The home range of males may be as much as 15 acres (6.1 ha), whereas that of females may be less than 1 acre (0.4 ha) (Ingles, 1941). Ingles reported that in his study area the species rarely used holes, relying on thick brambles for cover. Little difference in the size of home ranges was found for males and females on the San Joaquin Experimental Range; the size was 8 or 9 acres (3.2 to 3.6 ha) for both sexes (Fitch, 1947). Young individuals have smaller foraging ranges than do adults (Fitch, 1947).

Homing ability was reported by Fitch (1947). Three rabbits displaced distances of from 4400 ft. (1341 m) to 3150 ft. (960 m) returned to their original home ranges. However, 10 others established themselves at the release sites. Fitch (1947) observed shifting of home ranges, which he believed resulted from changes in critically needed food or succulence.

On the San Joaquin Experimental Range, the following number of cottontails on 80 acres (32.4 ha) was reported: 1939, 153; 1940, 53; and 1941, 95 (Fitch, 1947). The following densities per hectare were calculated: 1939, 4.7; 1940, 1.6; and 1941, 2.9. A density of 6.6 desert cottontails per acre (16.3 per ha) was reported by Flinders and Hansen (1973) for northeastern Colorado.

Seasonal availability of food plants was the most important influence of feeding cottontails according to Fitch (1947).

Orr (1940) also reported seasonal variation in desert cottontail diets, consisting of various unidentified grasses, foxtail grass (*Hordeum murinum*), galingale (*Cyperus* sp.), sedge (*Carex* sp.), rush (*Juncus* sp.), willow, valley oak (*Quercus lobata*), miner's lettuce (*Montia perfoliata*), blackberry (*Rubus vitifolius*), California wild rose (*Rosa californica*), hoarhound (*Marrubium vulgare*), *Baccharis douglasii*, and California mugwort (*Artemisia vulgaris*). Cottontails living in fields depended almost entirely on grasses for food (Orr, 1940).

In the Sacramento Valley, California, the following plants are important foods: Johnson grass (*Holcus halepensis*), Bermuda grass (*Cynodon dactylon*), blue grass (*Poa pratensis*), rigput grass (*Bromus rigidus*), wheat grass (*Agropyron caninum*), morning glory (*Convolvulus* sp.), bull mallow (*Malva borealis*), honey suckle (*Lonicera* sp.), and sow thistle (*Sonchus asper*). In addition, cultivated hollyhock, carrots (pulled), acorns of valley oak and fruit of almond and peach are eaten (Ingles, 1941).

Hall (1916), Herman and Jankieurecz (1943), Stiles (1896), and Erickson (1947) reported the following internal parasites from *S. audubonii*: cestodes, *Cittotaenia variabilis*, *Raillietina retractilis*, and *Taenia pistiformis*; nematodes, *Dermatoxys veligera*, *Nematodirus leporis*, *Obeliscoides cuniculi*, and *Passalurus ambiguus*. Fitch (1947) also reported two intestinal protozoans (*Trichomonas* and *Chilomastix*). Fleas, *Spilopsyllus* sp. and *Ctenocephaloides felis*, and bots, *Cuterebra* sp. (Hall, 1921; Ingles, 1941; Fitch, 1947) also have been reported.

Mammalian predators include: coyote, *Canis latrans*; gray fox, *Urocyon cinereoargenteus*; badger, *Taxidea taxus*; bobcat, *Lynx rufus*; raccoon, *Procyon lotor*; skunk, *Mephitis mephitis*; mink, *Mustela vison*; and kit fox, *Vulpes macrotis*. Avian predators include: red-tailed hawk, *Buteo borealis*; Cooper's hawk, *Accipiter cooperi*; marsh hawk, *Circus hudsonius*; Swainson's hawk, *B. swainsoni*; golden eagle, *Aquila chrysaetos*; horned owl, *Bubo virginianus*; and barn owl, *Tyto alba*. Reptilian predators include rattlesnakes (*Crotalus confluenti*) and gopher snakes (*Pi-*

uophis catenifer). Domestic dogs and cats also prey on *S. audubonii*. Records of predation are from Orr (1940); Ingles (1941), and Fitch (1947).

Ingles (1941) believed that this cottontail is short-lived. The greatest age in his study was 19 months and only seven of 29 rabbits lived longer than one year.

BEHAVIOR. The desert cottontail is most active in the early morning and evening (Ingles, 1941). Rabbits sought shelter when it rained, especially if the rain was accompanied by high winds. There was also clear evidence that the rabbits preferred still nights for their activities. They were inactive at temperatures above 80°F (Ingles, 1941).

These cottontails swim with rapid strokes, much as does a dog, and move the legs alternately (Ingles, 1941). They also climb trees and brush piles (Sumner, 1931; Ingles, 1941). The only other member of the genus known to do this is the brush rabbit, *S. bachmani* (Chapman, 1974).

Individuals take advantage of the alarm calls of other species (Orr, 1940; Ingles, 1941): the alarm behavior of sparrows warned cottontails on at least one occasion observed by Ingles, and they react also to the alarm signals of California ground squirrels (*Spermophilus beecheyi*) according to Orr (1940). The tail of *S. audubonii* is used as an alarm signal. When the tail is raised so as to expose the maximum amount of white, the animals run for cover; when the tail points toward the ground showing little white, the rabbits move about leisurely.

Freezing, a rigid posture adopted during times of uncertainty or possible danger, has been reported for *S. audubonii*. However, when an animal is truly alarmed, it dashes toward the nearest brush (Cushing, 1939). Orr (1940) reported that brush-inhabiting cottontails invariably ran for cover when alarmed.

On one occasion, Ingles (1941) heard a desert cottontail squeal while being removed from a trap. Orr (1940) reported that wounded rabbits often emitted a short, high-pitched squeal. One rabbit also attempted to bite while being handled (Ingles, 1941). Orr (1940) reported a thumping of the hind feet as an alarm signal.

Ingles (1941) observed as many as three females foraging together without antagonism. Interaction between males was observed; on one occasion, one male chased another away from a favored station. These rabbits may occasionally fight each other, although Ingles did not observe this.

In open situations, these rabbits frequent burrows during most of their daily periods of inactivity (Orr, 1940). They hide by sitting in forms, small cleared places on the ground. Desert cottontails are more wary in the late morning and early evening than at dawn or dusk (Orr, 1940).

With regard to locomotion, Orr (1940:133) stated: "When running, members of this species take small bounds into the air in order to clear tufts of grass and other obstacles which may be in their way. As open patches of ground are chosen for running, cottontails seldom appear to travel in a straight line. Individuals were observed at times running as far as 100 yards [91 m] in the open, pursuing a somewhat zig-zag course." The speed of a running cottontail was estimated at 15 miles (24.13 km) per hour (Grinnell and Storer, 1924).

Orr (1940:133) reported that: "At dawn or dusk, the white tails of these animals appear to be especially prominent as the rest of the body blends well in color with the landscape. Cottontails seen at such times were frequently undiscernable when viewed from the side at a distance of ten yards [9 m], whereas individuals which were running directly away from the observer were easily followed by the eye to a distance of 70 yards [64 m] because of the white tail. Immediately upon their stopping, however, such rabbits are lost to sight. This may be an adaptation to confuse pursuing enemies. One, upon watching a running cottontail under such circumstances, tends to look only at a conspicuous white tail. When this suddenly disappears, due either to their stopping or veering off their course, the animal seems to vanish completely."

In cottontail territories, low prominences, such as logs and tree stumps, invariably had feces deposited on them (Orr, 1940). These places were believed to be lookout posts used after dark. Desert cottontails are not gregarious. They and jackrabbits have been observed feeding together without animosity. Similar observations have been made with regard to the California ground squirrel.

The type of cover is an important factor in determining feeding sites. In areas of brushy cover adjacent to open grassland, much of the late morning and early evening feeding takes place under the shelter of brush. Habitat, season of the year, fog, rain,

and wind are important factors that affect daily periods of feeding. Maximum numbers of these cottontails always were observed feeding at dawn, if the mornings were not foggy or windy. Wind appeared to interfere greatly with normal feeding. Light intensity was also an important factor determining the distance from shelter a cottontail will venture for food. After dark, cottontails were observed to travel up to 110 yards (100 m) from cover (Orr, 1940).

In open situations, desert cottontails feed by taking a number of successive mouthfuls. The head is then elevated and chewing begins. The terminal portions of plants are generally taken. When feeding on low-growing grass, rabbits appear to extend the body along the ground. The neck is stretched out and the front feet edge forward. When food can no longer be reached, the hind feet are brought forward with a hop. When eating, brush rabbits were frequently seen standing on their hind legs. Rabbits feeding in this manner leave a twig characteristically cut at a 45° angle (Orr, 1940).

GENETICS. The desert cottontail has a diploid chromosome number of 42 (Worthington and Sutton, 1966) with five metacentric pairs, 11 submetacentric pairs, and four acrocentric pairs of autosomes. *Sylvilagus audubonii* differs from *S. nuttallii* in having one exceptionally large pair of acrocentric chromosomes. The Y chromosome is dotlike (Worthington and Sutton, 1966).

Chapman and Morgan (1973) electrophoretically examined the blood of several species and subspecies of cottontails. They studied 18 individuals of *S. audubonii neomexicanus* and reported that the species had a unique serum protein pattern when compared to the serum of four subspecies of *S. floridanus* and *S. transitionalis*. The *S. a. neomexicanus* serum contained 20 serum proteins with several variant protein systems including a polymorphic transferrin. Electrophenograms and schematic drawings were presented for several members of *Sylvilagus* including *S. audubonii*. Johnson (1968) also electrophoretically examined several *Sylvilagus* including one *S. audubonii*.

REMARKS. The desert cottontail has been inadvertently (along with *S. floridanus*) introduced widely into Maryland and probably other regions of the eastern United States. However, there is no evidence that this species has become established as a result of these introductions.

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Sylvilagus floridanus. By Joseph A. Chapman, J. Gregory Hockman, and Magaly M. Ojeda C.

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Sylvilagus floridanus (J. A. Allen)

Eastern Cottontail

- Lepus sylvaticus* Bachman (1837:403). No type or type locality. Name given to the "common gray rabbit" of eastern United States. Name preoccupied by *Lepus borealis sylvaticus* Nilsson, 1832, from Sweden.
- Lepus orizabae* Merriam (1893:143). Type from Mt. Orizaba, 9500 ft., Puebla, Mexico.
- Lepus nigronuchalis* Hartert (1894:40). Type from Aruba Island, Netherlands, off the coast of Venezuela near the Paraguana Peninsula.
- Lepus cumanicus* Thomas (1897:552). Type from Cumana, Sucre Prov., Venezuela.
- Lepus margaritae* Miller (1898:97). Type from Margarita Island, Venezuela.
- Lepus (Sylvilagus) superciliaris* J. A. Allen (1899a:196). Type from Bonda, near Santa Marta, Magdalena Prov., Colombia.
- Sylvilagus orinoci* Thomas (1900:356). Type from Maipures, upper Rio Orinoco, Vichada Prov., Colombia.
- Lepus simplicianus* Miller (1902:81). Type from Brownsville, Texas.
- Lepus (Sylvilagus) durangae* J. A. Allen (1903:609). Type from Rancho Bailon, northwestern Durango, Mexico.
- Lepus (Sylvilagus) russatus* J. A. Allen (1904:31). Type from Pasa Nueva, southern Veracruz, Mexico.
- Sylvilagus cognatus* Nelson (1907:82). Type from [Tajique] near summit of Manzano Mountains, 10,000 ft., New Mexico.
- Sylvilagus avius* Osgood (1910:29). Type from Testigo Grande, Islas de los Testigos, Venezuela.
- Sylvilagus cumanicus* Allen (1911:249). Type from near Maracaibo, Lake Maracaibo, northern Zulia, Venezuela.
- Sylvilagus valenciae* Thomas (1914:413). Type from El Trompillo, southeast of Lake Valencia, Carabobo Prov., 1300 ft., Venezuela.
- Sylvilagus boylei* J. A. Allen (1916:84). Type from La Playa, northwest of Barranquilla, Colombia.
- Sylvilagus purgatus* Thomas (1920:32). Type from Purificacion, Rio Magdalena, Tolima Prov., 292 m, Colombia.

CONTEXT AND CONTENT. Order Lagomorpha, Family Leporidae, Genus *Sylvilagus*, Subgenus *Sylvilagus*. There are about 14 recognized living species in the genus and 35 recognized subspecies of *S. floridanus* (Hall, 1951; Hall and Kelson, 1959; Hershkovitz, 1950; Hoffmeister and Lee, 1963) as follows:

- S. f. alacer* (Bangs, 1896:136). Type from Stilwell, Indian Territory [Boston Mountains, Adair County, Oklahoma].
- S. f. ammophilus* A. H. Howell (1939:365). Type from "Oak Lodge," on Peninsula opposite Micco, Florida.
- S. f. avius* Osgood (1910:29), see above.
- S. f. aztecus* (J. A. Allen, 1890a:188). Type from Tehuantepec [City], Oaxaca, Mexico.
- S. f. chapmani* (J. A. Allen, 1899b: 12). Type from Corpus Christi, Nueces County, Texas (*caniculus* Miller and *simplicianus* Miller are synonyms).
- S. f. chiapensis* (Nelson, 1904:106). Type from San Cristobal, Chiapas, Mexico.
- S. f. cognatus* Nelson (1907:82), see above.
- S. f. connectens* (Nelson 1904:105). Type from Chichicastle, central Veracruz, Mexico.
- S. f. continentis* Osgood (1912:57). Type from near Maracaibo, Lake Maracaibo, northern Zulia, Venezuela.
- S. f. costaricensis* Harris (1933:3). Type from Hacienda Santa Maria, Province of Guanacaste, 3200 ft., Costa Rica.
- S. f. cumanicus* (Thomas 1897:552), see above (*margaritae* Thomas and *superciliaris* Thomas are synonyms).
- S. f. floridanus* (J. A. Allen 1890b:160). Type from Sebastian River, Brevard County, Florida.

- S. f. hesperius* Hoffmeister and Lee (1963:140). Type from 5.25 mi. SE Kingman, Hualpai Mountains, Mohave County, Arizona.
- S. f. hitchensi* Mearns (1911:227). Type from Smiths Island, Northampton County, Virginia.
- S. f. holzneri* (Mearns, 1896:554). Type from Douglas spruce zone, near summit of Huachuca Mountains [Cochise County], Arizona (*rigidus* Mearns and *durangae* J. A. Allen are synonyms).
- S. f. hondurensis* Goldman (1932:122). Type from Monte Redondo, approximately 30 mi. NW Tegucigalpa, 5100 ft., Honduras.
- S. f. llanensis* Blair (1938:1). Type from old "F" Ranch headquarters, Quitaque, Briscoe County, Texas.
- S. f. mallurus* (Thomas, 1898:320). Type from Raleigh, Wake County, North Carolina (*sylvaticus* Bachman is a synonym).
- S. f. margaritae* (Miller, 1898:97), see above.
- S. f. mearnsi* (J. A. Allen, 1894:171). Type from Fort Snelling, Hennepin County, Minnesota.
- S. f. nelsoni* Baker (1955:611). Type from 22 mi. S, 5 mi. W Ocampo, 5925 ft., Coahuila.
- S. f. nigronuchalis* (Hartert, 1894:40), see above.
- S. f. orinoci* Thomas (1900:356), see above.
- S. f. orizabae* (Merriam, 1893:143). Type from Mt. Orizaba, 9500 ft., Puebla, Mexico (*persultator* Elliot is a synonym).
- S. f. paulsoni* Schwartz (1956:147). Type from 6 mi. N Homestead, Dade County, Florida.
- S. f. purgatus* Thomas (1920:32), see above.
- S. f. restrictus* Nelson (1907:82). Type from Zapotlan, Jalisco, Mexico.
- S. f. robustus* (Bailey, 1905:159). Type from 6000 ft. Davis Mountains, Jeff Davis County, Texas.
- S. f. russatus* (J. A. Allen, 1904:31), see above.
- S. f. similis* Nelson (1907:82). Type from Valentine [Cherry Co.], Nebraska.
- S. f. subcinctus* (Miller, 1899:386). Type from Hacienda El Molino, near Negrete, Michoacan.
- S. f. superciliaris* (Allen, 1899a:196), see above (*boylei* Allen is a synonym).
- S. f. valenciae* Thomas (1914:413), see above.
- S. f. yucatanicus* (Miller, 1899:384). Type from Merida, Yucatan.



FIGURE 1. *Sylvilagus floridanus*. Photo by Leonard Lee Rue II.

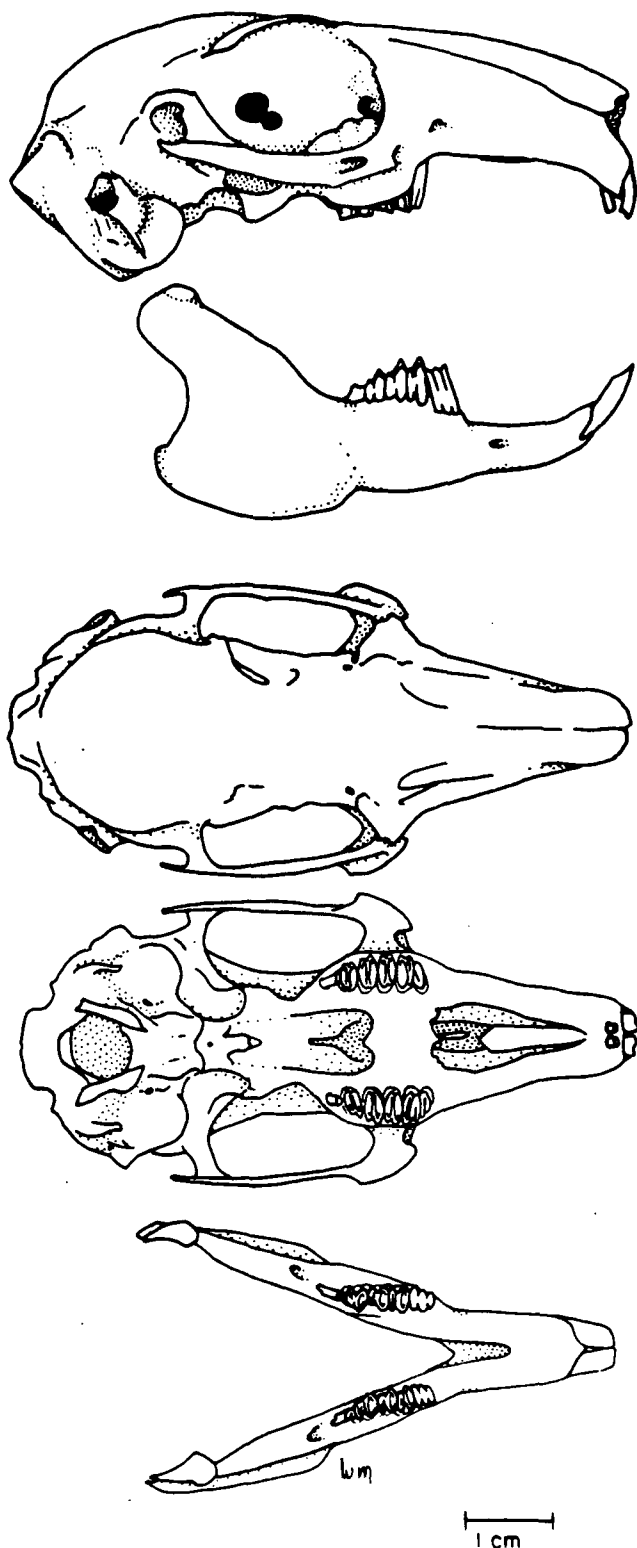


FIGURE 2. Skull and mandible of *Sylvilagus floridanus* (male [AEL-940] from St. Clements Island, Potomac River, St. Marys County, Maryland). Drawing by Wilma Martin. Above, lateral view of cranium and mandible; middle dorsal view; below, ventral view of cranium and dorsal view of mandible.

DIAGNOSIS. This is a large cottontail (Fig. 1). The pelage is long and dense, brownish to greyish on the upper parts and white on the underside of the body and tail. The South American forms have a nuchal patch which varies from yellowish-brown to black in the different subspecies. The skull has a transversely

thickened, posterior extension of the supraorbital process of the frontal. Because this species has the widest distribution of any *Sylvilagus*, characteristics which are diagnostic for the species vary according to locality. However, in local areas it is generally easy to distinguish *S. floridanus* from other sympatric rabbits. The only exception is the separation of *S. floridanus* and *S. transitionalis* on the basis of pelage where the two occur sympatrically along the Appalachians and in New England. These two rabbits are easily identified on the basis of cranial characters (for a detailed description of the differences between these species and photographic illustrations see Chapman, 1975). The skull is illustrated in Fig. 2.

GENERAL CHARACTERS. Descriptions are given in Nelson (1909), Hall (1951), and Hall and Kelson (1959). Females are about 1% larger than males (Chapman and Morgan, 1973). The dental formula is $i\ 2/1, p\ 3/2, m\ 3/3$, total 28.

Some average external measurements (in mm) for 33 to 35 *S. floridanus* males, with ranges in parentheses, are: total length, 427.0 (395 to 456); length of tail, 44.9 (25 to 54); length of hind foot, 95.4 (90 to 105); length of ear (from notch), 61.5 (55 to 67). Corresponding measurements for 41 to 42 females are: 433.2 (400 to 477); 44.8 (28 to 61); 95.4 (90 to 104); 61.1 (56 to 67) (Chapman and Morgan, 1973). Weight of 64 adult males averaged 1,134.4 g (range, 801 to 1,411), and 36 adult females averaged 1,244.0 (842 to 1,533) (Chapman and Morgan, 1973).

Mean cranial measurements (in mm \pm SD) of 59 to 78 adult *S. floridanus* from Maryland are: basilar length, 56.17 ± 1.98 ; zygomatic breadth, 36.30 ± 1.10 ; postorbital constriction, 12.24 ± 0.87 ; length of nasals, 31.51 ± 1.43 ; width of nasals, 15.00 ± 0.89 ; length of maxillary toothrow, 13.95 ± 0.58 ; diameter of external auditory meatus, 4.11 ± 0.19 ; breadth of brain case, 23.62 ± 0.68 ; length of palatal bridge, 6.33 ± 0.62 ; depth of rostrum, 14.66 ± 0.67 ; parietal breadth, 24.24 ± 0.87 ; length of bulla, 10.22 ± 0.46 (Chapman and Morgan, 1973). Additional measurements of North and Central American forms may be found in Nelson (1909), Hall (1951), Hall and Kelson (1959), and Chapman and Morgan (1973). Measurements of South American forms may be found in Hummelinck (1940), Hershkovitz (1950), and Bracamonte (1972).

DISTRIBUTION. The eastern cottontail has the widest distribution of any species of *Sylvilagus* (Hall, 1951; Hershkovitz, 1950). It is unique among the rabbits of the world in that it inhabits diverse areas, occurring over broad geographic provinces from southern Canada into Central and northwestern South America, including some islands north of Venezuela (Figs. 3 and 4). This cottontail is generally thought of as a mammal of farmlands, fields, and hedge rows; however, historically it occurred in natural glades and woodlands, deserts, swamps, prairies, hardwood forests, rain forests, and boreal forests. The species has been widely introduced and populations are now established in Oregon (Graf, 1955) and Washington (Dalquest, 1941).

The eastern cottontail occurs sympatrically with many other rabbits. Its range overlaps that of six species of *Sylvilagus* and six species of *Lepus*. No other species occurs sympatrically with this many other leporids. Recent studies have shown that widely separated populations of *S. floridanus* have different genetic compositions which may account for the species' ability to occupy diverse habitats (Chapman and Morgan, 1973).

FOSSIL RECORDS. The fossil history of *S. floridanus* is well documented from Pleistocene deposits. Specimens of *Sylvilagus* from the Pleistocene of Schulze Cave, Edwards County, Texas (Dalquest et al., 1969), the Duck Creek local fauna of Kansas (McMullen, 1978), the Ileta Caves fauna, New Mexico (Harris and Findley, 1964), and the Melbourne fauna, Florida (Gazin, 1950) have been referred to *S. floridanus*. The early Holocene record of *S. floridanus* is well documented (Guilday and Bender, 1958; Guilday and Parmalee, 1965; Gilmore, 1946; Parmalee, 1962). Fossil remains of *S. floridanus* from the late Irvingtonian to Recent have been reported in Arkansas, Illinois, Maryland, Wisconsin, Nebraska, Pennsylvania and Tennessee (Kurtén and Anderson, in press).

FORM AND FUNCTION. Adult eastern cottontails undergo two distinct molts per year (Negus, 1959). The spring molt from winter to summer pelage is a gradual process taking place from March to August (Dalke, 1942). The fall molt begins in late September; full winter pelage is attained by the first week in November (Negus, 1959). Reproductive activity is related to the onset of the adult molt (Negus, 1959).

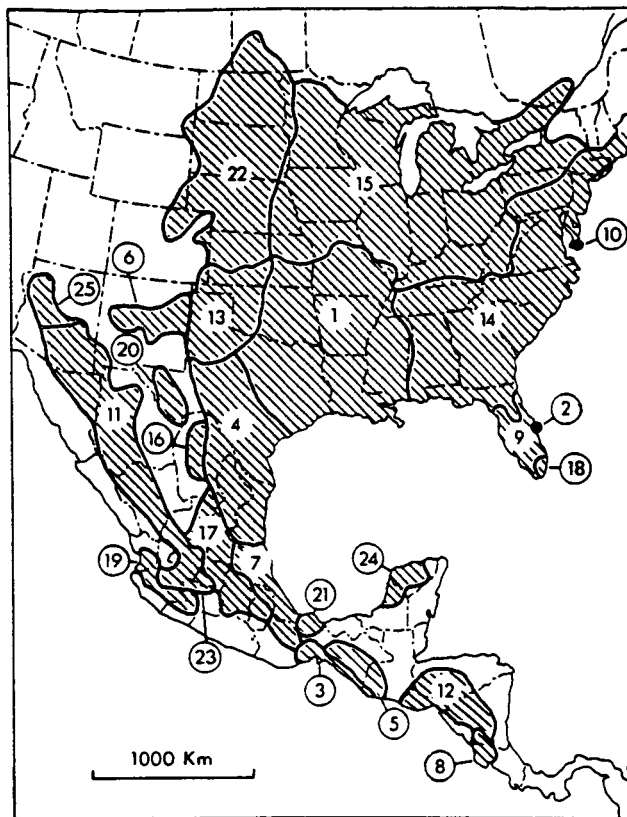


FIGURE 3. Distribution of *Sylvilagus floridanus* in North and Central America: 1, *S. f. alacer*; 2, *S. f. ammophilus*; 3, *S. f. aztecus*; 4, *S. f. chapmani*; 5, *S. f. chiapensis*; 6, *S. f. cognatus*; 7, *S. f. connectens*; 8, *S. f. costaricensis*; 9, *S. f. floridanus*; 10, *S. f. hitchensi*; 11, *S. f. holzneri*; 12, *S. f. hondurensis*; 13, *S. f. llanensis*; 14, *S. f. mallurus*; 15, *S. f. mearnsi*; 16, *S. f. nelsoni*; 17, *S. f. orizabae*; 18, *S. f. paulsoni*; 19, *S. f. restrictus*; 20, *S. f. robustus*; 21, *S. f. russatus*; 22, *S. f. similis*; 23, *S. f. subcinctus*; 24, *S. f. yucatanicus*; 25, *S. f. hesperius*. Adapted from Hall and Kelson (1959); Hall (1951); Hoffmeister and Lee (1963); Anderson (1972); Armstrong (1971), and Findley et al. (1975).

A partial *bursa ovarica* with a very large orifice is found medial to the ovary. Ovaries are found in the lumbar region and are fusiform in shape. Ripe graffian follicles remain small and maintain a medium size antrum with several radiating trabeculae. A thick thecal gland is present within the generally smooth surfaced ovary (Mossman and Duke, 1973).

Chapman et al. (1977) found *S. floridanus* was in its best condition in spring according to a weight-length condition index (K). Adrenal index curves showed that eastern cottontails exhibited highest stress during the winter and second highest stress during the breeding season (spring). Body fat index for *S. floridanus* peaked in fall, adrenal index peaked in winter and condition peaked in spring. Females remain in better condition during the breeding season than males according to the three physiological indices. Males have significantly higher mean adrenal indices year-round than females.

ONTOGENY AND REPRODUCTION. In Maryland, the mean ovulation rate was 5.75, with 6% of the ova being resorbed and approximately 7% failing to implant or being resorbed prior to becoming visible (Chapman et al., 1977). The ovulation rate of Missouri cottontails was 4.18, with a partial litter resorption rate between 5% and 12% (Conaway and Wight, 1962; Evans et al., 1965). Pelton (1969) reported 3.3% of the fetuses were resorbed in cottontails from Georgia. Ovulation rates in Texas varied from 1.47 to 4.09 (Bothma and Teer, 1977).

The mean gestation period is 28 to 29 days with a range from 25 to 35 days (Dice, 1929; Dalke, 1942; Bruna, 1952; Evans, 1962; Marsden and Conaway, 1963).

Bruna (1952) reported the number of litters per year was three or four. The average number of litters produced in Maryland

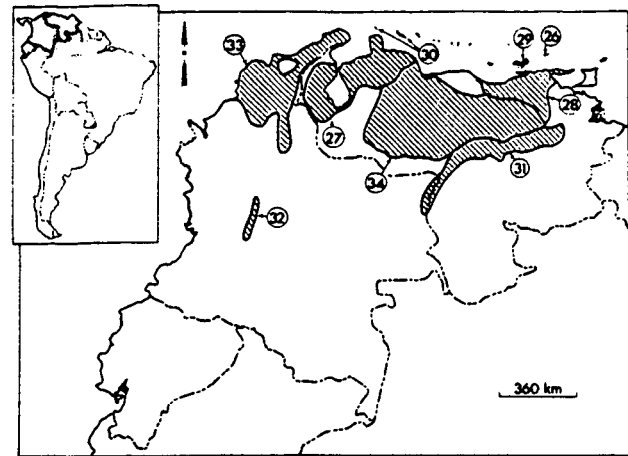


FIGURE 4. Distribution of *S. floridanus* in South America: 26, *S. f. avius*; 27, *S. f. continentis*; 28, *S. f. cumanicus*; 29, *S. f. margaritae*; 30, *S. f. nigronuchalis*; 31, *S. f. orinoci*; 32, *S. f. purgatus*; 33, *S. f. superciliaris*; 34, *S. f. valenciae*. Adapted from Cabrera (1961); Gimenez-Bracamonte (1972); Hershkovitz (1950); Hummelinck (1940); and Musso (1962).

was 4.6 per female per year (Chapman et al., 1977). Litter numbers of five to seven per year were reported by Sheffer (1957), Conaway et al. (1963), Evans et al. (1965) and Trethewey and Verts (1971). The litter size of the first pregnancy of the year is influenced by age and, or, previous reproductive experience (Lord, 1961a; Conaway and Wight, 1962). The size of the first litter increases when there is a delay in the onset of reproduction (Conaway and Wight, 1962).

The mean size of the first litter varies from about three in Alabama to five or greater in Maryland and North Dakota (Chapman et al., 1977; Chapman and Morgan, 1974; Conaway et al., 1974; Hill, 1972). Conaway et al. (1974) found mean annual litter sizes to be correlated with latitude and with other factors such as conception dates, body weight, elevation and on a single occasion, longitude. In the United States, mean annual litter size varies from 3.1 in Georgia to 5.6 in Illinois (Ecke, 1955; Pelton and Jenkins, 1971). As a rule South American forms have 2 young per litter, rarely 1 or 3 (Hummelinck, 1940).

Ecke (1955) gave the following description and average measurements of neonates: weight, 35 to 45 g; total length, 90 to 110 mm; and hind foot, 21 to 23 mm. Young at birth were covered with fine hair, their eyes were tightly closed, and their legs were developed enough to enable them to crawl into the nest. Their eyes opened on day 4 or 5 and young were able to leave the nest on days 14 to 16 after birth. Nestlings from Kentucky opened their eyes at days 7 to 8 and were able to move out of the nest at day 14 (Bruna, 1952). Nestling rabbits in southern Texas opened their eyes between days 6 and 7 and moved away from the nest at day 12 (Bothma and Teer, 1977).

Initial reproductive activity occurs later at higher elevations and at higher latitudes (Conaway et al., 1974). In Alabama the breeding season begins in the first week of January (Barkalow, 1962) and continues to the last week in March in southern Wisconsin (Rongstad, 1966). The breeding season in Connecticut lasts from mid-March to mid-September (Dalke, 1942), in New York, from February through September (Schierbaum, 1967), and in western Maryland from late February through August (Chapman et al., 1977). In the southern latitudes the breeding seasons are of longer duration. In Georgia, cottontails have a nine-month breeding season (Pelton and Provost, 1972) while in south Texas they breed year-round (Bothma and Teer, 1977). An introduced population in western Oregon began to breed in late January and ceased in early September (Trethewey and Verts, 1971). The onset of breeding varies between different populations and within the same population from year to year (Conaway and Wight, 1962; Hill, 1966). Hill (1966) suggested that temperature, rather than diet, is the primary factor controlling the onset of breeding. Many studies have correlated severe weather with delays in the onset of the breeding season (Hamilton, 1940; Wight and Conaway, 1961; Conaway and Wight, 1962). Ecke (1955) believed that the limits of the breeding season are closely related to the availability of succulent vegetation. Change in photoperiod is an important factor in regulating cottontail breeding (Bissonnette and Csech,

1939). The major environmental factors controlling breeding activity in south Texas are temperature and rainfall. Rainfall affects the amount of succulent vegetation available (Bothma and Teer, 1977).

Many studies have reported breeding in young-of-the-year juveniles: Negus (1959) found that 50% of juveniles bred; Stevens (1962), Lord (1963), and Trethewey and Verts (1971) observed that 44%, 27%, and 52% of juveniles bred, respectively. Other investigations found that breeding of juveniles was substantially lower than that of adults in terms of total productivity. Bothma and Teer (1977) reported 7.6% of all pregnant females were young-of-the-year. Juvenile females accounted for 3.9% of the pregnancies and only 2.7% of total ovulations in Maryland (Chapman et al., 1977). Pelton (1969) reported that 4.4% of the total young-of-the-year showed indications of breeding.

Annual production in Missouri was 35 young per adult female (Conaway et al., 1963). Pelton and Jenkins (1971) reported a lower potential productivity by Georgia cottontails (15 to 21 young per adult female per year) than cottontails from Missouri. Adult females in Oregon produced 24 to 35 young in five to seven litters (Trethewey and Verts, 1971). Bothma and Teer (1977) calculated that the potential productivity of adult females was 9.4 young per female per year. Chapman et al. (1977) estimated 23.9 young were produced per breeding female per year in an average of 4.6 litters. In Texas, potential productivity of juvenile females was found to be 6.2 young per female per year (Bothma and Teer, 1977). These authors concluded that the juvenile contribution to the production of young was mainly dependent upon their proportion in the overall female population.

Conaway et al. (1963) found synchronized breeding behavior. Photoperiod is thought to regulate synchronization of the initial pre-estrus stage on all populations over a wide geographic area (Conaway and Wight, 1962). A cycle of recurring pre-estrus has been postulated as explaining synchronous conceptions of approximately fourteen-day intervals (Conaway and Wight, 1962; Evans et al., 1965). Marsden and Conaway (1963) suggested a 7-day behavioral rhythm during the onset of breeding and first pregnancy. This 7-day rhythm is apparently absent in postpartum breeding cycles. Cottontails from Georgia and Missouri exhibited synchrony throughout the breeding season (Wight and Conaway, 1962; Conaway et al., 1963; Pelton and Provost, 1972). Once breeding begins, synchronous peaks of conception are determined by the length of gestation (Conaway and Wight, 1962; Evans, 1962).

Trent and Rongstad (1974) reported mean annual survival rates for adults of 0.20. Average life span in the wild is 15 months (Bruna, 1952). Lord (1963) stated that the potential life span of cottontails was at least 10 years. Salo (1965) concluded that females have greater longevity than males.

ECOLOGY. *Sylvilagus floridanus* is widely distributed throughout various habitats within its range. No single habitat type may be classed as preferred cover. Habitat preferences vary from season to season, between latitudes and regions, and with differing behavioral activities.

Nests are slanting holes in the ground with average measurements of: length, 180 mm; width, 126 mm; depth, 119 mm (Friley, 1955). In Texas, five nests averaged 125 mm long, 104 mm wide, and 91 mm deep (Bothma and Teer, 1977). Casteel (1966) found the average measurements from 21 nests to be 102 mm deep, 121 mm wide, and 146 mm long. There is no relationship between size of the nest and size of litter (Bothma and Teer, 1977). Nest holes in farming areas in southern Michigan contained an outer lining of grass or herbaceous stems covering all sides and a heavy, inner layer of belly or side fur from the female (Friley, 1955). Nests from Illinois were lined first with leaves, then with an inner lining of fur plucked from the female (Ecke, 1955). Casteel (1966) determined that residual vegetative cover was the preferred nest material, especially grass stems when available. Casteel (1966) found that females pulled fur from almost every part of their body, except the abdomen, for nest construction.

In Connecticut, brushpiles were apparently preferred as shelter and resting cover. Where brushpiles were absent, cleared spots or forms under herbaceous and shrubby vegetation were used as hiding and resting places. Brushpiles in cut-over woodlands provide winter shelter and an adequate supply of winter food consisting of stump sprouts and exposed shrubby and herbaceous vegetation (Dalke, 1942).

In southern Michigan farming areas, forms composed of native herbaceous vegetation, with dense herbaceous cover on all sides, were preferred. Grass was the basic construction material.

Spring forms were constructed of brush and briars and winter forms of herbaceous vegetation (Friley, 1955).

Bruna (1952) stated that use of cover is probably determined by availability and location, rather than any individual preference. Broomsedge and woods in Kentucky were utilized frequently throughout all seasons (Bruna, 1952).

Smith (1950) concluded that the habitat requirements for cottontails in the Hudson Valley of New York include grasslands, hedgerows, areas of low, dense brush, and dens for escape. Old field situations were also reported as highly-preferred habitat by Friley (1955), Heard (1962), and Nugent (1968). Woodchuck holes provide the best dens for escape cover and shelter (Smith, 1950).

Cottontail habitat has been improved by interspersing of old fields and briar thickets, creation of edge and by establishment of open food plots or by breaking up large, continuous parcels of monotypic habitat (Smith, 1950; Bruna, 1952; Friley, 1955; Heard, 1962; and Nugent, 1968). Burning followed by grazing was found to be destructive to habitat quality (Heard, 1962).

South American forms inhabit arid and semi-arid regions of Colombia, Venezuela, and some adjacent islands, from sea level to 1000 m (Hershkovitz, 1950). Handley (1976) found that in South America, the species composition of rabbits varied with habitat, with *S. floridanus* accounting for 97% of the rabbits in dry upland habitats, 76% in thorn forest, 20% in savannas and pastures, and 4% in orchards and deciduous forests.

There have been numerous studies of the home range size of the eastern cottontails involving radio-telemetry, trapping and direct observation. In general, yearly mean home ranges for adult males varied from 0.95 ha (2.34 acres) to 2.8 ha. Adult female yearly home range size varied from 0.95 to 1.2 ha (Lord, 1963; Trent and Rongstad, 1974).

Home range size is near the maximum in a rabbit's first winter (Janes, 1959). Home range size and movements of adult rabbits varies by season, sex, and individual (Chapman and Trethewey, 1972a). Trent and Rongstad (1974) reported that home range size of males increased with the onset of sexual activity. Habitat quality and sexual behavior influence the home range size of males during the breeding season. These findings support those of Janes (1959). Home ranges overlap indiscriminately after breeding activity has ended (Trent and Rongstad, 1974). Cottontails do not maintain territories (Allen, 1939; Janes, 1959).

Janes (1959) reported homing ability for two rabbits in Kansas. A male and female were displaced 586.3 m (1800 ft) and 358.3 m (1100 ft) respectively, and were found one month later in their original home ranges. Hill (1967) reported that a female cottontail returned to its original capture site after escaping from an enclosure 3.74 km (2.33 mi) distant.

In southern Wisconsin, fall population densities of rabbits were 8.9/ha (Trent and Rongstad, 1974). The peak density for a small island in Maryland was 10.18/ha (Bittner and Chapman, 1979).

Cottontails feed upon a wide variety of plant species. In New York herbaceous species were chosen during the growing season, and woody species were chosen during the dormant season. Woody plants, in order of importance as food are: apple (*Malus pumila*), staghorn sumac (*Rhus typhina*), red maple (*Acer rubrum*), blackberry (*Rubus allegheniensis*), red raspberry (*R. strigosus*). Herbaceous species of importance are: Kentucky bluegrass (*Poa pratensis*), Canada bluegrass (*P. compressa*), timothy (*Phleum pratense*), quack grass (*Agropyron repens*), orchard grass (*Dactylis glomerata*), red clover (*Trifolium pratense*), and wild carrot (*Daucus carota*). Staghorn sumac was chosen over smooth sumac (Smith, 1950).

In Ohio, herbaceous plants, except when snow covered, comprised almost the entire diet. Bluegrass was the most important all-season food. Orchard grass, timothy, and nodding wild-rye (*Elymus canadensis*) are all-season foods of lesser importance. Red clover and Korean lespedeze (*Lespedeza stipulacea*) were utilized seasonally (Dusi, 1952). Young cottontails preferred dandelion (*Taraxacum officinale*) and prickly lettuce (*Lactuca scariola*), but also ate giant ragweed (*Ambrosia trifida*), red clover, Rugel's plantain (*Plantago rugelii*), and curly dock (*Rumex crispus*), also (Bailey and Siglin, 1966).

Dalke and Sime (1941) observed two pronounced feeding periods, the first was 3 to 4 h after sunrise and second was from sunset to 1 h after. Feeding habits varied with changes in seasons and the succession of plants. Spring through October diets consisted of herbaceous plants, mainly clover, timothy and alfalfa. The fall period, November and December, was a transition period from herbaceous to woody plant materials. Winter diets consisted mainly of tree species, including gray birch (*Betula populifolia*), red maple, apple, aspen (*Populus tremuloides*), choke cherry

(*Prunus virginiana*), and wild black cherry (*P. serotina*); and the shrubs and vines, blackberry, dewberry (*Rubus villosus*), willow (*Salix*), black alder (*Ilex verticillata*), male berry (*Lyonia ligustrina*), and highbush blueberry (*Vaccinium corymbosum*).

Coprophagy has been reported for the genus *Sylvilagus* (Hamilton, 1955). Cottontails excrete two types of pellets, hard, brown fecal pellets and soft, greenish food pellets. Digestion has extracted the nutrients from hard pellets, which comprise approximately 60% of the total fecal excretion (Bailey, 1969). According to P. R. Cheeke (pers. comm.) soft pellets are produced in the caecum and provide vitamin B supplementation.

The following ectoparasites were reported from *S. floridanus*: ticks, *Haemaphysalis leporispalustris*, *Dermacentor variabilis*, and *Ixodes dentatus*; fleas, *Ceratophyllus multispinosus*, *Cediopsylla simplex*, *Odontopsyllus multispinosus*, *Hoplopsyllus affinis*, and *Ctenocephalides canis*; botflies, *Cuterebra buccata*, *Haemaphysalis justakochi*, *Amblyomina paruum*, *Amblyomma americana*, *Ornithodoros puertoricensis*, *Ctenophthalmus pseudagrytes*, and *Neotrombicula whartoni* (Jones et al., 1972; Morgan and Waller, 1940; Stannard and Pietsch, 1958; Heard, 1962; Jacobson and Kirkpatrick, 1974; Jacobson et al., 1978). Internal parasites include: cestodes, *Ctenotaenia ctenoids*, *C. variabilis*, *Mosgovoyia pectinata*, *Multiceps serialis*, *Taenia pisiformis*, *Citiotenia perplexa*, *C. pectinata*, *Cysticercus dearmasi*, *Hydatigera lyncis*, and *Taenia hydatigena*; trematode, *Hasstilesia tricolor*; nematodes, *Dermatoxylus veligera*, *Nematodirus triangularis*, *N. leporis*, *Obeliscoides cuculi*, *Passalurus ambiguus*, *P. nonnulatus*, *Physaloptera* sp., *Trichostrongylus affinis*, *T. calcitrans*, *Dirofilaria scapiceps*, *Trichuris leporis*, *T. sylvilagi*, *Baylisascaris procyonis*, and *Ascaris columnaris* (Morgan and Waller, 1940; Erickson, 1947; Heard, 1962; Novelsky and Dyer, 1970; Jacobson and Kirkpatrick, 1974; Jacobson et al., 1974; Nettles et al., 1975; Jacobson et al., 1976; Diaz-Ungria, 1973).

Bacterial and viral infections such as tularemia (*Francisella tularensis*), Tyzzer's disease (*Bacillus piliformis*), *Herpesvirus sylvilagus*, and *Staphylococcus* have also been reported for *S. floridanus* (McCoy and Steenbergen, 1969; Pelton and Hubbard, 1969; Ganaway et al., 1976; Lewis and Hinze, 1976).

Jacobson et al. (1978) suggested that the pathologic effects of high infestation of parasites impair cottontail reproduction. Changes in physiologic measurements associated with disease infestations have been reported by Jacobson et al. (1978).

Cottontails are a stable food item of most carnivorous mammals found within the cottontail's range. Mammalian predators include raccoons (*Procyon lotor*), ring-tailed cats (*Bassariscus astutus*), marten (*Martes americana*), fisher (*M. pennanti*), weasels (*Mustela*), red fox (*Canis vulpes*), gray fox (*Canis cinereogenteus*), coyotes (*Canis latrans*), bobcats (*Felis rufus*), and feral cats (*Felis catus*) (Martin et al., 1961). Avian predators include red-tailed hawks (*Buteo jamaicensis*), red shouldered hawks (*B. lineatus*), rough-legged hawks (*B. lagopus*), Cooper's hawks (*Accipiter cooperi*), goshawks (*A. gentilis*), and golden eagles (*Aquila chrysaetos*), marsh hawks (*Circus cyaneus*), and crows (*Corvus brachyrhynchos*) (McAtee, 1935; Hagar, 1957; Gates, 1972; Trent and Rongstad, 1974; Johnson, 1978).

BEHAVIOR. Lord (1964) suggested that activity was not controlled by the onset of darkness. Activity was greatest in the summer months when nights were shortest. Lord speculated that the process of food assimilation might regulate the daily activity patterns of rabbits. Janes (1959) noted that activity was greatest at dawn and dusk, with increased activity on moonlit nights. Greatest activity occurred when air temperatures were between 0°F and 33°F. Rain apparently reduces activity. Janes (1959) stated that "activity increased as the percentage of ground covered by snow increased and as the abundance of food decreased." Lord (1961b) found that roadside activity was much greater in winter than in summer. Johnson and Hendrickson (1958) reported increased trap success, indicating increased activity, during or following rises in barometric pressure.

Exploratory males exhibit extensive chinning and paw-raking displays as described by Marsden and Holler (1964). Females also exhibit exploratory behavior when searching for nest sites (Marsden and Holler, 1964). Searching behavior by dominant males was also reported by Casteel (1966).

There are two general types of escape behavior, flushing and slinking. The flush is a "rapid, often zigzag movement to one of the established travel lanes, on which rabbits move at maximum speed to cover." When slinking towards cover the body remains close to the ground and the ears are laid back (Marsden and Holler, 1964).

Dog-like rolling in dusty areas (dusting) was also reported by Marsden and Holler (1964).

Marsden and Holler (1964) observed four distinct patterns of grooming: face grooming with front paws from eyes to muzzle, preceded by licking of paws; licking of the body and legs; scratching with the hind legs; and biting and cleaning of feet. Nursing females exhibited extended grooming sessions. Displacement activities of rapid face grooming and short feeding frenzies have also been noted (Marsden and Holler, 1964).

Male cottontails displayed alert posture, which involves raising the rump above the level of the shoulders and holding the ears upright, usually during confrontations with females or subordinate males (Marsden and Holler, 1964). Subordinate males displayed submissive posture (crouched position with ears reclined and tail held downward) when confronted by a dominant male. When males approached other males, the approaching rabbit assumed the alert posture. Sexually excited males were observed to dash past females when met with aggression by the females. During the dash, the male swung his rump in front of the female and urinated toward her. Rushes of a male directly at a female were also observed. Attempted mountings by males upon females were made without thrusting. Males, when interacting with females or subordinates, marked vegetation by rubbing it with the corner of the eye. Dominant males were also observed scratching and paw-raking with forepaws. This display occurred in the presence of other rival males (Marsden and Holler, 1964).

Female social behavior includes: threat posture consisting of a deep crouch position with chin up and ears laid back; boxing with approaching males, which entails striking out with forepaws from a raised threat position; charging in the threat position directly toward approaching males; jumping in response to a male's rush; and presentation of genitals to males by females in estrus (Marsden and Holler, 1964).

Three types of vocalizations have been reported, consisting of distress cries, squeals, and grunts. Distress cries are high-pitched screams emitted by frightened or injured rabbits which alert other rabbits. Squeals are sounded during copulation by either the female or the male. Nesting females emit grunts when their nest is approached by an intruder (Marsden and Holler, 1964).

Adult social interactions include those related to reproduction and to social hierarchies. Reproductive interactions consist of a sequence of patterns which precede and culminate in copulation. Initially, the male approaches the female and she turns, in a threat posture, to face the male (facing off). Immediately following the face-off, the male continues his advance towards the female. The female responds by boxing or charging the approaching male until he retreats. Females follow-up by chasing the retreating male. Males turn and dash at the passing female, urinating during the dash. After the dash, females shake their head, groom, and then retreat from the male. With more receptive females, jump sequences usually follow the male dash. In this chain of events, the male and female face-off, the male then rushes the female, the female jumps over the male, and finally they face-off again. When the female retreats from the male after a face-off, the male follows the female from behind, close enough to smell her hind quarters. A short reproductive chase of the estrous female by one or more males precedes copulation. During the copulatory act, the estrous female presents herself to the male, approaching from the rear. When mounting, the male clasps the female's flanks with his forelegs and initiates several rapid thrusts. Females then breakaway and are again pursued by the male (Marsden and Holler, 1964). Casteel (1966) reported successful copulatory chases lasting 10 sec to 7 min.

Dominant-subordinate interactions have been reported by Marsden and Holler (1964). Displays of aggression and submission usually indicate dominance. Subordinates move away from dominants, or crouch in a submissive posture. Dominant males often charge subordinates, forcing them to retreat (dislodgement). The dominant male then sniffs the vacated area. Pursuit does not follow dislodgement. Dislodgement by females is essentially the same as for males. Aggressive chases differ from dislodgement in that dominant animals aggressively pursue the subordinate. Male-male chases are of longer duration than female-female chases. Fighting does occur although it is not a part of normal social activity. Biting and kicking and striking with the feet have been observed, but extensive fighting does not develop because one animal always gives ground quickly (Marsden and Holler, 1964).

Male hierarchies prevent reproductive fighting. Nearly all male aggression is initiated by dominant males. Challenges for social status have only been observed between the top two males.

Dominant males copulate with the majority of females (Marsden and Holler, 1964).

Interspecific aggressive behavior was observed between introduced *S. floridanus* and native brush rabbits (*S. bachmani*) in Oregon (Chapman and Verts, 1969). One such aggressive encounter within an enclosure resulted in the death of the brush rabbit.

Chapman and Trethewey (1972b) studied the responses to traps by introduced eastern cottontails in the Willamette Valley of Oregon. They found that females were more frequently recaptured than males, and that juveniles were more frequently recaptured than adults. All sex and age groups of cottontails were most easily captured in January. A positive correlation was found between cottontail captures and barometric pressure. As temperatures became colder, individuals were trapped more frequently.

Kirkpatrick (1956) observed coprophagy in *S. floridanus*. Soft pellets were eaten directly from the anus before they touched the ground, and was limited to two or three pellets at a time.

GENETICS. The eastern cottontail has a diploid chromosome number of 42, with six metacentric or nearly metacentric pairs, 11 submetacentric pairs, and three acrocentric pairs of autosomes (Holden and Eabry, 1970). *S. floridanus* differs from *S. transitionalis* in that the latter has 52 chromosomes. The Y chromosome is acrocentric and is the smallest of the complement, while the X chromosome is a medium sized submetacentric. Four pairs of submetacentric chromosomes have secondary constrictions in the long arms and two pairs of acrocentric chromosomes have prominent satellites on the short arms (Holden and Eabry, 1970).

Chapman and Morgan (1973) examined the blood sera of several species and subspecies of *Sylvilagus* by electrophoresis, including 277 individuals of *S. floridanus* (42 *S. f. alacer*, 18 *S. f. mearnsi*, 5 *S. f. chapmani*, and 212 intergrades between various subspecies). All of the *S. floridanus* examined had unique protein systems, with intergrades of *S. floridanus* showing more polymorphism than all others they examined, including *S. audubonii* and *S. transitionalis*. The polymorphism found in the intergrade *S. floridanus* included variant transferrins. Detailed electropherograms and schematic drawings were presented for several members of the genus *Sylvilagus*, including four subspecies of *S. floridanus*. Johnson (1968) also examined blood sera from 17 *S. floridanus* and several other *Sylvilagus*, and reported that they differed significantly from *Brachylagus idahoensis*.

REMARKS. The eastern cottontail is an important game animal and provides millions of hours of recreational sport each year. This species has been more intensively studied than any other rabbit. These studies include numerous M.S. and Ph.D. theses as well as hundreds of Federal Aid to Wildlife Restoration reports (Pittman/Robertson). Because of page limitations here, and the nature of many of the reports, we have not cited most. Contribution Number 947-AEL, Center for Environmental and Estuarine Studies, University of Maryland.

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Microtus pennsylvanicus. By Lawrence M. Reich

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Microtus pennsylvanicus (Ord, 1815)

Meadow Vole

- Mus pennsylvanicus* Ord, 1815:292. Type locality meadows below Philadelphia, Pennsylvania.
- Microtus pennsylvanicus* Rhoads, 1895:940. First use of current name combination.
- Mynomes pratensis* Rafinesque, 1817:45. Type locality meadows and seashore below Philadelphia, Pennsylvania.
- Lemmus noveboracensis* Rafinesque, 1820:3. Type locality New York or New Jersey.
- Arvicola riparius* Ord, 1825:305. Type locality not given.
- Arvicola palustris* Harlan, 1825:136. Type locality swamps along shores of Delaware River.
- Arvicola hirsutis* Emmons, 1840:60. Type locality Massachusetts.
- Arvicola albo-rufescens* Emmons, 1840:60. Type locality Williamstown, Massachusetts.
- Arvicola fulva* Audubon and Bachman, 1841:96. Type locality "One of the Western states; we believe Illinois."
- Arvicola nasuta* Audubon and Bachman, 1841:96. Type locality near Boston, Massachusetts.
- Arvicola rufescens* DeKay, 1842:85. Type locality Oneida Lake, New York.
- Arvicola oneida* DeKay, 1842:88. Type locality Oneida Lake, New York.
- Arvicola drummondii* Audubon and Bachman, 1854:166. Type locality "Valleys of the Rocky Mountains."
- Arvicola dekayi* Audubon and Bachman, 1854:298. Type locality New York or Illinois.
- Arvicola modesta* Baird, 1858:535. Type locality Cochetopa Pass, Saguache Co., Colorado.
- Arvicola riparia* var. *longipilis* Baird, 1858:524. Type locality West Northfield, Illinois or Racine, Wisconsin.
- Arvicola rufidorsum* Baird, 1858:526. Type locality Holmes Hole, Martha's Vineyard, Massachusetts.
- Arvicola (Mynomes) aztecus* Allen, 1893:73. Type locality Aztec, San Juan Co., New Mexico.
- Arvicola insperatus* Allen, 1894:347. Type locality Custer, Custer Co., South Dakota.
- Arvicola (Mynomes) microcephalus* Rhoads, 1894:286. Type locality Lac LaHache, British Columbia.
- Arvicola terraenovae* Bangs, 1894:129. Type locality Codroy, Newfoundland.
- Microtus enixus* Bangs, 1896a:1051. Type locality Hamilton Inlet, Labrador.
- Microtus fontigenus* Bangs, 1896b:48. Type locality Lake Edward, Quebec.
- Microtus stonoi* Allen, 1899:5. Type locality Liard River, British Columbia.
- Microtus aphorodemus* Preble, 1902:52. Type locality 50 mi. S Cape Eskimo, near mouth Thlewiaza River, Keewatin.
- Microtus provecus* Bangs, 1908:20. Type locality Block Island, Newport Co., Rhode Island.
- Microtus admiralitiae* Heller, 1909:256. Type locality Windfall Harbor, Admiralty Island, Alaska.
- CONTEXT AND CONTENT.** Order Rodentia, Suborder Myomorpha, Family Muridae, Subfamily Microtinae. The genus *Microtus* includes 8 subgenera, approximately 47 species, and 238 subspecies, distributed throughout the northern two-thirds of Eurasia, and in North America south to Guatemala. *M. pennsylvanicus* is included in the subgenus *Microtus* (Hall and Kelson, 1959; Ellerman and Morrison-Scott, 1951; Ellerman, 1940). Recognized subspecies are (Hall and Kelson, 1959; Youngman, 1967; Bradley and Cockrum, 1968):
- M. p. acadicus* Bangs, 1897:239. Type locality Digby, Nova Scotia.
- M. p. admiralitiae* Heller, 1909:256, see above.
- M. p. alcorni* Baker, 1951:105. Type locality 6 mi. SW Kluane, Yukon.
- M. p. aphorodemus* Preble, 1902:521, see above.
- M. p. arcticus* Cowan, 1951:353. Type locality Kidluit Bay, Richards Island (69°31'N, 133°49'W) Mackenzie.
- M. p. aztecus* (Allen), 1893:73, see above.
- M. p. chihuahuensis* Bradley and Cockrum, 1968:1. Type locality 3 mi. SE Galeana, NW Chihuahua, Mexico.
- M. p. copelandi* Youngman, 1967:579. Type locality North Head, Grand Manan Island, New Brunswick.
- M. p. drummondii* Audubon and Bachman, 1854:166, see above. (*stonei* Allen is a synonym; *microcephalus* Rhoads, *rubidus* Dale, and *arcticus* Cowan may be synonyms.)
- M. p. enixus* Bangs, 1896a:1051, see above.
- M. p. fnitus* Anderson, 1956:96. Type locality 5 mi. N, 2 mi. W Parks, Dundy Co., Nebraska.
- M. p. fontigenus* Bangs 1896b:48, see above.
- M. p. funebris* Dale, 1940:338. Type locality Coldstream, 3.5 mi. SE Vernon, British Columbia.
- M. p. insperatus* (Allen), 1894:347, see above.
- M. p. kincaidi* Dalquest, 1941:145. Type locality 10 mi. S Moses Lake, Grant Co., Washington.
- M. p. labradorius* Bailey, 1898:88. Type locality Fort Chimo, Quebec.
- M. p. magdalenensis* Youngman, 1967:579. Type locality Grindstone Island, Magdalen Islands, Quebec.
- M. p. microcephalus* (Rhoads), 1894:286, see above.
- M. p. modestus* (Baird), 1858:535, see above. (*aztecus* Allen may be a synonym.)
- M. p. nigrans* Rhoads and Young, 1897:307. Type locality Currituck, Currituck Co., North Carolina.
- M. p. pennsylvanicus* (Ord), 1815:292, see above. (*pratensis* Rafinesque, *noveboracensis* Rafinesque, *riparius* Ord, *palustris* Harlan, *hirsutis* Emmons, *albo-rufescens* Emmons, *fulva* Audubon and Bachman, *nasuta* Audubon and Bachman, *rufescens* DeKay, *oneida* DeKay, *dekayi* Audubon and Bachman, *longipilis* Baird, and *rufidorsum* Baird are synonyms.)
- M. p. provecus* Bangs, 1908:20, see above.
- M. p. pullatus* Anderson, 1956:97. Type locality 12 mi. N and 2 mi. E Sage, Lincoln Co., Wyoming.
- M. p. rubidus* Dale, 1940:339. Type locality Sawmill Lake, near Telegraph Creek, British Columbia.
- M. p. shattucki* Howe, 1901:201. Type locality Tumble Down Dick Island, Penobscot Bay, Maine.
- M. p. tananaensis* Baker, 1951:107. Type locality Yerrick Creek, 21 mi. W, 4 mi. N Tok Junction, Alaska.
- M. p. terraenovae* (Bangs), 1894:129, see above.
- M. p. uligocola* Anderson, 1956:94. Type locality 6 mi. W, 0.5 mi. S Loveland, Larimer Co., Colorado.
- Anderson and Hubbard (1971) placed *M. p. aztecus* within the synonymy of *M. p. modestus*, Martell (1975) placed *M. p. arcticus* within the synonymy of *M. p. drummondii*, Weaver (1940) placed *M. p. fontigenus* within the synonymy of *M. p. pennsylvanicus*, and Cowan and Guiguet (1956) placed *M. p. microcephalus* and *M. p. rubidus* within the synonymy of *M. p. drummondii*.
- DIAGNOSIS.** The following characters are diagnostic of *M. pennsylvanicus* (Hall and Kelson, 1959; Hall and Cockrum, 1953): first lower molar with 5 closed triangles, third lower molar with 3 transverse loops and no triangles, second upper molar with 4 closed triangles and a posterior loop, third upper molar with 3 closed triangles. Incisive foramen long and not constricted posteriorly. Nasals rounded posteriorly (Fig. 1). Plantar tubercles 6.
- GENERAL CHARACTERS.** External measurements in mm for adult *M. pennsylvanicus* (Fig. 2) vary as follows: total length, 140 to 195; length of tail, 33 to 64; length of hindfoot, 18 to 24; length of ear, 12 to 16. The length of body is about 2 to 3 times the length of tail, and the tail is 1.9 to 2.7 times as long as the hindfoot. Mean (\pm SD) adult weight is 44.2 \pm 6.29 g for males, and 44.0 \pm 10.25 g for females. Cranial measurements (mm) for males (mean \pm SD) are: greatest length of skull, 27.4 \pm 0.63;

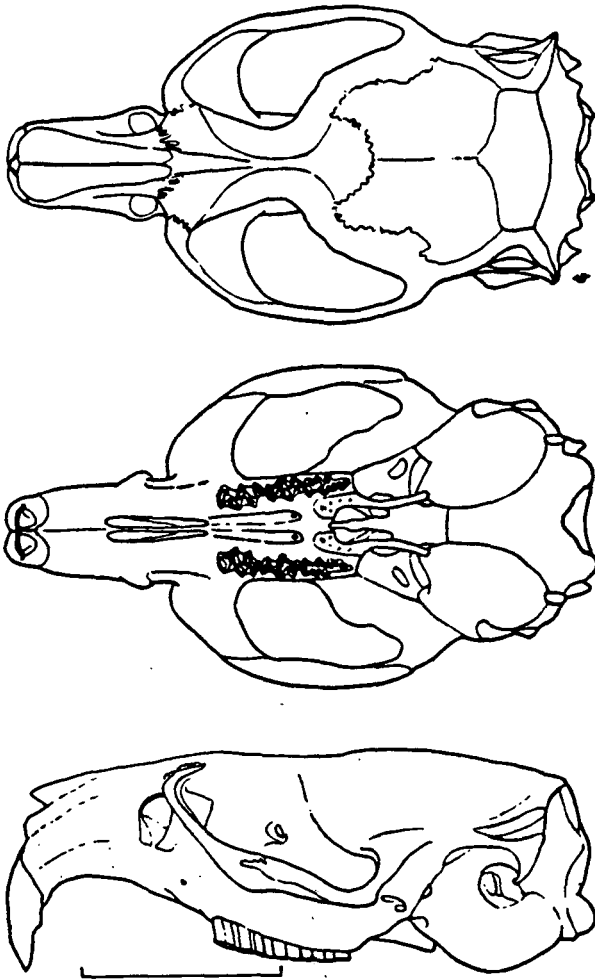


FIGURE 1. Dorsal, ventral, and lateral views of skull of male *Microtus pennsylvanicus pullatus* (from Hall and Kelson, 1959, by permission). Line at bottom represents 1 cm.

condylozygomatic length, 21.3 ± 0.52 ; length of nasal, 7.7 ± 0.42 ; length of incisive foramen, 5.2 ± 0.28 ; length of diastema, 8.3 ± 0.27 ; length of rostrum, 6.0 ± 0.23 ; cranial breadth, 11.0 ± 0.29 ; interorbital breadth, 3.7 ± 0.12 ; zygomatic breadth, 15.2 ± 0.47 , and cranial height, 10.1 ± 0.27 (Hall and Kelson, 1959; Snyder, 1954). Adult males average slightly larger than females in cranial measurements (Snyder, 1954).

Upper parts vary in color from bright yellowish chestnut to dull bistre with black-tipped hairs (Hall and Kelson, 1959). Northern subspecies were said to be more blackish or grayish (Hall and Kelson, 1959), although Hooper (1941) and Dale (1940) reported that southern forms were blacker. Burt and Grossenheider (1976) noted that western subspecies are notably lighter than eastern subspecies. The tail is bicolored. Pelage color varies with age, young animals being darker than older animals (Starrett, 1958). The sexes are colored alike (Starrett, 1958). Dale (1940) showed that body size increased along a cline from north to south and from high to low altitudes.

DISTRIBUTION. *Microtus pennsylvanicus* has the largest range of any American species in the genus *Microtus* (Fig. 3), occurring throughout Canada, the northern and eastern regions of the United States, and into Mexico (Hall and Kelson, 1959; Bradley and Cockrum, 1968; Youngman, 1967). It is most commonly found in grasslands, preferring moister areas, but may also be found in woodlands (Burt and Grossenheider, 1976).

FOSSIL RECORD. Martin (1968) summarized the Late Pleistocene records of *M. pennsylvanicus*, which has been reported from Florida, Louisiana, Texas, Kansas, Nebraska, Pennsylvania, Virginia, Indiana, Oklahoma, and Tennessee. Martin (1972) compared Pleistocene remains of *M. pennsylvanicus* with



FIGURE 2. Adult male *Microtus pennsylvanicus pennsylvanicus* from Plymouth, Massachusetts. (Photographed by the author and Peter V. August.)

the extinct *M. paroperarius*, which he concluded is an ancestral form. Guthrie (1971) presented a model of the evolution of tooth cusp patterns in microtine rodents, and pointed out that no ancestor common to Old World and New World microtines is known.

FORM. The pelage of *M. pennsylvanicus* consists of two types of hair—short, flexible underhair (tricolored on the dorsum with dark gray bases, central bands of orange or yellow-brown, and short, dark tips, gradually becoming bicolored towards the venter, with gray bases and white tips) and longer, stiffer guard hairs (bicolored with short gray bases and long, dark brown tips), which occur predominantly on the dorsum (Starrett, 1958). The seasonal molt results from changes in the underhair with little change in the guard hair. Summer pelage is sparser and coarser than winter pelage (Starrett, 1958).

Anderson (1960) gave a detailed quantitative description and line drawings of the baculum, comparing it to those of other rodents. Snyder (1954) found considerable variability in linear cranial measurements within a population, and even greater variation between populations. By examining ontogenic variation, he concluded that the best craniometric characters for age determination are lengths of the paroccipital process and occipital crest. A detailed account of macro- and micro-anatomy of molars was presented in Phillips and Oxberry (1972). Oppenheimer (1965) studied within- and between-population variation in molar patterns, discussed the relationship between molar patterns and adaptive radiation, and suggested that there is a trend toward reduced molar complexity in microtine evolution. Guilday (1951) described sexual differences in innominate bone morphology.

The circulatory system was described on a biochemical level by Genaux and Morrison (1973), who constructed a complete peptide map of the hemoglobin of *M. pennsylvanicus*, and by Dieterich (1972) and Dieterich and Preston (1977), who reported on mean concentrations of various blood cells and plasma constituents. Carotid circulation was described by Guthrie (1963), and inner ear morphology by Hooper (1968).

Golley (1960a) reported both on macro- and micro-anatomical aspects of the digestive tract, including details of the mouth, tongue, esophagus, stomach, intestine, caecum, and liver. He found the caecum was unusually long and the colon and rectum were short. The large caecum is likely responsible for the high digestive efficiency (86 to 90%) of *M. pennsylvanicus*. Barry (1976) gave a histological description of the small intestine, and concluded that the villous and mucosal surface morphology was typical for an herbivore.

Zimny (1968) studied the renal glomerular capillaries, and concluded that the presence of an extracellular polysaccharide coat on the plasma membrane of the epithelial cells, and a central dense zone of basal lamina, are both adaptations to reduce urine output in cold weather.

Spermatogenesis was investigated by Beach (1931), and Arata (1964) described the structure of male accessory reproductive glands. There is one pair each of preputial, vesicular, and am-

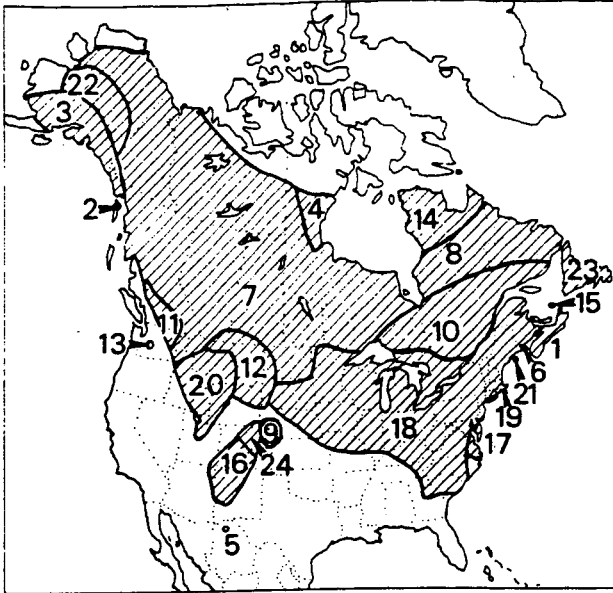


FIGURE 3. Distribution of *Microtus pennsylvanicus*, modified from Hall and Kelson, 1959 (Anderson and Hubbard, 1971; Bradley and Cockrum, 1968; Youngman, 1967). Subspecies are: 1, *M. p. acadicus*; 2, *M. p. admiraltiae*; 3, *M. p. alcorni*; 4, *M. p. aphorodemus*; 5, *M. p. chihuahuensis*; 6, *M. p. copelandi*; 7, *M. p. drummondii*; 8, *M. p. enixus*; 9, *M. p. finitus*; 10, *M. p. fontigenus*; 11, *M. p. funebris*; 12, *M. p. insperatus*; 13, *M. p. kincaidi*; 14, *M. p. labradorius*; 15, *M. p. magdalensis*; 16, *M. p. modestus*; 17, *M. p. nigrans*; 18, *M. p. pennsylvanicus*; 19, *M. p. proectus*; 20, *M. p. pullatus*; 21, *M. p. shattucki*; 22, *M. p. tananaensis*; 23, *M. p. terraenovae*; 24, *M. p. uligicola*.

pullary glands, and four pairs of prostate glands. The glans penis was described by Hooper and Hart (1962).

Christian and Davis (1966) noted that weight of adrenal glands of females increased sharply in response to estrogen secretion. Most variations in adrenal weight were due to changes in the cortical layer, primarily in the fasciculata and reticular zones. Cells of the hyperplastic inner cortical portion often contained small lipid vacuoles in the zona fasciculata, with fewer in the zona reticularis.

Dieterich and Preston (1977) reported on mean weights for many organs and organ systems of *M. pennsylvanicus*.

FUNCTION. The wound healing ability of *Microtus pennsylvanicus* was studied by Rose and Hueston (1978). Most skin punctures and scars were undetectable after one month.

Winter acclimatization and thermoregulatory strategies were studied by Narayansingh and Aleksuik (1972), who described temperature-related changes in DNA and protein synthesis rates in the liver, small intestine, and brown fat masses, concluding that low ambient temperatures induce a reorganization of metabolic activity, such that energy available for heat production is maximized at the temporary expense of growth. Mean body weights are reduced in winter (Iverson and Turner, 1974). Brown fat weight decreases with higher body weight and higher ambient temperature (Didow and Hayward, 1969). The thermoneutral zone is 25 to 29°C (Wiegert, 1961). Pearson (1947) reported a 24-h mean oxygen consumption rate of 2.4 to 3.7 cc g⁻¹ h⁻¹. Oxygen consumption is directly related to body weight, is highest at night, and decreases in response to huddling (Wiegert, 1961). Golley (1960b) reported a basal metabolic rate of 10 cal/day and an average tissue caloric value of 4.65 cal/g.

Holleman and Dieterich (1973) reported a mean total body water content of 63.0% body weight and a mean rate of water exchange of 8.1 ml/day. Getz (1963) found that evaporative water loss was 0.0125 g/cm² surface area per 6 h period at 28°C, and 0.0119 g/cm² at 33°C. Ernst (1968) calculated a water consumption rate of 0.21 ± 0.02 ml/g body weight/day.

Several studies found increased adrenocortical activity with increased population densities (Louch, 1958; Christian and Davis, 1966), although To and Tamarin (1977) presented evidence to the contrary. Seabloom (1965) found that peaks in adrenal activity

corresponded with reduced motor activity and noted higher levels of corticosterone in females than in males. Seabloom et al. (1978) observed a spring peak in adrenal activity with a rapid decline into summer, except in subadult males, who showed an early summer peak. Levels of ACTH are higher in adults than in juveniles, and higher in non-pregnant females than in pregnant females (Seabloom et al. 1978). Olsen and Seabloom (1973) noted that confinement caused increased adrenal activity, especially in males. Ungar et al. (1978) determined that corticosterone is the major adrenal steroid produced. The weight of the thymus gland was lower at high population density, in winter months, and in breeding individuals, and arterial blood pressure was higher in artificial populations kept at high densities than at low densities (Blaine, 1973).

ONTOGENY AND REPRODUCTION. Copulation in *M. pennsylvanicus* consists of intra-vaginal thrusting, no lock, and multiple ejaculations (Gray and Dewsbury, 1975). First ejaculation is preceded by multiple intromissions, but subsequent ejaculations require only a single insertion. Ovulation is induced (Clulow and Mallory, 1974), and occurs 12 to 18 hours after coitus (Lee et al., 1970). A male-induced, pregnancy-block mechanism (the Bruce effect) was demonstrated by Mallory and Clulow (1977). Pre- and post-implantation mortality rates were estimated to be 0.3 and 0.1 ova per pregnancy, respectively (Tamarin, 1977a).

Gestation is 21 days (Dieterich and Preston, 1977). Manly (1953) described parturition. The six young in the litter he observed were all born within 40 minutes; birth of a litter observed by Hamilton (1941) took 7 hours. Manly (1953) observed the mother construct a nest and place the neonates within it in the 2 hour period following parturition. Using radio-telemetry, Madison (1978a) noted that female movement sharply decreased at parturition. Mean litter sizes range from 4.0 to 6.2, with extremes of one to 11 young per litter (Hamilton, 1941; Kott and Robinson, 1963; Tamarin, 1977a). Litter size is not significantly correlated with latitude or elevation (Innes, 1978). Keller and Krebs (1970) noted that fall, winter, and spring litters averaged 14% smaller than summer litters. They also noted that litter size was positively correlated with body size, was not significantly different in primiparous and multiparous females, and was constant in summer breeding periods at different population densities.

Neonates of *M. pennsylvanicus* are pink and hairless, with closed eyes and ear pinnae, and weigh from 1.6 to 3.0 g (Hamilton, 1941). Fur begins to appear at day 4, and the entire body with the exception of the belly is covered with juvenile hair by day 7. The eyes and ears open by day 8, and vocalization ability appears at day 4 (Hamilton, 1941; Manly, 1953). Pepin and Baron (1978) described the development of motor activity during the first 21 days. According to Hamilton (1941), weaning occurs between 12 and 14 days after birth. An average of 2.6 young per litter (63% of the litter) is successfully weaned (Morrison et al. 1976).

Getz (1960) reported a mortality rate of 88% for the first 30 days after birth, and Krebs et al. (1969) found that early juvenile mortality was not related to changes in population density. Growth rates for the first 25 to 30 days after birth range from 0.2 to 0.5 g per day (Barbehenn, 1955) to 1 g per day (Hamilton, 1941). Brown (1973) found that young born in spring and early summer attained adult weight in 12 weeks, and underwent a fall weight loss. Young born in late summer continued growing into the fall, and maintained their weight through the winter. Myers and Krebs (1971a) reported a more rapid growth rate in juvenile males than in juvenile females.

Reproductive rate is sensitive to adrenal activity (Pasley, 1974), and depends on season and population density, with winter breeding occurring at high population density (Tamarin, 1977a), particularly in individuals of greater body weight (Keller and Krebs, 1970). Tamarin (1977a) estimated an average pregnancy rate of 60%. Post-partum estrus was observed in 55% of the females in a laboratory colony (Morrison et al., 1976).

Estimates of mean longevity range from 2 to 3 months (Beer and MacLeod, 1961) to 10 to 16 months (Hamilton, 1941). Survival rates for laboratory bred voles for a period of 144 weeks were given in Morrison et al. (1977). For field populations, Tamarin (1977b) determined that females had greater survival rates than males, but juvenile survival rates did not vary with sex.

ECOLOGY. *Microtus pennsylvanicus* is locally sympatric with a variety of small mammals over its wide geographic range. This vole is often restricted to moister habitats when sympatric with *M. ochrogaster* or *M. montanus* (Findley, 1954), and ex-

cludes *Clethrionomys gapperi*, *Peromyscus leucopus*, and *P. maniculatus* from grasslands (Morris and Grant, 1972; Bowker and Pearson, 1975; Grant, 1971). *M. pennsylvanicus* also coexists with *Sigmodon hispidus*, *Zapus hudsonius*, *Synaptomys cooperi*, and *Orzomys palustris* (Terman and Johnson, 1971; Shure, 1971; Getz, 1961a; Harris, 1953). *M. pennsylvanicus* appears to avoid locations frequented by *Blarina brevicauda* in the field, and avoids its scent in the laboratory (Fulk, 1972). Annual population densities of *M. pennsylvanicus* seem to be inversely related to the number of short-tailed shrews present (Eadie, 1952).

Microtus pennsylvanicus is prey for many hawks, owls, and carnivores, and is also taken by some snakes (Madison, 1978b). *Blarina brevicauda* may be a predator (Eadie, 1952). There is extensive documentation of ecto- and endo-parasites (for example, Kinsella, 1967; Rausch and Tiner, 1949; Whitaker and Wilson, 1974; Timm, 1973). These parasites include several species of the following groups: trematodes, cestodes, nematodes, acanthocephalans, anoplura, siphonaptera, diptera, and acarina. The ecology of botfly (*Cuterebra*) infection was studied by Getz (1970a). Protozoan, bacterial, and viral infections have been reported (Kirner et al., 1958; Whitney et al., 1970).

Microtus pennsylvanicus populations are characterized by cyclic fluctuations in density with a period of 2 to 5 years. These cycles were summarized by Krebs and Myers (1974). Many factors have been mentioned as being important in the population regulation of microtine rodents. Batzli and Pitelka (1971) suggested that food quality is important, with population cycles being caused by a lag in nutrient-recovery time. Pearson (1966) stressed the importance of predation in microtine cycles, noting that predators are responsible for determining the timing and the amplitude of the cycle in *M. californicus*. Krebs and Myers (1974) describe how climatic events can be of importance in the timing of various demographic changes. Christian (1970) emphasized the importance of physiological stress, noting that an increase in population density raises the level of endocrine stress in the population, which ultimately results in a decline in density. Chitty (1967) and Krebs et al. (1973) suggested that behavioral and genetic factors are important in causing cyclic fluctuations. The behavior-genetic model of Chitty (1967) maintains that at different population densities selection differentially favors voles which differ in their respective genetically-determined intraspecific behavior. Changes in behavior and gene frequencies of electrophoretic loci have been observed (Krebs et al., 1973). The importance of dispersal as a regulation factor was discussed by Krebs et al. (1973) and Tamarin (1977c). Normal population cycles do not occur when dispersal is prevented, and under normal conditions, dispersers have been shown to be behaviorally, genetically, and demographically different from residents.

The dispersal tendency of *M. pennsylvanicus* is well documented. Myers and Krebs (1971b) and Reich and Tamarin (1980) noted behavioral differences between dispersing and resident subpopulations of *M. pennsylvanicus*, and differences in frequencies of alleles have been noted by Keith and Tamarin (In press) and Myers and Krebs (1971b). Tamarin (1977b) noted seasonally related size differences in dispersers and residents, and observed that males contributed a disproportionately larger portion of the dispersal population in the winter, whereas females were more common among dispersers in summer. A positive relationship between dispersal rate and population density was noted by Tamarin (1977b). Hilborn (1975) emphasized the similarity in dispersal tendency between siblings, especially during population increases. Grant (1978) studied dispersal in relation to carrying capacity and energetics.

A review of home range dynamics was provided by Van Vleck (1969), who reported home ranges of 405 to 3,480 m² (0.10 to 0.86 acres) for males, and 160 to 3,115 m² (0.04 to 0.77 acres) for females. Home range size depends on season (summer ranges are larger than winter ranges), habitat (ranges in marshes are larger than ranges in meadows), and population density (ranges are smaller at higher population densities) (Tamarin, 1977c; Getz, 1961b). Getz (1961b) observed that roughly 20% of the population (mostly males) shifted their home range each month. Getz (1961b) estimated the size of a defended area to be less than 7 m in diameter, and found that the degree of territoriality was independent of population density or environmental conditions.

Robinson and Falls (1965) studied the homing ability of *M. pennsylvanicus*, and noted no successful homing at a displacement distance of greater than 305 m. They concluded that homing is accomplished through prior knowledge of the terrain and through random wandering. The ability of *M. pennsylvanicus* to use the sun for sun-compass orientation was demonstrated by Fluharty et al. (1976).

Microtus pennsylvanicus appears to eat most available species of grasses, sedges, and herbaceous plants. Riewe (1973) found that herbaceous vegetation is eaten primarily in summer and autumn. He recorded 64 vascular and 9 non-vascular plant species in the diet, and noted that among the plants eaten, many are typical of the forest. Zimmerman (1965) found that the grasses *Poa*, *Panicum*, and *Muhlenbergia* predominated in the diet. The occurrence of fungi, primarily *Endogone*, in the diet of *M. pennsylvanicus* has been noted (Bakerspigel, 1956). Meadow voles also eat insects (Zimmerman, 1965), and sometimes scavenge on animal remains (Riewe, 1973). At high population densities, *M. pennsylvanicus* may seriously damage woody vegetation, especially in fruit orchards, by girdling (Byers, 1979).

By studying mineral levels in stomach contents, Bergeron (1976) determined that nitrogen, calcium, phosphorus, and magnesium levels are a function of the concentrations in food plants while potassium levels are consistent throughout the year. Grant (1978) proposed several methods by which *M. pennsylvanicus* can minimize mineral deficiencies.

Habitat selection may be influenced by relative ground cover of grasses and herbs (Getz, 1970b), soil moisture (Wrigley, 1974), soil sodium levels (Aumann and Emlen, 1965), soil pH and potassium levels (Krebs et al., 1971), surface temperature and humidity (Getz, 1971), and inter-specific competition (Grant, 1971). Woodland populations have a lower reproductive success and lower adult survival rates than do grassland populations (Grant, 1975).

Maintenance of *M. pennsylvanicus* as a laboratory animal was described by Lee and Horvath (1969). Meadow voles were found to be useful as bioassay organisms to test for the nutritive quality of, and presence of toxins in, food plants (Schillinger and Elliott, 1966; Kendall and Sherwood, 1975). Chemical regulation of vole populations in commercial fruit orchards was discussed in Byers (1979).

BEHAVIOR. *Microtus pennsylvanicus* acts aggressively in intraspecific encounters (Getz, 1962). Intraspecific male aggression varies directly with population density (Krebs, 1970), and reproductive activity (Turner and Iverson, 1973). In interspecific encounters, *M. pennsylvanicus* was subordinate to other *Microtus* species (D. Colvin, 1973).

Microtus pennsylvanicus can be active at any time of day although short-term activity cycles with a mean of 4.8 h (Ambrose, 1973) have been reported. Ambrose (1973) determined that at any given moment at least 50% of the population was active. Kavanau and Havenhill (1976) found a dual light-preference curve, with activity peaks at darkness and at 15% starlight. Voles may be more active in the daytime (Ambrose, 1973) or at night (Seabloom, 1965). Graham (1968) suggested that the time of major activity depends on the amount of vegetative cover present. Under dense cover activity will be mostly diurnal, whereas under sparse cover, activity will be mostly crepuscular. Getz (1961c) noted that *M. pennsylvanicus* switched from diurnal to nocturnal activity when ambient temperatures were above 20°C, but that they were not active when temperatures dropped below 0°C. Voles were more active during a new moon than during a full moon, regardless of nighttime cloud cover (Doucet and Bider, 1969). Myers and Krebs (1971b) found a greater level of activity in dispersing voles compared to resident voles, and Ambrose (1973) found a positive correlation between activity and population density.

Krebs (1970) observed that vocalizations often accompany aggressive threats. The average threat vocalization has a duration of 0.068 seconds, has a fundamental frequency of 1.5 kHz, and a maximum frequency of 1.8 kHz (Houseknecht, 1968). There are few vocalizations in interspecific encounters (Houseknecht, 1968). M. Colvin (1973) found that ultrasonic vocalizations were produced in response to a variety of stressful conditions, and described four acoustically distinct calls.

Microtus pennsylvanicus may select foods based on low alkaloid content (Kendall and Sherwood, 1975), low fiber content (Keys and Van Soest, 1970), and high nutritive quality (Schillinger and Elliott, 1966). Voles can detect the presence of various solutes added to their drinking water (Laughlin et al., 1975).

Weilert and Shump (1977) described nest-building and the physical parameters of the nest.

GENETICS. The transferrin (Tf) locus consists of 6 alleles, and is inherited as a codominant, autosomal trait (Gaines and Krebs, 1971). Maurer (1969) studied temporal and geographic variation at this locus in 24 separate populations from North Dakota to Massachusetts. He found no evidence of temporal variation, but did detect macrogeographic trends in the frequencies

of certain alleles and significant microgeographic differences in three populations in New York. Gaines and Krebs (1971) determined that the leucine amino peptidase (LAP) locus was dimorphic and was controlled by two codominant autosomal alleles. Changes in the allele frequencies at the transferrin and leucine amino peptidase loci are correlated with differences in population density, sex, survival rates, growth rates, breeding activity index, body weights, and resident or dispersing individuals (Gaines and Krebs, 1971; Myers and Krebs, 1971b; Tamarin and Krebs, 1969; Kohn and Tamarin, 1978; Birdsall, 1974). Kohn and Tamarin (1978) studied a total of 15 loci, and except for Tf and LAP, all were monomorphic. A case of dimorphism at the hemoglobin (Hb) locus was noted for *M. pennsylvanicus* from Montana (Stratton and Duffy, 1976), and the 6-phosphogluconate dehydrogenase (6PGD) locus was found to be dimorphic in *M. pennsylvanicus* from Nebraska (Nadler et al., 1978).

Little (1958) summarized coat color mutations and assigned them to probable loci known from other rodents. The following mutations were described: yellow (*A*^y), brown (*b*), complete albino (*C*^a), himalayan rabbit (*C*^h), extreme dilute (*c*^e), blue dilute (*d*), yellow (*e*), pink-eye (*p*), extreme white piebald (*s*^m), and black-eyed white (*W*). Barrett (1976) found a population in Ohio with the extreme dilute phenotype in 5 of 19 individuals. Breeding experiments suggested that the trait was inherited as a recessive.

Microtus pennsylvanicus has a diploid chromosome number of 46 with a fundamental number of 50. Its autosomes consist of two pairs of large submetacentrics, one pair of large metacentrics, and 19 pairs of small to large telocentrics. The X is a large submetacentric and the Y is a small telocentric (Hsu and Benirschke, 1967).

REMARKS. The genus name *Microtus* is derived from the Greek *micro* (small) and *otus* (ear). The species name is derived from Pennsylvania, the state from which the species was first described.

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Reithrodontomys megalotis. By Wm. David Webster and J. Knox Jones, Jr.

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Reithrodontomys megalotis (Baird, 1858)

Western Harvest Mouse

- Reithrodon megalotis* Baird, 1858:451. Type locality between Janos, Chihuahua, and San Luis Springs, Grant Co., New Mexico.
- Reithrodontomys megalotis* Allen, 1893:79; first use of current name combination.
- Reithrodon longicauda* Baird, 1858:451. Type locality Petaluma, Sonoma Co., California.
- Reithrodontomys aztecus* Allen, 1893:79. Type locality La Plata, San Juan Co., New Mexico.
- Reithrodontomys pallidus* Rhoads, 1893:835. Type locality Santa Ysabel, San Jacinto Mts., San Diego Co., California.
- Reithrodontomys dychei* Allen, 1895:120. Type locality Lawrence, Douglas Co., Kansas.
- Reithrodontomys arizonensis* Allen, 1895:134. Type locality Rock Creek, 8,000 ft, Chiricahua Mts., Cochise Co., Arizona.
- Reithrodontomys saturatus* Allen and Chapman, 1897:201. Type locality Las Vigas, 8,000 ft, Veracruz.
- Reithrodontomys klamathensis* Merriam, 1899:93. Type locality Big Spring, Shasta Valley, Siskiyou Co., California.
- Rhithrodontomys peninsulæ* Elliot, 1903:164. Type locality San Quintin, Baja California del Norte.
- Rhithrodontomys catalinae* Elliot, 1904:246. Type locality Santa Catalina Island, Santa Barbara Islands, California.
- Reithrodontomys amoles* Howell, 1914:40. Type locality Pinal de Amoles, about 7,500 ft, Querétaro.

CONTEXT AND CONTENT. Order Rodentia, Family Muridae, Subfamily Cricetinae, Tribe Hesperomyini. Sixteen subspecies (but see Remarks section) of *R. megalotis* currently are recognized (Hall and Kelson, 1959; Jones and Mursaloglu, 1961), as follows:

- R. m. alticolus* Merriam, 1901:556. Type locality Cerro San Felipe, 10,000 ft, Oaxaca.
- R. m. amoles* Howell, 1914:40, see above.
- R. m. arizonensis* Allen, 1895:134, see above.
- R. m. aztecus* Allen, 1893:79, see above (*caryi* Howell is a synonym).
- R. m. catalinae* (Elliot, 1904:246), see above.
- R. m. distichlis* von Bloeker, 1937:155. Type locality salt marsh at mouth of Salinas River, Monterey Co., California.
- R. m. dychei* Allen, 1895:120, see above (*nebrascensis* Allen and *pectoralis* Hanson are synonyms).
- R. m. hooperi* Goodwin, 1954:1. Type locality Rancho del Cielo, 5 mi NW Gómez Farias, 3,500 ft, Tamaulipas.
- R. m. limicola* von Bloeker, 1932:133. Type locality Playa del Rey, Los Angeles Co., California.
- R. m. longicaudus* (Baird, 1858:451), see above (*klamathensis* Merriam and *pallidus* Rhoads are synonyms).
- R. m. megalotis* (Baird, 1858:451), see above (*deserti* Allen, *nigrescens* Howell, and *sestiniensis* Allen are synonyms).
- R. m. peninsulæ* (Elliot, 1903:164), see above.
- R. m. ravus* Goldman, 1939:355. Type locality north end of Stansbury Island, 4,250 ft, Great Salt Lake, Tooele Co., Utah.
- R. m. santacruzæ* Pearson, 1951:366. Type locality Prisoners Harbor, Santa Cruz Island, Santa Barbara Co., California.
- R. m. saturatus* Allen and Chapman, 1897:201, see above (*cineurus* Merriam is a synonym).
- R. m. zacatecae* Merriam, 1901:557. Type locality Sierra de Valparaíso, Zacatecas (*obscurus* Merriam is a synonym).

DIAGNOSIS. *Reithrodontomys megalotis* (Fig. 1) is a small, long-tailed rodent with medial grooves on the anterior surface of the upper incisors. The ears are prominent; the tail is slender, scaly, and scantily haired. Western harvest mice have six tubercles on the soles of the hindfeet, and three pairs of mammae, one pectoral and two inguinal. The braincase (Fig. 2) is rounded and

smooth; the zygomata are slender, but possess broad zygomatic plates. The long incisive foramina are separated by a thin septum and terminate anterior to the maxillary toothrow. The pterygoids are nearly parallel and the pterygoid fossae are broad. The posterior border of the palate is truncate. The tympanic bullae are moderately inflated and angled obliquely to the longitudinal axis of the skull. The coronoid process is reduced. The dental formula is $i\ 1/1, c\ 0/0, p\ 0/0, m\ 3/3$, total 16.

Two subgenera of New World harvest mice, *Reithrodontomys* and *Aporodon*, currently are recognized. The former includes *R. megalotis* and is distinguished cranially from the latter (Hooper, 1952; Howell, 1914) as follows: zygomatic plate broader than mesopterygoid fossa; mesopterygoid fossa narrower, equal in width to the crown length of M2; pterygoid fossa more than twice as broad as mesopterygoid fossa, and pterygoid hamulae inflated slightly and not reflexed laterally. *Reithrodontomys* also has a simpler molar pattern than *Aporodon*, with reduced mesolophids (mesolophids) and mesostyles (mesostylids), and an incomplete third molar. Additionally, the zygomasseteric musculature of *Reithrodontomys* is distinct from that of *Aporodon* (Rinker and Hooper, 1950).

It sometimes is difficult to distinguish *R. megalotis* from other members of the subgenus. "There are no absolute characters by which this species can be distinguished from certain congeners; usually close comparison must be made and identification based on the summation of characters" (Hall and Kelson, 1959). Breadth of braincase separates *R. megalotis* (10.7 mm or less) from *R. chrysopsis* and *R. sumichrasti* (greater than 10.7). The third molar in *R. megalotis* has a faint or absent first primary fold that always is shorter than the second primary fold, whereas *R. fulvescens* and *R. hirsutus* have a well-developed first primary fold. *R. burti*, *R. humulis*, and *R. montanus* are smaller than *R. megalotis*. The latter differs from *R. raviventris* in that the total pelage is shorter and the ears are buffy to reddish-brown rather than blackish; also, the tail of *megalotis* is more distinctly bicolored. See Hall (1981), Hall and Kelson (1959), and Hooper (1952) for diagnostic keys to the species of harvest mice.

GENERAL CHARACTERS. The dorsal pelage is one of two types, grayish to blackish guard hairs that are less numerous than shorter cover hairs. The latter are gray basally, with a buffy terminal band or a buffy subterminal band and a black terminal tip. In addition, *R. m. dychei* east of the Missouri River (Hoffmeister and Warnock, 1955) and *R. m. hooperi* from southwestern



FIGURE 1. *Reithrodontomys megalotis dychei* from Lawrence, Douglas Co., Kansas.



FIGURE 2. Dorsal, ventral, and lateral views of skull, and lateral view of lower jaw of *Reithrodontomys megalotis megalotis* (TTU 32227, female) from 6 mi N, 6 mi E Ft. Davis, Jeff Davis Co., Texas. The greatest length of skull is 21.9 mm.

Tamaulipas (Goodwin, 1954) frequently have a buffy pectoral spot, as do many individuals of *R. m. longicaudus* from the San Francisco Bay area (Fisler, 1965). Albinism is a rare recessive condition similar to that found in *Mus* (Egoscue, 1958).

Selected average and extreme external and cranial measurements (mm) from a series ($n = 85$) of *R. megalotis* from Indiana (Whitaker and Mumford, 1972), followed by one ($n = 15$) from western Texas and another ($n = 11$) from southern Oaxaca, both after Hooper (1952), are, respectively: total length, 126.8 (114 to 146), 133 (120 to 152), 144 (135 to 154); length of tail, 58.3 (50 to 69), 68 (61 to 78), 73 (64 to 83); length of hindfoot, 16.3 (15 to 18), 17 (16 to 18), 17 (15 to 18); length of ear from notch, —, 14 (12 to 15), 14 (13 to 15); greatest length of skull, 20.4 (19.0 to 21.4), 20.5 (19.6 to 21.2), 21.3 (20.0 to 22.5); zygomatic breadth, —, 10.4 (10.0 to 11.0), 10.5 (10.1 to 10.8); breadth of braincase, 10.0 (9.6 to 10.7), 9.9 (9.5 to 10.3), 9.7 (9.0 to 10.1); interorbital breadth, 3.2 (2.7 to 3.8), 3.0 (2.9 to 3.2), 3.0 (2.8 to 3.2); length of palate, 3.6 (3.2 to 4.0), 3.4 (3.2 to 3.7), 3.3 (2.9 to 3.5); length of maxillary toothrow, 3.1 (2.8 to 3.5), 3.3 (3.2 to 3.5), 3.3 (3.0 to 3.4).

Fisler (1965) and Jones and Mursaloğlu (1961) listed measurements for large series from California and the Central Great Plains, respectively. The latter authors found secondary sexual variation in mensural characters to be less than individual variation in populations on the Great Plains.

DISTRIBUTION. The distribution of the western harvest mouse is mapped in Fig. 3. It is known from southwestern Canada (British Columbia, Alberta, and Saskatchewan) southward to southern México (Oaxaca and Veracruz), and from California eastward to recently-invaded Indiana (Ford, 1977; Whitaker and Mumford, 1972).

The species is known altitudinally from 250 feet (about 77 m) below sea level at Death Valley, California, to approximately

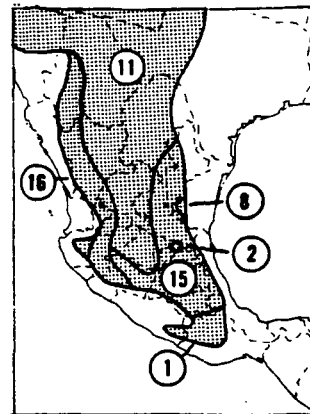
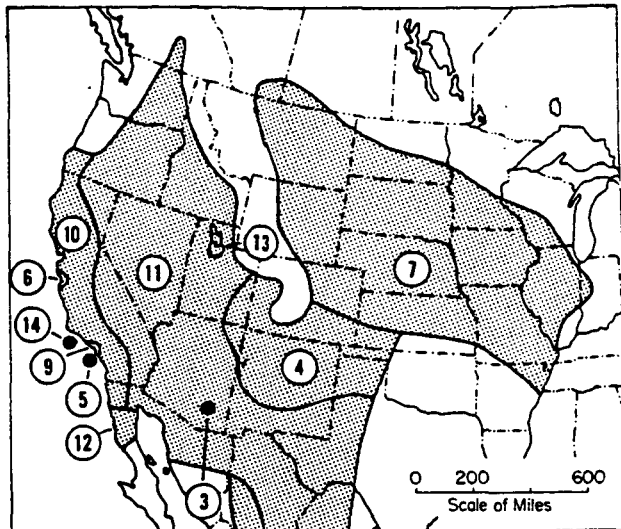


FIGURE 3. Distribution of *Reithrodontomys megalotis* in Canada and the United States (above) and México (below). Subspecies are: 1, *R. m. alticola*; 2, *R. m. amoles*; 3, *R. m. arizonensis*; 4, *R. m. aztecus*; 5, *R. m. catalinae*; 6, *R. m. distichlis*; 7, *R. m. dychei*; 8, *R. m. hooperi*; 9, *R. m. limicola*; 10, *R. m. longicaudus*; 11, *R. m. megalotis*; 12, *R. m. peninsulae*; 13, *R. m. ravus*; 14, *R. m. santacruzae*; 15, *R. m. saturatus*; and 16, *R. m. zacatecae*. Note that the ranges of *saturatus* and *zacatecae* are thought to overlap in Jalisco.

13,000 feet (4,000 m) on volcanos Popocatepetl and Orizaba in México (Hooper, 1952).

FOSSIL RECORD. *Reithrodontomys* cf. *megalotis* is known from Sangamon fossil beds in the Cragin Quarry Fauna, Kansas (Hibbard and Taylor, 1960). Illinoian remains from the Mt. Scott Fauna, Kansas, are referable to *Reithrodontomys*, and have styles and stylids similar to those of *megalotis* (Hibbard, 1963). Jakway (1958) assigned late Pleistocene remains from San Josecito Cave, Nuevo León, to *R. megalotis*.

FORM. The glans penis and os penis, figured by Hooper (1959) and Burt (1960), respectively, are morphologically similar to those of *Peromyscus*. The elongate phallus is rod-shaped and four to five times greater in length (6.0 mm) than in diameter (1.3 mm). The shaft is armored with small proximally-directed spines, but the terminal segment is aspinous. The os penis is a simple bone of uniform thickness that gradually arches upward from a dorsoventrally flattened and laterally expanded base; it lacks a cartilagenous tip. Geographic variation in total length of baculum (6.2 to 9.2 mm) and basal width (0.5 to 1.1 mm) is moderate, with specimens from México averaging slightly larger than those from the United States (Burt, 1960).

Males have a well-developed vesicular, paired ampullary and Cowper's glands, and four pairs of ventral prostate glands; however, they lack preputial glands (Arata, 1964). Average vagina length of seven estrus females was 17.3 mm (Fisler, 1965). The

hyoid apparatus, albeit slightly smaller, is similar to that of the subgenus *Peromyscus* (Sprague, 1941). There are small sebaceous, sudoriferous, and mucous glands associated with the buccal cavity (Quay, 1965). Small intestine and recto-colon lengths are 3.1 and 1.4 times that of the body length, respectively (Fisler, 1965).

FUNCTION. According to Fisler (1965), western harvest mice maintain a normal body temperature (35 to 38°C) when exposed to variable laboratory temperatures (17 to 29°C); however, individuals kept at 4.8°C for 14.5 h became torpid with a rectal temperature of 26.5°C. Hibernation has been reported in Nevada (O'Farrell, 1974), and in captive animals torpor has been recorded (Coulombe, 1970) in response to osmotic stress or water deprivation.

Pearson (1960b) found the minimum oxygen consumption for *R. megalotis* to be 2.5 cc g⁻¹ h⁻¹ at an ambient temperature of 33°C, with a metabolic increase of 0.27 cc g⁻¹ h⁻¹ for each 1°C decrease in ambient temperature. Also, oxygen consumption decreased if mice huddled or utilized a nest, but increased approximately 35% in experimental animals from which the fur had been removed.

Adult and fetal body compositions (percent dry weight) are, respectively: water, 68 and 88; ash, 14 and 11; lipid, 21 and one (Flehart et al., 1973). Adult lipid content, however, is higher in winter than summer. Western harvest mice preferably consumed fresh water during controlled experiments, but some salt water can be tolerated (Fisler, 1963). In fact, *R. m. limicola* consumed approximately twice as much 25% sea water than tap water in such experiments, and maintained constant body weight on 1.0 M NaCl solution (MacMillen, 1964). Western harvest mice have an exceptionally high evaporative water loss of 1.35 mg H₂O/cc O₂ consumed (Coulombe, 1970), and may reduce water loss in salt marshes by concentrating urine chlorides (MacMillen, 1964).

R. megalotis can perceive soundwaves of 35,000 and 23,000 vibrations per second on hot-dry and cold-rainy days, respectively (Davis, 1927). Young mice squeak frequently, but adult vocalizations are rare unless courting, fighting, or injured.

ONTOGENY AND REPRODUCTION. Most reproductive activity occurs from early spring to late autumn, with reduced midsummer activity, but these mice do breed year-round in the warmer parts of their geographic range. Females become sexually mature in just over four months of age and are polyestrous. Each of two females kept in optimal captive conditions gave birth to 14 litters in a single year (Bancroft, 1967); one produced a total of 58 young (litter size ranged from two to six) and the other 57 (litter size two to five).

Males are polygamous, and dominant males copulate with females in estrus (Fisler, 1965). The male venter contacts the female lower back when copulating; there is no locking or thrusting. Ejaculation occurs after the first intromission and multiple ejaculations are possible (Dewsbury, 1975). Postpartum estrus is known.

One to nine fetuses (Long, 1962) have been reported; 75 pregnant females from Nebraska had an average of 4.3 (Jones, 1964), whereas 41 from California averaged 3.8 (Fisler, 1965). Young are born after a gestation period of 23 to 24 days. Neonates are pink, hairless (except vibrissae), and have closed eyes and ears. They weigh 1.0 to 1.5 g and are 7.0 to 8.0 mm in length at birth (Jackson, 1961). Lightly haired young begin to crawl after five days and have erupting mandibular incisors (Smith, 1936; Svihla, 1931). The eyes and ears open between day 11 and 12, and weaning is complete in 24 days. The sex ratio evidently is about even at birth, but males were found by Fisler (1971) to predominate in all age classes thereafter except among old animals, when there was a predominance of females.

Western harvest mice have three characteristic pelages during their lifetime. The juvenile pelage is short, relatively sparse, and grayish brown. Postjuvenile molt "occurs at an early age, perhaps frequently before the young leave the nest" (Jones and Mursaloğlu, 1961). The subadult pelage is thicker, longer, and brighter than that of juveniles but duller than the pelage of adults.

Adults molt twice annually—in spring and autumn (Jones and Mursaloğlu, 1961). Spring molt proceeds posteriorly on the dorsum and venter, the latter being completed first. Autumnal molt is irregular. Molt is delayed in pregnant or lactating females. In summer the dorsal pelage is short (5 to 6 mm), sparse, and brownish to dark brownish on the dorsum, sides, and flanks; the venter is grayish. The pelage of winter is long (8 to 9 mm), denser, buffy dorsally and laterally, and the venter is whitish; also, the tail is more distinctly bicolored in the winter.

Senility in western harvest mice begins to occur at about 45

weeks of age and is accompanied by reduced litter size in females (Bancroft, 1967). Jones and Mursaloğlu (1961) suggested that old animals may have difficulty in completing seasonal molt. Fisler (1971) found essentially a complete turnover of individuals annually in California populations, few mice reaching the age of 12 months.

ECOLOGY. Western harvest mice typically inhabit grassy and weedy habitats such as overgrown pastures, meadows, fence-rows, fallow fields, and borders of agricultural and riparian areas, and not infrequently represent one of the most common mammals in such habitats. Individuals also are known from deserts, salt marshes, and pine-oak forests. *R. megalotis* is partially sympatric with at least eight other species of harvest mice, and although "there are records of occurrence of *megalotis* with each of these species" (Hooper, 1952), it is separated ecologically from *raviventris* (Fisler, 1965) and *montanus* (Hill and Hibbard, 1943). Multiple captures with *R. fulvescens* and *Baiomys taylori* have been reported in live traps in Durango (Peterson, 1975).

Spherical nests usually are located on the ground under heavy grass, bushes, weeds, or fallen logs, and are approximately 125 mm in diameter. Some nests are built (up to 1 m) above the ground in small shrubs. The nest is composed of plant fibers with an inner layer of finer plant "down." There are one or more openings near the base. Individuals have been reported as nesting in burrows in Illinois (Birkenholz, 1967).

Meserve (1977) reported circular or elliptical home ranges in California that averaged about 3,525 m². Density estimates vary from 4.8 per acre (about 11.9 per ha) in Washington (Gray, 1943) to 4.0 per ha in New Mexico (Whitford, 1976); the New Mexico population, however, increased to 60 per ha when ground vegetation became dense after September rains. Fisler (1966) recorded 330 feet (about 102 m) as the farthest distance between captured points of mice on a study area in California, although Brant (1962) earlier estimated 225 feet (about 70 m) as the average maximum distance between captures for *R. megalotis*. "Homing" ability was demonstrated by mice displaced by Fisler (1966) up to 1,000 feet (about 308 m) from their home areas.

This species is primarily granivorous, but individuals also consume herbaceous material and lepidopteran larvae (Meserve, 1976; Whitaker and Mumford, 1972). Natural predators include owls, hawks, snakes, canids, mustelids, felids, and scorpions (Hall, 1946). Cannibalism infrequently occurs among cagemates; in fact, *R. megalotis* is among the most tolerant of small mammals in that individuals in captivity frequently huddle together and even do so with mice of other species. When placed in an artificial enclosure with *Onychomys leucogaster*, western harvest mice were killed within three hours (Ruffer, 1968). No antagonistic behavior was reported when caged under conventional conditions with *Mus musculus* (Catlett and Shellhammer, 1962); however, water deprivation resulted in cooperative interspecific attacks and cannibalism on female *R. megalotis* and then on female *M. musculus*. *R. megalotis* frequently uses the runways of *Microtus* and *Sigmodon* (Hall, 1946), but does not assist in runway maintenance (Pearson, 1959). There appears to be no tendency for western harvest mice to avoid *Microtus* in Californian runways (Pearson, 1960a).

Numerous parasites are reported from *Reithrodontomys megalotis*. Endoparasites include the protozoan *Trypanosoma* sp. (Davis, 1952), acanthocephalan *Moniliformis clarkii* (McKeever, 1963), cestode *Hymenolepis diminuta*, and nematodes *Syphacia obveleta* and *Rictularia coloradensis* (Rankin, 1945). Ectoparasites found on western harvest mice include fleas (Siphonaptera) *Eptedia wenmani* and *Orchopeas leucopus*, and chiggers (Acarina) *Leeuwenhoekia americana*, *Trombicula alfreddugesi*, *T. lipovskyi*, *T. peromysci*, *T. diversa*, and *T. hungerfordi* (Loomis, 1956), and *Trombicula autumnalis* and *T. loomisi* (Kardos, 1954). Mites (Acarina) known to occur on *Reithrodontomys megalotis* include *Dermacarus* sp., *Androlaelaps fahrenheitii*, *Radfordia subuliger*, *Myocoptes* sp., *Hirstionyssus incomptus*, *H. occidentalis*, *H. eutamiae*, *H. isabellinus*, *H. tricanthus*, *H. utahensis*, *Macrocheles* sp., *Eubrachylaeps debilis*, and *Myobia musculi* (Whitaker and Mumford, 1972). Verts (1960) also reported *Heploleura hesperomydis* (Anopleura).

BEHAVIOR. Western harvest mice are nocturnal, and more active on moonless and rainy nights in California (Pearson, 1960a). In addition, increased activity was apparent when live traps were set adjacent to rodent runways.

Holes in nests are repaired immediately and, because several nests are constructed and utilized on different occasions, only old nests are fouled with excrement. "Breeding females are partic-

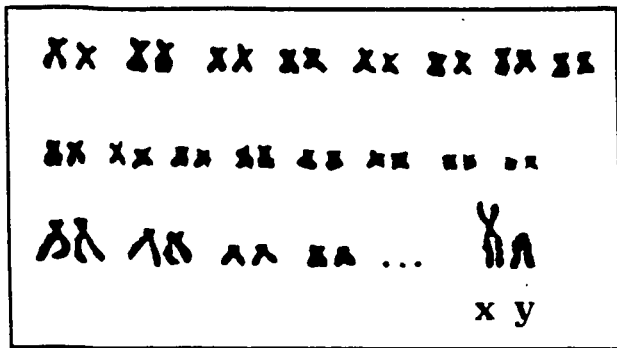


FIGURE 4. Karyotype of *Reithrodontomys megalotis megalotis* (TTU 4678, male) from Mt. Locke, Ft. Davis State Park, Jeff Davis Co., Texas. Note the three supernumerary chromosomes. Photograph courtesy of Robert J. Baker.

ularly careful in nest building and repair" (Fisler, 1965). He found *R. megalotis* to be more "tense" than *R. raviventris*. For example, when placed in water, *R. megalotis* swam erratically, did not use its tail to facilitate swimming, and struggled to keep its head above water. Also, as compared to the aforementioned species, *R. megalotis* attempted frequent escapes from captivity and, when successful, darted directly to the nearest cover.

GENETICS. The basic diploid number of chromosomes in *Reithrodontomys megalotis* is 42, although up to four supernumerary chromosomes may be present (Blanks and Shellhammer, 1968; Matthey, 1961). The basic complement of 40 autosomes includes 18 metacentrics, 16 submetacentrics, and six subtelocentrics. The X-chromosome is submetacentric and the Y-chromosome is subtelocentric (Shellhammer, 1967). The karyotype of *R. m. megalotis* from Texas shown in Fig. 4 includes three supernumeraries.

REMARKS. *Reithrodontomys* combines three Greek words to mean "grove-toothed mouse." The specific name *megalotis* is derived from the Greek words *mega* and *otis*, "large eared."

We recognize only 16 subspecies of *R. megalotis* although Hall (1981) listed 17. Following Jackson (1961), he included *R. m. pectoralis*, which we regard as a synonym of *R. m. dychei* (see Hoffmeister and Warnock, 1955).

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Odocoileus hemionus. By Allen E. Anderson and Olof C. Wallmo

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Odocoileus hemionus (Rafinesque, 1817)

Mule Deer

- Cervus hemionus* Rafinesque, 1817:436. Type locality near mouth of the Big Sioux River, South Dakota.
- Cervus auritus* Warden, 1820:640. Type locality "... la contré situé a l'ouest des montagnes Rocky, piès des bords de la rivière de Kooskooské."
- Cervus macrotis* Say, 1823:88. Type locality Mora River, near present town of Mora, New Mexico.
- Cervus Lewisii* Peale, 1848:39. Applied to specimens from Feather River and San Francisco Bay, California.
- Cariacus punctulatus* Gray, 1852:239. Type locality California.
- Cervus Richardsoni* Audubon and Bachman, 1848:table of contents and plate 106. Type locality California.
- Eucervus pusilla* Gray, 1873:157. Type locality North America (perhaps British Columbia).
- Dorcelaphus crooki* Mearns, 1897:2. Type locality summit Dog Mts., 6,129 feet, Hidalgo County, New Mexico.
- Cariacus virgultus* Hallock, 1899:404. Type locality near Hallock, Kittson County, Minnesota.

CONTEXT AND CONTENT. Order Artiodactyla, Family Cervidae, Subfamily Odocoileinae, Tribe Odocoileini. The genus *Odocoileus* includes two extant species, *O. hemionus*, as defined here, and *O. virginianus* (= *Dama virginiana* Zimmerman, 1780) that occurs over most of the southern half of North America and southward to northern South America and is sympatric with *O. hemionus* in much of the western half of North America. Subspecies recognized by Hall (1981) and Wallmo (1981a) are:

- O. h. californicus* (Caton, 1876:464). Type locality near Gaviota Pass, 40 mi W Santa Barbara, Santa Barbara County, California. California mule deer.
- O. h. cerrosensis* Merriam, 1898:101. Type locality Cedros Island, west coast of Baja California, Mexico. (Wallmo, 1981a, suggested that the distinction of *cerrosensis* from *peninsulae* be reconsidered). Cedros Island deer.
- O. h. columbianus* (Richardson, 1829:257). Type locality Cape Disappointment, Pacific County, Washington (*lewisii* Peale, *punctulatus* Gray, *richardsoni* Audubon and Bachman, *pusilla* Gray, and *scaphiotus* Merriam are synonyms). Columbian black-tailed deer.
- O. h. crooki* (Mearns, 1897:468). Type locality Dog Mountains, Hidalgo County, New Mexico (*eremicus* Mearns and *canus* Merriam are synonyms according to Hoffmeister, 1962, although Hall, 1981, recognized *O. h. eremicus*).
- O. h. fuliginatus* Cowan, 1933a:326. Type locality Barona Ranch, 30 mi E San Diego, San Diego County, California. Southern mule deer.
- O. h. hemionus* (Rafinesque, 1817:436). Type locality near mouth of Big Sioux River, South Dakota (*auritus* Warden, *macrotis* Say, *montanus* Caton, and *virgultus* Hallock are synonyms). Rocky Mountain mule deer.
- O. h. inyoensis* Cowan, 1933b:69. Type locality 10 mi W Big Pine, Inyo County, California (pers. comm. from I. McT. Cowan, W. Macgregor, and A. S. Leopold, to O. C. Wallmo question the validity of *inyoensis*). Inyo mule deer.
- O. h. peninsulae* (Lydekker, 1898:900). Type locality between La Laguna and Victoria Mountain, Sierra Laguna, Baja California, Mexico. Peninsula mule deer.
- O. h. sheldoni* Goldman, 1939:497. Type locality Tiburon Island in Gulf of California, Sonora, Mexico. (Wallmo, 1981a, suggested that the distinction of *sheldoni* from *peninsulae* be reconsidered). Tiburon Island mule deer.
- O. h. sitkensis* Merriam, 1898:100. Type locality Sitka, Alaska. Sitka black-tailed deer.

DIAGNOSIS. The following characters define the genus (Cowan, 1936; Hall, 1981): face long and narrow; rhinarium well developed; vomer high, dividing nostrils into two chambers posteriorly; upper canines usually absent; lacrimal pits and preorbital glands small; two lacrimal ducts on rim of orbit (Fig. 1); antlers normally present only in males, beam rising at marked angle to plane of face; generally dichotomously forked, with subbasal snag; anterior prong of main forks usually larger than posterior prong; main prongs with secondary forking. Skull, teeth, and antler characters do not reliably discriminate between all forms of *O. hemionus* and *O. virginianus* (Cowan, 1956a). Ears variable in size and hairiness; tarsal and metatarsal glands present; interdigital glands present on both fore- and hindfeet; noviculocuboid of tarsus free from cuneiform; coat uniformly colored; young spotted.

Odocoileus hemionus is distinguished from *O. virginianus* by a tail that is white to black above and tipped with black (in opposition to tail brown above, fringed with white laterally, and white below), ears approximately $\frac{3}{4}$ length of head (as opposed to $\frac{1}{2}$ length of head), antlers that branch dichotomously (Fig. 2) rather than one main beam with vertically rising tines, no external indication of the interdigital glands in contrast to orifices surrounded by white hairs, and deeper (ca 23 mm) preorbital pits. Metatarsal glands more than 25 mm in length separate *O. hemionus* from *O. virginianus* (Hall, 1981). The northern forms of *Odocoileus* spp. may have larger metatarsal glands (Anderson et al., 1964; Cowan, 1956a; Hershkovitz, 1958).

The western subspecies, or black-tailed deer (*O. h. columbianus* and *O. h. sitkensis*), have amply haired tails and raise them in flight, as does *O. virginianus*, but they do not wave them from side to side as the latter does. Geist (1981) described the unique bounding gait of *O. hemionus* as stotting. Stotting is a highly modified gallop (Eslinger, 1976), common in mule deer and, to a lesser extent, in Columbian black-tailed deer. In Sitka blacktails, stotting apparently is seen rarely. Stotting may be an alarm behavior that alerts conspecifics. Mule deer and white-tailed deer have essentially the same gallop but mule deer may lack the speed of whitetails (Geist, 1981).

GENERAL CHARACTERS. *Odocoileus hemionus* is a medium-sized cervid; adult males stand about 1 m at the shoulders and commonly attain 70-150 kg live weight (Fig. 2). The pelage of the back and sides ranges from gray to dark brown, or even black in median dorsal zone. The summer coat is more reddish-brown. According to Geist (1981), individual mule deer range from dark brown gray, dark and light ash-gray to brown and even reddish; the rump patch may be white or yellow and some have one white throat patch, but others have two. The white tails of most mule deer terminate in a tuft of black hair, or less commonly in a thin tuft of white hairs, or the barest admixture of black hairs. On other mule deer a dark dorsal line runs from the back down the top of the tail to the black tail tip. All markings vary considerably among individuals, but remain constant throughout life. A V-shaped dark mark extends from a point between the eyes upward and laterally; it is more characteristic and more conspicuous in males.

Growth in *O. h. hemionus* in Colorado (Anderson et al., 1974) was roughly parallel in males and females the first year. Thereafter, males, in general, exceeded females in carcass weight, chest girth, neck circumference, body length, head length, cranial breadth, shoulder height, hindfoot length, and hoof length. The largest male (bled carcass weight) was 112.3 kg and the largest female 75.2 kg; in shoulder height, the largest male was 106 cm and the largest female 100 cm (Anderson et al., 1974).

DISTRIBUTION. *Odocoileus hemionus* occurs over most of North America west of the 100 meridian from 23° to 60°N (Fig. 3). The most southerly records are from northern San Luis Potosi, Mexico (Cowan, 1956a) and the most northerly from southern

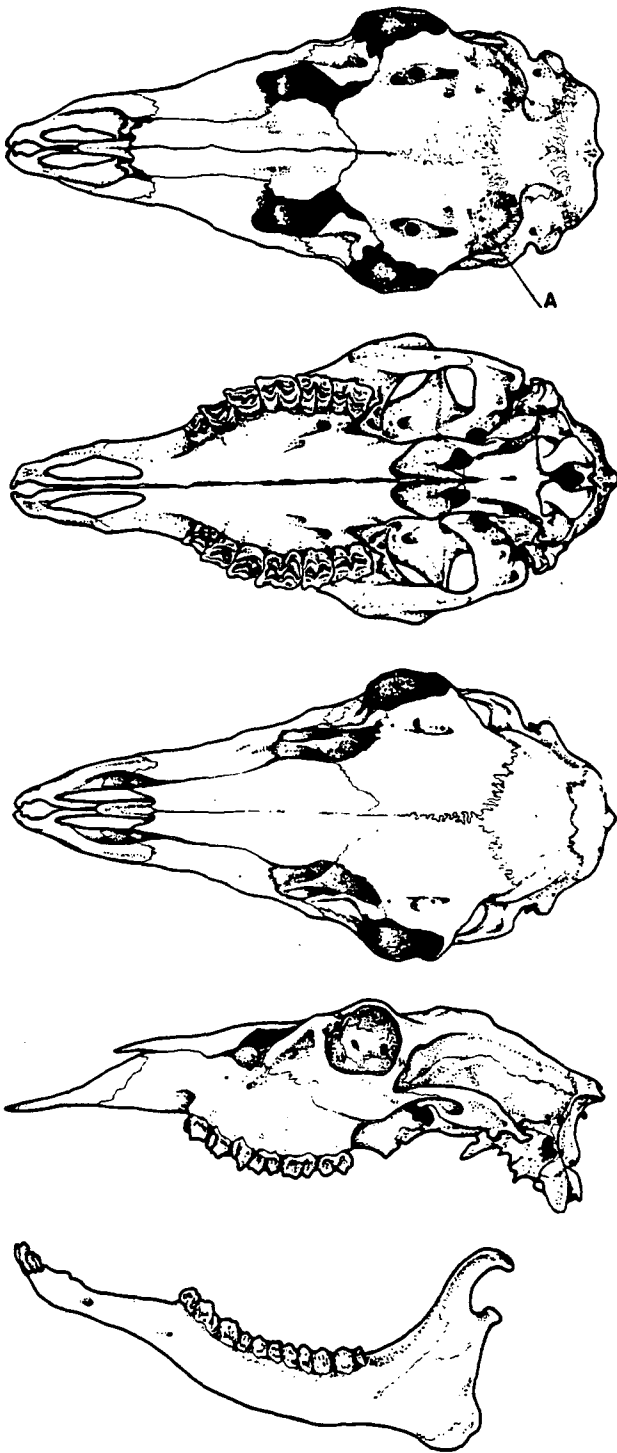


FIGURE 1. Dorsal and ventral views of cranium of male *Odocoileus hemionus hemionus* with antler pedicel (A) denoted (Dept. Anatomy, Colorado State Univ.), and dorsal and lateral views of cranium and lateral view of mandible of female (UCM 5387, from Converse County, Wyoming). Drawn by Gwen A. Anderson.

Yukon Territory, Canada (Wallmo, 1981a) but boundaries are provisional. The eastern edge of the usually occupied range extends from southwestern Saskatchewan through central North and South Dakota, Nebraska, Kansas, and western Texas, but isolated occurrences are reported from Minnesota, Iowa, and Missouri (Wallmo, 1981a). Major gaps in geographic distribution are in the Mojave and Sonoran deserts in southern Nevada, southeastern California, southwestern Arizona and northwestern Sonora, the Central Valley of California, and probably the Great Salt Lake desert region. Oth-



FIGURE 2. Three male Rocky Mountain mule deer (*Odocoileus hemionus hemionus*). Photo by Geoffrey Tischbein, Colorado Division of Wildlife.

erwise, the species occurs in all of the biomes of western North America north of central Mexico, except the Arctic tundra.

FOSSIL RECORD. The earliest fossil remains of *Odocoileus* in North America, from Arizona, California, and Kansas, were estimated to be ≥ 2 million years old (mid- to late Pliocene), and the genus was speculated to be of Old World origin (Opdyke et al., 1977). An early Blancan (late Pliocene) antler base from southwestern Washington, assigned to *Odocoileus ensifer* (Cope), was recognized by Fry and Gustafson (1974) as similar to a recent specimen of *O. hemionus*, though they considered *O. ensifer* to be distinct. A basal portion of an antler from late Pliocene deposits in the San Francisco Bay region compared well with recent specimens of *O. hemionus* (Savage, 1951). Pleistocene fragments of antler, teeth, and lower jaw (from near Aguascalientes in central Mexico) that resembled *O. hemionus* were referred to *O. ensifer* (Mooser and Dalquest, 1975). The fossil trace of *O. hemionus* is poor until it appears abundantly in recent sites within its present range. The race with the largest distribution, *O. h. hemionus*, now occupies an area that was covered by ice in the Pleistocene, whereas several races occur to the south where glaciation was either limited or did not occur (Cowan 1956a).

FORM AND FUNCTION. Cowan and Raddi (1972) identified four types of adult hairs and the annual cycle of follicles producing the natal, juvenile, adult summer and adult winter pelages. The pelage of adult deer is composed of woolly underhairs, mane type hairs (18 to 44 mm in length), intermediate guard hairs of the same length and the major component of the pelage, and large guard hairs up to 80 mm in length. Guard hairs have a sensory function and are distributed over the body about 2 cm apart and appear first for each molt. Among fawns, the characteristic white spots disappeared at 83 to 87 days and the pelage turned gray at 92 to 98 days (Robinette et al., 1977). Among adults, two hair cycles are completed annually, alternating between a summer pelage for 5 months and a winter pelage for 7 months. The abundance of woolly underhair in winter and its absence in summer is largely

responsible for the distinctly different coloration of winter and summer pelages (Cowan and Raddi, 1972).

The udder has four separate quarters each with a single teat and teat canal. The posterior quarters are the largest (Mueller and Sadleir, 1977). The udder averaged 12 cm long, 11 cm wide, and 4 cm deep, with teat lengths of 1.4 cm (anterior) and 1.6 cm (posterior) (Anderson et al., 1974).

Milk yield averaged $59 \text{ g kg}^{-0.75} \text{ day}^{-1}$ in *O. h. columbianus* (Sadleir, 1980) and most of the milk was produced in the posterior quadrants (Mueller and Sadleir, 1977). Those authors noted that nutrient composition of deer milk increased with fawn growth. Milk of *O. h. columbianus* contained 1.4% ash, 5.4% lactose, 7.6% protein, and 10.9% fat (Jeness and Sloan, 1970). The relatively high fat, hence high energy levels ($1,650 \text{ kcal kg}^{-1}$), of deer milk (Short, 1981) may have survival value for the neonate because feeding can occur at relatively long intervals (Mueller and Sadleir, 1977).

In *O. h. hemionus*, total muscle and bone averaged 46.9% and 10.3%, respectively, of the carcass weight of four adults (Hakonson and Whicker, 1971a) and 34.5% and 17.7%, respectively, of the carcass weight of three fetuses (Hakonson and Whicker, 1971b).

Mule-deer-antler (pedicel) primordia were visible in both sexes 73 to 83 days after conception (Hudson and Browman, 1959). Growth of the male pedicel from the frontal bones began about 80 to 93 days from birth (Davis, 1962; Robinette et al., 1977). The fawn antler is typically skin-covered and consists of the pedicel and the base of the yearling antler beam (Cowan, 1936) ranging from about 3.5 to 8.0 cm in length in *O. h. hemionus* (Anderson and Medin, 1971). Occasionally, fawns about 5 to 7 months of age may have 1.0 to 2.5 cm of either hard antler or bony tips attached to skin-covered pedicels (Anderson and Medin, 1971). In the mature male, antler growth begins from the concave pedicel about 2 weeks (Linsdale and Tomich, 1953) to 2 months (Leopold et al., 1951) after antler shedding. Among races of *O. hemionus*, antler growth begins from about 23 February (Linsdale and Tomich, 1953) to 15 July (Swank, 1958) and terminates from 28 July (Linsdale and Tomich, 1953) to 22 October (Anderson and Medin, 1971).

The growing antler is covered with velvet, a modified extension of normal skin of the head and pedicels that is shed after growth ceases (Bubenik, 1966). The annual cycle of antler growth in *Odocoileus* is initiated and controlled by changes in day length acting on several cell types of the anterior pituitary (Nicolls, 1971). Hypothetically, those cell types secrete growth-stimulating hormones that act mainly on the antler and incidentally on the testes (Nicolls, 1971). Antler hardening, shedding, and the breeding period are mediated by decreasing day length through action of gonadotropins on Leydig cells, thus producing androgens (Goss, 1963, 1980; Markwald et al., 1971; Nicolls, 1971; West and Nordan, 1976). Androgens induce secondary ossification, accelerate maturation, induce behavioral changes to shed antler velvet, and aid in the maintenance of osteoblasts and osteocytes to maintain antlers in hard bone condition (West and Nordan, 1976). Withdrawal of androgens at the end of the breeding season permits resorption of bone at the pedicel-antler junction (Fig. 1) and antler shedding (West and Nordan, 1976). Extreme dates of antler shedding were from about 20 October (Robinette et al., 1977) to 20 April (Swank, 1958) and may encompass 16 weeks (17 December to 10 April) for individual populations (Anderson and Medin, 1971).

Costal cortical bone was mobilized during antler growth and replaced after growth while maintaining a constant skeletal bone mineral composition throughout the cycle (Banks et al., 1968a). This cyclic physiological osteoporosis occurred even though dietary intake of minerals was adequate (Banks et al., 1968a, 1968b; Hillman et al., 1973).

Completely ossified (mature) antler has a sheath 7 to 10 mm thick and a base of solid hard bone that extends to the external burr or corona. The sheath completely surrounds a core of spongy bone at its tip that grades into coarser spongy bone to the corona (Cowan, 1936; Modell, 1969).

Antler development in *Odocoileus* was related experimentally to nutritional levels (French et al., 1956) especially during the late-summer stage of antler growth (Long et al., 1959). Anderson and Medin (1969) reported strong positive correlations between various antler measurements and antler weight, eviscerated carcass weight and antler weight, and estimated age and antler weight.

All but 2 of 17 antlered deer reported as females had poorly

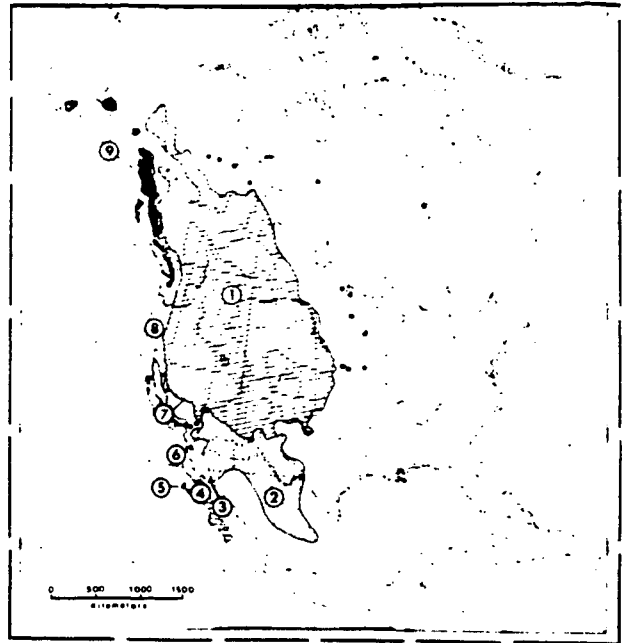


FIGURE 3. Distribution of *O. hemionus*. Lines enclose more or less continuously occupied range; outlying points are locations of specimens referenced by Hall (1981) where persistent populations do not occur; 1, *O. h. hemionus*; 2, *O. h. crooki*; 3, *O. h. sheldoni*; 4, *O. h. peninsulae*; 5, *O. h. cerrosensis*; 6, *O. h. fuliginatus*; 7, *O. h. californicus*; 8, *O. h. columbianus*; 9, *O. h. sitkensis*.

developed antlers in velvet; six were with fawns, had fetuses, or were lactating, but antlers were known to be deciduous in only one individual (Anderson, 1981). The latter female bore fawns, had a normal karyotype, and histologically normal endocrine glands (Mierau, 1972).

Mule deer have heterodont and brachydont dentition whose histologic development resembles that in other mammals (Rees et al., 1966a). The permanent dental formula for the genus *Odocoileus* is: i 0/3, c 0/1, p 3/3, m 3/3, total 32.

Hudson and Browman (1959) and Short (1970) noted that enamel tips of incisors were visible at about 161 days and were erupted partially approximately 180 days from conception. Lower incisors and canines were erupted fully among seven 10-day-old mule deer fawns. The second, third, and fourth deciduous premolars were erupted fully and mineralized at about 2.5 to 3 months of age (Rees et al., 1966b). Eruption and formation of the teeth of *O. h. hemionus* were complete at about 29 months (Rees et al., 1966b). Although unreliable, subjective estimates of the relative wear of the molariform teeth and the chronology of tooth replacement were used extensively to estimate ages of mule deer (Brown, 1961; Erickson et al., 1970; Robinette et al., 1957b; Taber and Dasmann, 1958; Thomas and Bandy, 1975).

Completely accurate age estimates were obtained from small samples of mule deer of known age by counting cementum annuli in the root of the first permanent incisor (Erickson and Seliger, 1969; Low and Cowan, 1963). However, the cementum-annuli technique is also somewhat subjective, and subsequent tests with 55 *O. virginianus* (Sauer, 1971) and 49 *O. h. hemionus* (Robinette et al., 1977) of known age revealed errors of 16% and 51%, respectively.

Ranges of mean values of selected cellular constituents of *O. hemionus* blood from several studies were: hemoglobin, 9.8 to 20.5 g/100 ml; packed cell volume, 30.6 to 58.2%; erythrocytes, 4.6 to 14.2 $10^6/\text{mm}^3$; and leukocytes, 3.0 to 5.8 $10^3/\text{mm}^3$ (Anderson, 1981). Similar values for selected serum constituents of *O. hemionus* were: total protein, 4.6 to 8.5 g/100 ml; blood urea nitrogen, 7.4 to 29.8 mg/100 ml; inorganic phosphorus, 5.2 to 11.2 mg/100 ml; and vitamin A, 151.9 to 367.7 IU (Anderson 1981).

In mature *O. h. hemionus*, mean (\pm SE) fresh brain weights (in grams) for 50 males and 89 females were 197.7 ± 2.7 and 189.3 ± 1.8 , respectively. Similar values for the right lung of 37

male and 62 females were 772.8 ± 50.6 and 636.6 ± 21.2 , respectively, and for the left lung of 38 males and 62 females 479.5 ± 28.0 and 408.5 ± 12.0 , respectively (Anderson et al., 1974).

The stomach of fawns less than 5 weeks old is monogastric and consists of the abomasum, an efficient organ for utilizing milk (Short, 1981). Over the next 11 weeks the digestive system develops into a highly specialized, four-compartment ruminant stomach with the same relative volume, functions, and appearance of that of adult deer (Short, 1981). The large and small intestines of *O. hemionus* are about 5 and 15 m in length, respectively (Short, 1981). The stomach of mule deer is relatively small compared with that of other ruminants (Short et al., 1965). Foods are often retained in the rumen of mule deer for less than 1 day (Short, 1981). During late spring, summer, and autumn, rapid rates of food consumption and passage of easily digestible foods through the gastrointestinal tract produce abundant assimilable nutrients in contrast with diminished levels in late autumn and winter (Short, 1981). Bacterial populations in the rumen of *O. h. hemionus* averaged about 11 billion and 12 billion per ml of rumen fluid during spring and late autumn and winter, respectively (Pearson, 1969).

In general, various carcass fat indices increased during maximum food intake in summer, and peaked during autumn just before the breeding period, decreased precipitously during the breeding period, and continued to decline until spring (Anderson et al., 1972; Short, 1981). Females generally lagged about 1 to 2 months behind males in the annual fat cycle (Anderson et al., 1972). Predicted annual weight losses for 5-year-old *O. h. hemionus* approximated 19% of the peak weight of males and 22% of the peak weight of females (Anderson et al., 1974). For deer, fat probably functions primarily as a store of energy for survival; the insulative subcutaneous fat layer essentially was depleted by early winter (Anderson et al., 1972).

Mule deer have excellent binocular (Cowan, 1956a) and probably color vision (Scott, 1981; Witzel et al., 1978). Apparently they usually are unable to detect motionless objects but are extraordinarily sensitive to movement. The sense of hearing is extremely acute (Cowan, 1956a; Moen, 1973).

The mean and range (in parentheses) of body core temperatures ($^{\circ}\text{C}$) of *O. h. hemionus* were 37.1 (36.3 to 42.1) for a semitame, captive, undisturbed yearling male (Thorne, 1975), and 38.9 (38.4 to 39.8) for two male fawns and 38.3 (37.8 to 39.3) for two adult female *O. h. columbianus* in captivity (Cowan and Wood, 1955).

Mean water intake (ml/kg body mass) of confined deer was 51 (Bissell et al., 1955): 24 to 35 in winter and 47 to 70 in summer (Nichol, 1938) for mule deer and 53 in winter and 104 in summer (Longhurst et al., 1970) for *O. h. columbianus*. Seasonal variations in water intake and forage intake are correlated (Short, 1981). Seasonally, free water may not be necessary in some habitats; wintering deer in temperate zones may meet their water requirements by eating snow (Cowan, 1956a). *O. h. crooki* may do so by eating cacti and other succulents (Short, 1977).

Daily mean defecation rates in *Odocoileus* from 24 studies ranged from 8.0 to 23.1 fecal pellet groups per deer; 12.0 to 13.0 groups per day were reported most frequently (Neff, 1968). High forage intake, high moisture content, high proportion of young in population, change from roughage to concentrated diets, and captivity were associated with high defecation rates (Neff, 1968). In spite of the variation, Neff (1968:597) reported "reasonable accuracy of estimate" of density of deer populations in enclosures with known numbers of deer by counts of groups of fecal pellets.

ONTOGENY AND REPRODUCTION. Most wild *O. hemionus* females conceive during their second year and only rarely during their first year (Nellis et al., 1976; Thomas and Smith, 1973) but up to 50% of captive *O. h. columbianus* fawns conceived in their first year (Mueller and Sadleir, 1979). Based on 23 studies, breeding records for the species extend from about 12 September to 7 March. The breeding peak in mule deer occurs mainly from late November through mid-December and during late November in black-tailed deer (Anderson, 1981).

Counts of corpora lutea exceeded counts of fetuses in 6 of 907 pregnant does indicating either monozygotic twinning or polyovular follicles. Determination of sex was possible for three of the six sets of twins; each pair was of the same sex suggesting monozygotic twinning (Robinette et al., 1977). Brown (1961) and Illige

and Erling (1955) reported similar instances in one *O. h. columbianus* and one *O. h. crooki*, respectively.

Mean gestation lengths for *O. hemionus* approximated 200 to 208 days with a range of 183 to 218 days based on 65 deer from five sets of data (Anderson, 1981). Fetal growth curves of *O. h. hemionus* were depicted qualitatively based on forehead-rump length of prenatal young of known age (Hudson and Browman, 1959) and quantitatively based on body mass of prenatal young of known age (Robinette et al., 1977). Length of forehead-rump and hindfoot were correlated more strongly with duration of gestation than with body mass in 21 *O. virginianus* fetuses with known dates of conception (Short, 1970).

Peak birth periods in *O. h. hemionus* were estimated as 19 to 20 June (Robinette et al., 1977) and 16 June to 6 July (Anderson and Medin, 1967). Extreme birth dates in that race were 16 May to early October et al., 1977). Most *O. h. columbianus* were born in June (Thomas and Cowan, 1975). Variation was associated partly with the diverse environments and phenology represented. For example, Robinette et al. (1977) calculated that a 305-m rise in elevation was associated with a 7-day delay in the birth period. Mean mass at birth for *O. h. hemionus* in six studies ($n = 358$) ranged from 2.74 to 3.99 kg with extremes of 2.27 to 5.00 kg. Similar values for *O. h. columbianus* in four studies ($n = 79$) were 2.97 to 3.29 kg and 2.04 to 4.54 kg (Anderson, 1981). Average mass at birth was affected by litter size and sex; singles averaged heavier than twins and, in sets of twins of opposite sex, males averaged heavier (Robinette et al., 1977). Malnutrition of dams reduced fetal weights and birth weights (Verme, 1963).

Average fetuses per doe for *O. hemionus* from 25 studies totaling 1,795 females ranged from 1.14 to 1.85 for all does examined and 1.43 to 1.89 per pregnant doe (Anderson, 1981). Mean numbers of fetuses per doe vary with nutritional levels (Robinette et al., 1973). The common litter size is two, with deer in their first or second breeding year most frequently producing singletons. Triplets occurred in 1.4% and quadruplets in 0.07% of the total examined; these were, with one exception, limited to *O. h. hemionus*. A preponderance of male fetuses are produced in most *O. hemionus* populations: 111:100, based on 2,299 fetuses from several western states (Robinette et al., 1957a). In *Odocoileus*, male neonates may predominate when poor nutrition prevails about 6 weeks before, and during, the breeding period (Verme, 1969), or when delayed breeding occurs (Verme and Ozoga, 1981).

Sperm production, serum testosterone, and testicular volume in both wild and captive *O. h. columbianus* were greatest during November and lowest in February and March, although sperm quality appeared adequate for successful breeding from September through January (West and Nordan, 1976). In *O. h. hemionus*, testicular mass and volume also were maximal during November but minimal during April-May; maximum size decreased with age following age 7 years (Anderson et al., 1974).

A mean daily gain of 0.22 kg for males and 0.21 kg for females was estimated from growth-in-weight curves for *O. h. hemionus* twins from birth to 150 days of age (Robinette et al., 1973). Based on 10 studies, gross estimates of gain in body mass for deer less than 1 year of age averaged 0.09 to 0.50 kg/day for *O. h. hemionus* and 0.05 to 0.27 kg/day for *O. h. columbianus* (Anderson, 1981).

Weaning begins at about 5 weeks of age and usually is completed at age 16 weeks (Short, 1981). However, deer were observed to nurse at about 32 (Mueller and Sadleir, 1977) and 36 to 56 weeks of age (Hanson, 1958).

In *O. h. hemionus*, full development of most skeletal attributes occurred at about age 49 months (male) and 37 months (female) (Anderson et al., 1974). However, predicted gains in carcass mass were continuous to about age 120 months for males and 96 months for females (Anderson et al., 1974).

Thomas and Cowan (1975:261) found that wild *O. h. columbianus* first ovulated in November but did not become pregnant "... even though some ova were penetrated by spermatozoa and began to cleave." The second ovulation occurred 8 to 9 days later during which 97% of 61 females conceived. During the second ovulation, about half of the does ovulated in a span of 7 to 8 days and most late ovulators were yearlings. Estrus occurred every third follicular cycle of 8 to 9 days in length. The length of the estrous cycle for confined *O. h. columbianus* thus was calculated as 23 to 29 days. As many as five periods of estrus may occur when does repeatedly fail to conceive. The period of estrus was 24 to 36 h in

captive *O. h. columbianus* (West, 1968). Ovulation in *Odocoileus* occurs about 12 to 14 h after estrus terminates (Verme and Ozoga, 1981). About 27 to 29 days elapsed between conception and implantation in *O. h. hemionus* (Hudson and Browman, 1959). Corpora lutea of pregnancy developed into corpora albicantia that equaled the number of implanted embryos and persisted for the life of the doe (Thomas and Cowan, 1975).

As estimated by the difference between counts of corpora lutea of pregnancy and of fetuses, losses of ova in *O. hemionus* ranged from 3.4 (Thomas, 1970) to 10.5% (Robinette et al., 1955). Annual rates of postnatal mortality among five "stable" *O. hemionus* populations ranged from 22 to 53% for males, 17 to 25% for females, and 45 to 69% for fawns of each sex (Connolly, 1981a).

Average longevity of *O. hemionus* has not been documented. Maximum longevity in the wild was 19 years for a male (Robinette et al., 1977) and 20 years for a female (Ross, 1934). A semi-captive female *O. h. columbianus* reached 22 years of age (Cowan, 1956b).

ECOLOGY. Optimum growth and productivity of individuals and populations are dependent upon adequate supplies of highly digestible, succulent forage (Robinette et al., 1973; Short, 1981). Diets consisting primarily of woody twigs cannot meet maintenance requirements of deer (Wallmo et al., 1977). Summaries of deer diets by Kufeld et al. (1973) and Longhurst et al. (1979) and several authors in Wallmo (1981b) show that the traditional characterization of these deer as "browsers," in the sense of subsisting mostly on woody forage, is inaccurate. Based on its stomach structure and its diet of woody and herbaceous forage in approximate equal proportions, *O. hemionus* is classified more aptly as an "intermediate feeder" (Hofmann and Stewart, 1972).

Because nutritious forage is in poor supply for much of the year, theoretically both *Odocoileus hemionus* and *O. virginianus* have an annual cycle of metabolic rates (Nordan et al., 1970; Silver et al., 1969) in which higher energy flux and food intake in summer (French et al., 1956; Nordan et al., 1970; Wood et al., 1962) enables deer to capitalize on abundant high-quality forage for growth, production, and fat storage. A lower energy flux in winter permits them to survive lower intake of poor-quality forage while minimizing the catabolism of stored fat for body functions. Although evidence for annual cycle is based primarily on experiments with tame animals, Anderson et al. (1974) demonstrated periodicity in growth and fat deposits in a wild population of *O. h. hemionus* in Colorado.

Estimated rate of food intake was about 22 g (air-dry basis) $\text{kg}^{-1} \text{ day}^{-1}$ (Alldredge et al., 1974; Nichol, 1938), equivalent to 1.5 kg of air-dry forage per day for a 68-kg deer. Fawns appear to consume more per unit of body mass year-round (ca 31 to 38 g/kg) and adults less in winter (ca 17 g/kg) (Alldredge et al., 1974). In adult males, food intake drops abruptly with onset of rut (Bandy et al., 1970; Nordan et al., 1970). Mean intake of dry matter for nonlactating black-tailed deer females was 67 g $\text{kg}^{-0.75} \text{ day}^{-1}$ that furnished 247 kcal digestible energy $\text{kg}^{-0.75} \text{ day}^{-1}$. Lactating females with singletons and twins consumed 135% and 170%, respectively, of the intake of nonlactating females (Sadleir, 1982). About 158 kcal digestible energy $\text{kg}^{-0.75} \text{ day}^{-1}$ is the maintenance requirement for mule deer fawns during winter (Baker et al., 1979). Kautz et al. (1981) estimated composite winter energy expenditures while bedded, standing, walking, and trotting of three tame fawn mule deer as 94 to 446 kcal $\text{kg}^{-0.75} \text{ day}^{-1}$. Heart rates of those deer ranged from 46 to 96 beats/min and were significantly ($P < 0.001$) correlated ($r = 0.69$) with energy expenditures.

Individuals of *O. hemionus* tend to confine their daily movements to discrete "home ranges." Where seasonally migratory, most deer with established home ranges use approximately the same winter and summer home ranges in consecutive years (Bertram and Rempel, 1977; Carpenter et al., 1979; Gruell and Papez, 1963; Robinette, 1966; Robinette et al., 1977; Zalunardo, 1965). Harestad and Bunnell (1979) calculated mean size of the annual home range from several studies as 58.8 ha ($n = 81$) for *O. h. columbianus* and 285.3 ha ($n = 110$) for *O. h. hemionus* and showed that male *Odocoileus* have larger home ranges. Other estimates of the size of annual mean home ranges ranged from 39 ha for yearling female *O. h. columbianus* in Oregon coastal forest (Miller, 1970) to 3,379 ha for adult female *O. h. hemionus* on the Great Plains (Severson and Carter, 1978). Variation in estimates of mean home range size of *O. hemionus* probably is associated with interactions

among sex, age, body mass, season, race, habitat, and method of computing home range size.

According to Dasmann and Taber (1956), a nonmigratory population of *O. h. columbianus* exhibited three types of movements outside the home range: breeding season travels, wandering, and dispersal. Bunnell and Harestad (1983:201) defined dispersal as "... individual movements out of an area larger than a home range that exhibit no predictable return." Movements of *O. h. columbianus* greater than 5 km were dispersive and averaged 15.2 and 12.2 km for males and females, respectively (Bunnell and Harestad, 1983). Male, but not female, dispersal increased with increases in density (Bunnell and Harestad, 1983). Robinette (1966) and Severson and Carter (1978) defined dispersal in *O. h. hemionus* as movements beyond the home range to distances of 1.6 km and 8.0 km, respectively, that resulted in establishment of a new home range. Male *O. h. hemionus* tagged as fawns dispersed (air line distances) from 97 to 217 km (Robinette, 1966), and a female *O. h. hemionus* moved 180 km (Severson and Carter, 1978). In one migratory population of that race, few deer dispersed as fawns but 60% of the yearling bucks and 35% of the yearling does apparently dispersed by 16 months of age (Robinette, 1966).

Seasonal movements exceeding about 15 km or involving migrations from higher elevations (summer ranges) to lower winter ranges are associated, in part, with decreasing temperatures, severe snowstorms, and snow depths that reduce mobility and food supply (Leopold et al., 1951; Russell, 1932). On the winter range, snow depths in excess of 25 to 30 cm impede movement (Loveless, 1967) and excess of 51 to 60 cm discourage continuous occupation (Gilbert et al., 1970; Loveless, 1967). Thus, deep snows ultimately limit useable range to a fraction of the total. The chronology of spring movement from lower (winter ranges) to upper (summer ranges) elevations presumably is an interaction of plant phenology, rate of snow melt, and, perhaps, impending birth period (Russell, 1932). Mule deer in the arid southwest may migrate in response to rainfall patterns (Longhurst and Chattin, 1941). Autumn and spring migrations may encompass 4 weeks in *O. h. hemionus* (Wright and Swift, 1942) or 6 or 7 weeks with delays enroute of about 40 days in *O. h. californicus*; individual deer appeared to follow the same route for both autumn and spring migrations (Bertram and Rempel, 1977). Migratory routes may (Leopold et al., 1951; Russell, 1932), or may not (Gruell and Papez, 1963; Bertram and Rempel, 1977) be confined to major drainages or ridgetops, and may cross other winter ranges enroute to traditional wintering areas (Gruell and Papez, 1963; Jensen, 1968). Air line distances between summer and winter ranges traveled by individual, marked, migrating *O. h. hemionus* varied greatly within and among herds; means and ranges of distances reported (km) were 29.8 (0.4 to 129) (Zalunardo, 1965) and 15.4 (1.6 to 241) (Jensen, 1968).

Some measured posthunting densities (mean number of deer/ km^2) of migratory *O. h. hemionus* on winter ranges were 10.0 (Kufeld et al., 1980), and 16.0 (Robinette et al., 1977). In migratory populations of this race, a variable and unmeasured proportion of deer may be permanent residents on winter ranges. Densities of nonmigratory *O. h. hemionus* were estimated at 3.9/ km^2 during winter in prairie-woodland riverbreaks in Montana (Maćkie, 1970). Densities of nonmigratory *O. h. columbianus* were estimated on relatively small areas as 18.5 deer/ km^2 in forest habitat (Brown, 1961), and 49.8/ km^2 (Longhurst et al., 1979) and 21.2 to 55.6 deer/ km^2 (Dasmann and Taber, 1956) in chaparral habitat.

Common predators of mule deer include pumas, *Felis concolor*; coyotes, *Canis latrans*; bobcats, *Felis rufus*; golden eagles, *Aquila chrysaetos*; domestic and feral dogs, *Canis familiaris*; and black bears, *Ursus americanus* (Connolly, 1981b).

Sources of mortality other than predation probably are more effective regulators of population density; at least, they are measured more easily. For example, legal hunting from 1950 to 1975 accounted for an estimated 1.73 million mule deer and 33,000 black-tailed deer on U.S. National Forests alone. No reliable estimates are available for the total kill of *O. hemionus* in the U.S. (Connolly, 1981c), Mexico, and Canada.

Additional unrecorded mortality associated with hunting includes "cripple-kills" (wounded deer that die), deer killed legally and abandoned by hunters, and illegal kills. Among five intensive field surveys, estimates of crippling loss plus illegal kills ranged from 8 to 92% of the estimated legal kill and were greater where a buck-only hunting regulation was in effect (Connolly, 1981a). Connolly (1981b) generalized that hunting can regulate local populations but

not cause general declines over large areas; hunting bucks may increase deer numbers, and hunting does may reduce deer numbers in proportion to the percentage of does killed annually.

Diseases and parasites of *O. hemionus* listed and discussed by Hibler (1981) include: viral—bluetongue; epizootic hemorrhagic disease; foot-and-mouth disease; malignant catarrhal fever; bovine virus diarrhoea/mucosal complex; neoplastic (non-malignant papillomas and fibromas); bacterial—pasteurellosis, *Pasteurella multocida*; brucellosis, *Brucella* spp.; necrobacillosis, *Fusibacterium necrophorum*; actinomycosis, *Actinomyces bovis*; blackleg and malignant edema, *Clostridium chauveii* and *Cl. septicum*; caseous lymphadenitis, *Corynebacterium ovis* and *C. pyogenes*; anthrax, *Bacillus anthracis*; parasitic—elaeophorosis, *Elaeophora schneideri*; setaria, *Setaria yehi*; parelaphostrongylosis, *Parelaphostrongylus tenuis*; gastrointestinal parasitism by nematodes of the genera *Haemonchus*, *Ostertagia*, *Trichostrongylus*, *Nematodirus*, *Nematodierella*, *Trichuris*, *Capillaria*; lungworms, *Dictyocaulus* spp., *Protostrongylus macroti*, *Parelaphostrongylus odocoilei*; foot worm, *Onchocerca cervipedis*; eye worm, *Thelazia californiensis*; tapeworms (larval stages of *Taenia hydatigena*, *T. krabbei* and adult *Moniezia* spp., *Thysanosoma actinioides*, *Echinococcus granulosis*); liver flukes, *Fasciola hepatica* and *Fascioloides magna*; sarcocystis, *Sarcocystis* spp.; toxoplasmosis, *Toxoplasma gondii*; myiasis, *Cephenemyia jellisoni*, *C. apicata*; bloodsucking diptera of the genera *Hybomitra*, *Tabanus* spp., *Simulium* spp., *Symphoromyia*, *Chrysops* spp., *Aedes*, *Culex*, *Culiseta*, *Leptoconops*; louse flies, *Lipoptena depressa*, *Neolipoptena ferrisi*; native lice of the genera *Haematopinus*, *Linognathus*, *Tricholipeuris*, *Cervophthirus*; fleas, *Pulex irritans*; ticks, *Otobius megnini*, *Dermacentor albipictus*, *D. andersoni*, *Ixodes scapularis*, *I. pacificus*, *Ornithodoros coriaceus*; and anaplasmosis, *Anaplasma marginale*. Hibler (1981) noted that an infectious or parasitic disease could be a primary mortality factor or the result of a predisposing factor. For example, heavy burdens of gastrointestinal nematodes may cause death, but usually are indicative of such predisposing factors as high deer densities and malnutrition. Livestock may transmit diseases to deer as in the foot-and-mouth disease epidemic in California in 1924 where over 22,000 deer were killed to control the disease (Hibler, 1981). Conversely, deer frequently are latent carriers of anaplasmosis, a disease often fatal to livestock. Infections of meningeal worm, *Parelaphostrongylus tenuis*, are tolerated by *O. virginianus* but may cause fatal neurologic disease in *O. hemionus* and other cervids where their natural or introduced ranges overlap (Hibler, 1981).

Anomalies of *O. hemionus* include sickle cell (Dougherty, 1939), brachygnathism (Short, 1964), retracted leg tendons, bowed leg bones, curved spine, cleft palate in fawns (Hines, 1975), stomach calculi (Draney and Robinette, 1955), vestigial first digit, splayed front hooves, two maxillary canines, two p1 (premolars), missing p2, and uterine eversion (Robinette et al., 1977).

The adequacy of "cover" and the degree of competition with other herbivores for forage, particularly domestic livestock, often are considered actual or potential regulators of density in *O. hemionus* populations. So far, cover requirements are hypothetical but not demonstrated (Moen, 1973; Thomas, 1979). The literature on the effects of range competition (Mackie, 1981) reveals only that they are understood poorly.

BEHAVIOR. *Odocoileus hemionus* is polygynous and, although Robinette et al. (1977:71) refer to harems in *O. h. hemionus*, the breeding system is generally regarded as the tending-bond type (Geist, 1981). Thus, courtship and mating occur within the group; the dominant buck tends an estrous doe until mating or displacement by another buck occurs (Kucera, 1978). Among *O. h. columbianus*, only the dominant buck exhibited territorialism during the breeding period (Miller, 1974). Dominance was largely a function of size; the largest bucks with the largest antlers performed most of the copulations (Kucera, 1978; Miller, 1974). Frequency of heterosexual behavior was strongly and positively correlated with antler size in *O. h. crooki* (Kucera, 1978). Serious fights were rare and limited to large bucks (Kucera, 1978; Wachtel et al., 1978).

The social system consists of "female clans related by maternal descent that are facultative resource defenders and bucks dispersed as individuals or in groups of unrelated individuals" (Geist 1981:213). During winter and spring, the stability of close-family and buck groups was maintained in *O. h. columbianus* with domi-

nance hierarchies (Miller, 1974). Increases in strife and alarm behavior and decreases in play among fawns occurred as population density increased (Dasmann and Taber, 1957; Miller, 1974). Pregnant and maternal does exhibited mutual intolerance and strong spatial regulation but bucks did not (Dasmann and Taber, 1956). Frequency of aggressive behavior between sexes remained low year-long in *O. h. californicus* (Koutnik, 1981).

Communication among *O. h. hemionus* is facilitated by the sebaceous and sudoriferous secretory cells of five integumentary glands. The cells of each gland produce specific scents (pheromones) that release specific reactions of conspecifics (Müller-Schwarze, 1971; Müller-Schwarze and Müller-Schwarze, 1975). The metatarsal (outer surface of each hindfoot) acts as an alarm pheromone, the tarsal (inner surface of each hock) aids in mutual recognition, the interdigital may leave a scent trail, and the function of the tail gland is uncertain (Müller-Schwarze, 1971). The pheromone from the forehead skin, in combination with the pheromone from the antorbital sac (anterior to the eye), may signal the home range of individual deer (Müller-Schwarze, 1971) or the presence of individual male deer (Volkman et al., 1978). Urine has a pheromone function at all ages and by both sexes (Müller-Schwarze, 1969); it is deposited on tufts of hair surrounding tarsal glands when the tufts are rubbed together (Müller-Schwarze et al., 1978; Geist, 1981). "Rub-urinating" may signal distress in fawns but threat in adults (Müller-Schwarze, 1971) and is a major dominance display of mule deer (Geist, 1981).

GENETICS. The diploid number in *O. hemionus* is 70. Autosomes are two submetacentrics and 66 acrocentrics or telocentrics. Sex chromosomes are a submetacentric X and a metacentric Y (Hsu and Benirschke, 1967).

Wild hybrid *O. hemionus* and *O. virginianus* were described (Cowan, 1962; Wishart, 1980), but those authors and Day (1980), Hoffmeister (1962), and Kramer (1973), believed such hybrids were rare. Hybrids are produced easily in captivity, but their survival (particularly fawns) is poor (Day, 1980; Nichol, 1938). Day (1980) reported that mature male and female F₁ hybrids were both fertile but two F₁ crosses were not successful. Wishart (1980) speculated that, in the wild, introgressive hybridization and eventual loss of *O. virginianus* characters are probable. Intergradation of *O. h. hemionus* and *O. h. columbianus* occurs in northeastern California and southern British Columbia (Cowan, 1936) and Oregon (Wallmo, 1981a). Little effort has been made to discriminate between phenotypic and genotypic variation among subspecies (Wallmo, 1981a). Melanism and albinism, including a true albino, were recorded for *O. h. hemionus* (Robinette et al., 1977).

REMARKS. We have followed usage of the generic name *Odocoileus* rather than *Dama* (Hall, 1981) because of opinion 581 of the International Commission on Zoological Nomenclature (Jones et al., 1982).

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Neotoma mexicana. By John E. Cornely and Robert J. Baker

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Neotoma mexicana Baird, 1855

Mexican Woodrat

- Neotoma mexicana* Baird, 1855:333. Type locality near Chihuahua, Chihuahua.
Neotoma ferruginea Tomes, 1862:282. Type locality Dueñas, Sacatepequez, Guatemala.
Neotoma torquata Ward, 1891:160. Type locality abandoned mine between Tetela del Volcán and Zacualpan, Morelos.
Neotoma tenuicauda Merriam, 1892:169. Type locality north slope Sierra Nevada de Colima, 12,000 ft, Jalisco.
Neotoma pinetorum Merriam, 1892:111. Type locality San Francisco Mountain, Coconino Co., Arizona.
Neotoma fallax Merriam, 1894:123. Type locality Gold Hill, Boulder Co., Colorado.
Neotoma fulviventer Merriam, 1894:121. Type locality Toluca Valley, México.
Neotoma orizabae Merriam, 1894:122. Type locality Volcán de Orizaba, Puebla.
Neotoma sinaloae J. A. Allen, 1898:149. Type locality Tatámeles, Sinaloa.
Neotoma navus Merriam, 1903:47. Type locality Sierra Guadalupe, Coahuila.
Neotoma distincta Bangs, 1903:89. Type locality Texolo [=Teocelo], near Jalapa (Hall and Kelson, 1959), Veracruz.
Neotoma picta Goldman, 1904:79. Type locality mountains near Chilpancingo, 10,000 ft, Guerrero.
Neotoma isthmica Goldman, 1904:80. Type locality Huiltepec, 100 ft, 8 mi S Tehuantepec, Oaxaca.
Neotoma parvidens Goldman, 1904:81. Type locality Juquila, 5,000 ft, Oaxaca.
Neotoma tropicalis Goldman, 1904:81. Type locality Totontepec, 6,500 ft, Oaxaca.

CONTEXT AND CONTENT. Order Rodentia, Family Muridae (considered Cricetidae by some authors), Subfamily Sigmodontinae. The genus *Neotoma* contains four Recent subgenera and approximately 22 Recent species. *Neotoma mexicana* is a member of the *mexicana* species group within the subgenus *Neotoma*. Currently, 24 subspecies of *Neotoma mexicana* are recognized (Hall, 1981):

- N. m. mexicana* Baird, 1855:333, see above (*madrensis* Goldman is a synonym).
N. m. ferruginea Tomes, 1862:282, see above.
N. m. torquata Ward, 1891:160, see above (*fulviventer* Merriam and *orizabae* Merriam are synonyms).
N. m. tenuicauda Merriam, 1892:169, see above.
N. m. pinetorum Merriam, 1893:111, see above.
N. m. bullata Merriam, 1894:122. Type locality Santa Catalina Mountains, Pima Co., Arizona.
N. m. fallax Merriam, 1894:123, see above.
N. m. sinaloae J. A. Allen, 1898:149, see above.
N. m. navus Merriam, 1903:47, see above.
N. m. distincta Bangs, 1903:89, see above.
N. m. picta Goldman, 1904:79, see above.
N. m. isthmica Goldman, 1904:80, see above.
N. m. parvidens Goldman, 1904:81, see above.
N. m. tropicalis Goldman, 1904:81, see above.
N. m. ochracea Goldman, 1905:30. Type locality Atemajac, 4,000 ft, near Guadalajara, Jalisco.
N. m. solitaria Goldman, 1905:31. Type locality Nentón, 3,500 ft, Guatemala.
N. m. chamula Goldman, 1909:141. Type locality mountains near San Cristóbal, 8,400 ft, Chiapas.
N. m. inopinata Goldman, 1933:471. Type locality Chuska Mountains, 8,800 ft, San Juan Co., New Mexico.

- N. m. vulcani* Sanborn, 1935:84. Type locality south slope Volcán Tajumulco, San Marcos, 13,200 ft, Guatemala.
N. m. inornata Goldman, 1938:60. Type locality Carmen Mountains, 6,100 ft, Coahuila.
N. m. atrata Burt, 1939:1. Type locality 4 mi W Carrizozo, Lincoln Co., New Mexico.
N. m. griseoventer Dalquest, 1951:363. Type locality Xilitla, San Luis Potosí.
N. m. scopulorum Finley, 1953:529. Type locality 3 mi NW Higbee, 4,300 ft, Otero Co., Colorado.
N. m. eremita Hall, 1955:328. Type locality 1 mi S San Francisco, 50 ft, Nayarit.

DIAGNOSIS. Form rat-like (Fig. 1); body of average size for genus; skull of medium size for genus; anterointernal re-entrant angle of M1 deep, extending more than halfway across the crown (Hall, 1981). According to Hall (1981), the upperparts are grayish, grayish buff, dull brown, russet, or bright rufous, usually darkened dorsally by an admixture of blackish hairs; underparts white or yellowish with hairs plumbeous basally, except that inguinal and gular hairs of some subspecies may be white to base; tail is black to dusky above and grayish to whitish below. A narrow dusky line usually borders the mouth (Finley, 1958). The combination of size, color, and deep anterointernal re-entrant angle of M1 distinguish this species from congeners (Hall, 1981).

GENERAL CHARACTERS. The following skull characteristics were reported by Finley (1958): skull light and smooth (Fig. 2); rostrum slender; interorbital region narrow; maxillovomarine notch present; posterior margin of bony palate convex or pointed; interpterygoid fossa narrowly rounded; sphenopalatine vacuities large; upper incisors small. The dental formula is $i\ 1/1, c\ 0/0, p\ 0/0, m\ 3/3$, total 16. Means and extremes of external measurements and selected cranial measurements (in mm) of individuals of *N. m. fallax* from El Paso Co., Colorado (Finley, 1958), are as follows: eight males—total length, 333 (314 to 351); length of tail, 143 (132 to 154); length of hindfoot, 35 (33 to 38); basilar length, 36.8 (35.3 to 38.0); zygomatic breadth, 22.8 (21.7 to 23.9); interorbital breadth, 5.5 (5.2 to 5.7); diastema, 12.6 (11.8 to 13.7); alveolar length of maxillary toothrow, 9.3 (9.0 to 9.7); length of incisive foramina, 9.6 (8.9 to 10.0); length of palatal bridge, 8.4 (7.7 to 9.3); six females—total length, 327 (307 to 350); length of tail, 148 (140 to 154); length of hindfoot, 33 (31 to 35); basilar length, 36.2 (35.0 to 37.3); length of nasals, 18.1 (17.1 to 18.8); zygomatic breadth, 23.3 (22.8 to 23.6); interorbital breadth, 5.2 (4.9 to 5.6); diastema, 7.0 (6.9 to 7.3); alveolar length of maxillary



FIG. 1. Photograph of a Mexican woodrat (*Neotoma mexicana*).

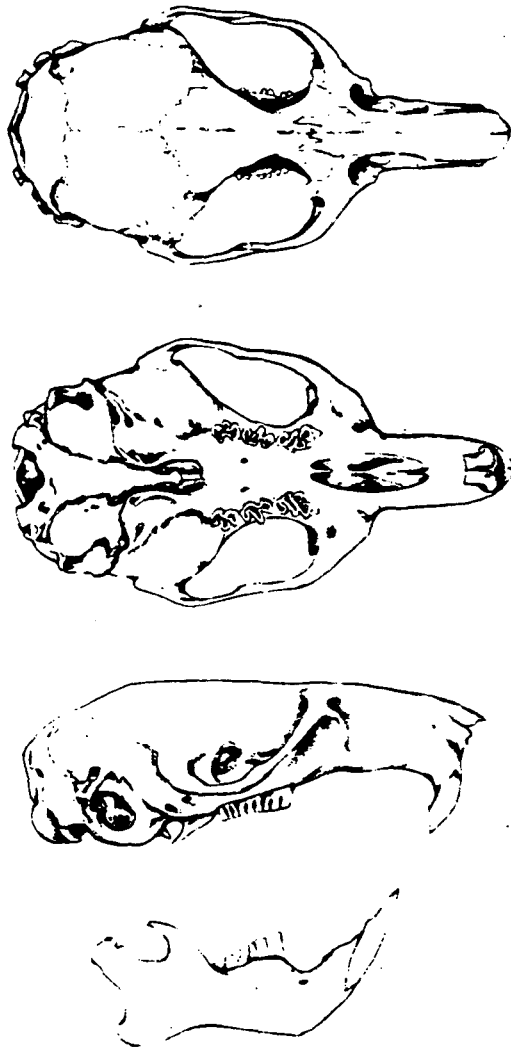


FIG. 2. Dorsal, ventral, and lateral views of the cranium and lateral view of lower jaw of a female *Neotoma mexicana fallax* (TTU 8126) from Jefferson Co., Colorado. Greatest length of skull is 46.2 mm.

toothrow, 9.2 (8.8 to 9.8); length of incisive foramina, 9.4 (9.0 to 9.6); length of palatal bridge, 8.2 (7.8 to 8.9). Mean external measurements of five adults of *N. m. mexicana* from Chihuahua (Anderson, 1972) are: total length, 324.5; length of tail, 148.0 (4); length of hindfoot, 34.9; length of ear, 32.0. Mean skull measurements of six adult *N. m. mexicana* from Chihuahua (Anderson, 1972) are: occipitonasal length, 42.66; alveolar length of maxillary toothrow, 8.73; length of rostrum, 14.55; breadth of braincase, 16.58; postdental breadth, 6.52; posterior zygomatic breadth, 21.58; breadth of molar teeth, 2.42; interorbital breadth, 5.38.

DISTRIBUTION. *Neotoma mexicana* occurs from northern Colorado south through western and central Mexico, through Guatemala into western Honduras (Fig. 3). In the United States, Mexican woodrats occur from the western tip of the Oklahoma panhandle (Blair, 1939) westward to the south rim of the Grand Canyon (Bailey, 1935; Hoffmeister, 1971). Their altitudinal distribution ranges from 15 m in Nayarit (Hall, 1955) to 4,025 m on Volcán Tajumulco in Guatemala (Hall, 1955; Sanborn, 1935).

FOSSIL RECORD. Hibbard (1967) suggested that the stock that gave rise to *Neotoma* must have separated from a generalized cricetine in the late Miocene. Fossil evidence of *Neotoma mexicana* is rare. Van Devender et al. (1977) reported remains of Mexican woodrats from Pleistocene deposits in Rampart Cave in Grand Canyon National Park, Arizona. They remarked that *N. mexicana*

apparently occurred at much lower elevations in that area during the Pleistocene than at present. Remains of Pleistocene Mexican woodrats were found in Wisconsin deposits in Burnet Cave (Murray, 1957; Schultz and Howard, 1935) in the Guadalupe Mountains in southern New Mexico. Harris (1984b) reported Pleistocene remains of *N. mexicana* from Baldy Peak Cave, New Mexico and Holocene remains from Dry Cave, New Mexico. According to Harris (1984b), *N. cinerea* abruptly disappeared from southern New Mexico and western Texas at the close of the Pleistocene and was replaced by *N. mexicana*. Logan and Black (1979) identified *N. mexicana* remains from Pleistocene deposits in Upper Sloth Cave, Guadalupe Mountains National Park, Texas. Dalquest and Stangl (1984) found *N. mexicana* represented by a single lower jaw in Pleistocene deposits in Fowlkes Cave in southern Culberson Co., Texas, and reported that *N. mexicana* does not occur in the desert habitat near the cave at present. A molar from Pleistocene deposits in Tlapacoya, México, was identified as that of Mexican woodrat (Alvarez, 1969). A newly described, extinct species (*N. findleyi*) from Dry Cave seems to be allied with *N. cinerea* or *N. mexicana* (Harris, 1984a, 1984b).

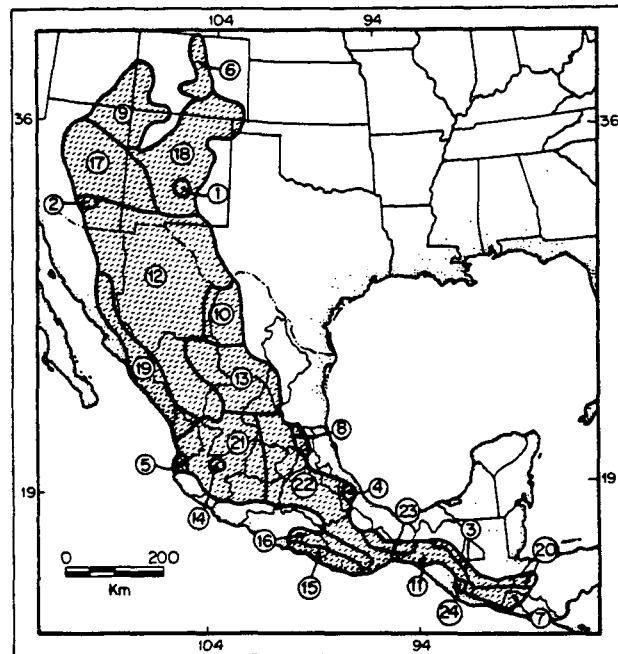


FIG. 3. Map showing the distribution of *Neotoma mexicana* (after Hall, 1981). Guide to subspecies: 1, *N. m. atrata*; 2, *N. m. bullata*; 3, *N. m. chamula*; 4, *N. m. distincta*; 5, *N. m. erimita*; 6, *N. m. fallax*; 7, *N. m. ferruginea*; 8, *N. m. griseoverter*; 9, *N. m. inopinata*; 10, *N. m. inornata*; 11, *N. m. isthmica*; 12, *N. m. mexicana*; 13, *N. m. navus*; 14, *N. m. ochracea*; 15, *N. m. parvidens*; 16, *N. m. picta*; 17, *N. m. pinetorum*; 18, *N. m. scopulorum*; 19, *N. m. sinaloae*; 20, *N. m. solitaria*; 21, *N. m. tenuicauda*; 22, *N. m. torquata*; 23, *N. m. tropicalis*; 24, *N. m. vulcani*.

FORM AND FUNCTION. Howe (1977) reported that males of *Neotoma mexicana* have prominent, midventral sebaceous glands. Melanistic specimens of *N. mexicana* were collected on dark lava flows in New Mexico (Blair, 1941; Burt, 1939; Dice, 1942; Hooper, 1941). Burt (1939) described a new subspecies, *N. m. atrata*, from two dark specimens collected on the malpais near Carrizozo, New Mexico. According to his description, *N. m. atrata* is distinctly darker than *N. m. mexicana* and *N. m. fallax*. The buffy subterminal bands on the hairs were reduced but not replaced entirely with black as in *N. albigula melas*. Hooper (1941), who obtained dark individuals of *N. m. fallax* from lava flows in Valencia Co., New Mexico, noted that the tendency for woodrats captured on dark substrates to be darker was more evident in juvenile pelage. Warren (1913) reported an instance of dichromatism in *N. m. fallax* from Colorado.

The baculum of *N. mexicana* is distinct (Burt and Barkalow, 1942); the shaft is nearly straight and the basal end is slightly expanded and inverted U-shaped in cross section. The bone narrows abruptly then more gradually from the lateral proximal projections to the distal tip. It differs from bacula of other *Neotoma* in that it is wider near the middle of the shaft then gradually narrows again near the distal end. A slight knob may be present near the distal end. Hooper (1960) reported that the shape of the osseous part of the baculum differed in each specimen examined. The ventral surface was flat on one specimen, shallowly concave in two, and more deeply concave in a fourth, but the dorsal surface was narrowly concave in all of them. The distal half was club-like with a slightly cleft terminal enlargement. Measurements (in mm) of bacula from two *N. m. mexicana* (Burt and Barkalow, 1942) are: length, 5.38, 5.6; dorsoventral diameter of base, 0.89, 1.09; lateral diameter of base, 1.84, 2.21; dorsoventral diameter of shaft near middle, 0.51, 0.55; lateral diameter of shaft near middle, 0.61, 0.70.

Hooper (1960) described the glans penis of *N. mexicana* as robust, oblong, and spinous. He reported that it generally resembled those of *N. albigula*, *N. floridana*, and *N. micropus* with the following exceptions: internal crater deeper, with the floor below the tip of os penis leaving the distal part of the bone and all of the terminal cartilagenous spine contained within the crater and free of its walls; urethral flap was shorter, blunt, and entire.

According to Cockerell et al. (1914), the malleus of *N. m. fallax* is bimarginate with no processus muscularis, but with a distinct tubercle present above the orbicular apophysis. The orbicular apophysis is large and the cephalic peduncle elongated, terminating in a relatively small head. The bony lamina is extensive and the processus gracilis is long.

The incus (Cockerell et al., 1914) has a thick, short processus brevis and a long stapedial process with a distinct and well-developed sylvian apophysis. A distinct broad groove is around the inner margin of the articular surface.

The stapes has a stout bony intercrural canal (Cockerell et al., 1914). One crus is shorter and straighter than the other, making the ossicle asymmetrical.

Sprague (1941) reported that the hyoid apparatus of *N. mexicana fallax* is about the same size as in *N. albigula*. The ceratohyals are long, slender, and slightly bifurcated distally. The thyrohyals are triangular, the thyrohyals straight, and the shoulders well developed. Measurements (in mm) of the hyoid apparatus of one specimen (Sprague, 1941) were as follows: width of basihyal, 6.2; length of thyrohyal, 5.0; length of ceratohyal, 3.0; arch of basihyal and thyrohyal, 5.4; thickness of basihyal through the entoglossal process, 2.4.

Carleton (1973) reported that Mexican woodrats have a bilocular-discoglandular stomach with incisora angularis and fornix ventricularis similar to those of *Peromyscus*. Stomachs of *N. mexicana* possessed a relatively greater area of glandular epithelium than those of *Peromyscus*.

Brownfield and Wunder (1976) calculated the following renal indices for *N. mexicana*: percent medullary thickness, 79; relative medullary thickness, 6.3; percent medullary area, 43.9; relative medullary area, 0.79. All of these values were lower than those for *N. albigula* indicating that *N. albigula* has greater urine concentrating ability than *N. mexicana*. Boice (1969) and Boice and Boice (1968) were unable to complete water-relation studies when specimens of *N. mexicana* given drinking water and dry food began to lose conditioning. They drank more readily after capture than individuals of *N. albigula* and *N. micropus*, but they could not be maintained in good health without succulent foods until habituated to the laboratory for several months.

ONTOGENY AND REPRODUCTION. At the northern limit of the range of the species in Colorado, adult females breed from March through May, producing two litters annually (Brown, 1969). Farther south, the breeding season is longer but few details are available. Pregnant females have been captured in January, and March through August (Baker, 1956; Birney and Jones, 1971; Cary, 1911; Davis, 1944; Finley, 1958; Genoways et al., 1979; Hoffmeister, 1971; Hooper, 1941; Warren, 1926). Males with enlarged testes were captured in June, July, August, and November, and subadults were observed or collected in every month except February and May (Baker, 1956; Birney and Jones, 1971; Burt and Hooper, 1941; Cary, 1911; Davis, 1944; Finley, 1958; Genoways et al., 1979; Hall and Dalquest, 1963).

The average gestation period of *N. mexicana* is 32.7 days with a range of 31 to 34 (Olsen, 1968). Data were collected in the laboratory from eight pregnancies of five different females obtained in the San Mateo Mountains of New Mexico. Mean litter size was 2.1 with a range of 1 to 3. A total of 17 young (eight males, nine females) was born in the eight litters. Brown (1969) reported mean litter sizes for adult females in Colorado based on counts of embryos (3.43; $n = 19$), corpora lutea (3.66; $n = 45$), and pigmented sites of implantation (3.47; $n = 22$). Juvenile females born in April or May in Colorado produced litters in June or July and had an average of 2.44 ($n = 14$) embryos and 2.52 ($n = 19$) corpora lutea. Some young females born late in the reproductive season failed to produce a litter even though they ovulated in September and October. Reproductive failure apparently was caused by an absence of fertile males at that season. Brown (1969) found that gonadal development of juvenile males progressed slowly with low testicular weight and activity through November (61.9 mg), accelerated in December (476.8 mg), and reached full development during the following breeding season. Peak testicular development in adult males was attained in April (1,540.2 mg), whereas minimum size and activity occurred in November (119.6 mg).

Finley (1958) described the molt patterns of *N. mexicana* as being much like those of *N. cinerea*. Both species usually have three molts the first year. In the postjuvinal and second molts, the inguinal region molts earlier in *N. mexicana* than in *N. cinerea*, but later than in *N. floridana* or *N. micropus*. Molt lines from the body sides meet on the dorsal surface at the lumbar region and rump before they join at the base of the tail. The third molt may begin on the belly before completion of the second molt, but follows the same pattern as the second molt (Finley, 1958). The third molt was recognized in specimens taken in the period September through January, and only in adults about 5 to 8 months of age.

ECOLOGY. Throughout its range, *N. mexicana* generally is saxicolous, preferring rock outcrops, rocky slopes, and cliffs (Baker, 1956; Baker and Greer, 1962; Birney and Jones, 1971; Blair, 1939; Findley et al., 1975; Finley, 1958; Genoways and Jones, 1973; Hall and Dalquest, 1963; Schmidly, 1977). These rats occur from the Upper Sonoran Life-zone to the upper limits of the Transition Zone (Bailey, 1931; Finley, 1958). In western Colorado, Finley (1958) reported them to be more abundant in the Upper Sonoran Zone, whereas in Arizona, New Mexico, and western Texas they are more abundant in the Transition Zone (Bailey, 1905, 1931; Findley et al., 1975). Mexican woodrats are predominantly montane and are associated most often with open woodland or shrub vegetation types.

The most widespread plant community occupied by *N. mexicana* in Colorado is piñon (*Pinus edulis*)-juniper (*Juniperus communis*) woodland (Armstrong, 1972; Finley, 1958). Finley (1958) found them commonly in scrub oak (*Quercus gambelii*) with scattered ponderosa pine (*Pinus ponderosa*).

In New Mexico, Mexican woodrats reach their greatest numbers in montane mixed coniferous forests (Findley et al., 1975). They are common in piñon-juniper woodland (Bailey, 1931; Dice, 1930, 1942; Thompson and Hier, 1981), ponderosa pine-scrub oak (Hill, 1942), and ponderosa pine (Bailey, 1931; Hooper, 1941). Ivey (1957) collected these woodrats in Douglas fir (*Pseudotsuga menziesii*)-Engelmann spruce (*Picea engelmannii*) forest.

In western Texas, Mexican woodrats occur in piñon, juniper, ponderosa pine, and mixed deciduous coniferous forest (Bailey, 1905; Blair, 1940; Cornely, 1979). They sometimes occur on relatively open, steep, rocky slopes. On one such slope in Guadalupe Mountains National Park, the dominant plants near active woodrat dens were *Nolina micrantha*, *Muhlenbergia pauciflora*, *Dasyliroium leiophyllum*, *Cercocarpus montanus*, and *Quercus undulata* (Cornely, 1979).

Mexican woodrats inhabit ponderosa-pine forest in montane areas of Arizona (Bailey, 1931, 1935; Cahalane, 1939; Hoffmeister, 1956, 1971; Hoffmeister and Goodpaster, 1954; Merriam and Stejneger, 1890). They occur also in piñon-juniper (Hoffmeister, 1971), oaks (Cahalane, 1939), and firs and aspens (Hoffmeister and Goodpaster, 1954).

In Coahuila, specimens were taken in the Sierra del Carmen in mixed oaks and conifers; in the Sierra de la Madera in an association of oaks, pine, and madroño (*Arbutus xalapensis*); and in the Sierra Madre Oriental in an association of pine, aspen, and fir (Baker, 1956). Hooper (1955) obtained these rats in a riparian

forest of fig trees and other tropical plants in Sinaloa; Birney and Jones (1971) found them in a tropical thorn forest above the Rio Piaxtla in the same state. They also have been taken in tropical deciduous thorn forest in Jalisco (Genoways and Jones, 1973). A specimen was collected from boreal forest in the state of México (Davis, 1944). In Morelos, Mexican woodrats were obtained in the Mixed Forest Association and in the Arid Tropical Scrub Association (Davis and Russell, 1954; Ward, 1891). Goodwin (1934) reported them in cactus hedges in Guatemala.

In Colorado, Cary (1911) noted that these rats ate acorns, piñon nuts, and juniper berries. Finley (1958) examined 51 dens in Colorado and inferred the diet from plant remains in the litter at each den. Foliage was utilized in much greater quantities than fruits, flowers, stems, or woody parts. Conifer needles were common, but cactus apparently was avoided. The most common food plants were those most abundant and most accessible in the scrub oak and piñon-juniper (Finley, 1958). Among those plants were scrub oak, skunkbush (*Rhus trilobata*), mountain mahogany (*Cercocarpus montanus*), and juniper. Finley (1958) concluded that the food of *N. mexicana* is relatively generalized, similar to that of *N. cinerea* and in contrast to the specialized food habits of *N. albigula* and *N. micropus*.

Bailey (1931) reported that food of these rats in New Mexico consisted of a great variety of green plants, berries, fruits, seeds, nuts, acorns, and mushrooms. At lower elevations, pine nuts, juniper berries, and cactus pulp and fruits were common foods. In the Guadalupe Mountains in southern New Mexico and western Texas, acorns and juniper berries were commonly eaten (Bailey, 1905, 1931). In The Bowl, in Guadalupe Mountains National Park, Texas, Cornely (1979) observed a young Mexican woodrat eating acorns from a large cache in an old log cabin. Schmidly (1977) reported that favorite foods included acorns, juniper berries, nuts, seeds, and mushrooms. Davis (1944) reported that Mexican woodrats in western Texas ate a variety of plants including green vegetation, nuts, berries, acorns, and fungi. He stated that cactus was eaten if available. According to Baker (1956), woodrats in the Sierra de la Madera, Coahuila, seemed to feed mostly on acorns.

Finley (1958) reported that Mexican woodrats in Colorado apparently cure and store large quantities of food. The greatest collecting activity occurred in the late summer and autumn. The stored food consisted almost entirely of dried cuttings of foliage.

Mexican woodrats generally do not build houses typical of most species of *Neotoma* (Bailey, 1931, 1935; Cornely, 1979; Finley, 1958; Schmidly, 1977), but construct nest chambers in well-protected rock crevices, tree cavities, or abandoned buildings. Finley (1958) reported that they have a relatively weak collecting instinct compared with that of other species of woodrats in Colorado. Sticks and other objects often are stuffed into crevices near the den. Although stick houses of *N. mexicana* rarely have been found, several authors reported that they are capable of building houses (Bailey, 1931; Davis, 1966; Hoffmeister, 1971). According to Finley (1958) individuals sometimes move into vacant houses constructed by other species of woodrats. Six nest chambers examined by Finley (1958) were either cup-shaped or ball-shaped and constructed mainly of shredded juniper bark.

Because Mexican woodrats are principally montane, the distribution is often disjunct, with adjacent populations isolated on the tops of mountain ranges. Often two or more species of woodrats with different altitudinal distributions occur in such areas. Mexican woodrats were reported in sympatry or contiguous allopatry with other species of woodrats in several localities (Cary, 1911; Cornely, 1979; Dice, 1942; Finley, 1958; Hill, 1942; Hoffmeister and de la Torre, 1960; Howe, 1977). Where *N. cinerea* is present, it apparently uses the higher vertical crevices in cliffs, whereas *N. mexicana* occupies the lower ledges and spaces under talus blocks (Finley, 1958). In the absence of *N. cinerea*, *N. mexicana* often occupies the higher vertical crevices and caves (Cornely, 1979; Finley, 1958). Finley (1958) reported *N. mexicana* and *N. albigula* in the same habitats at many localities in southwestern Colorado. In Dolores Canyon near Gateway, Colorado, he noted a clear distinction in habitats occupied by the two; Mexican woodrats occupied steep sides of canyons and cliff bases near the valley bottom and white-throated woodrats occupied the valley floor. The same pattern was reported in upper Dog Canyon in Guadalupe Mountains National Park, Texas (Cornely, 1979). Findley et al. (1975) described the distribution of these two species in New Mexico as "islands" of *N. mexicana* surrounded by a "sea" of *N. albigula*.

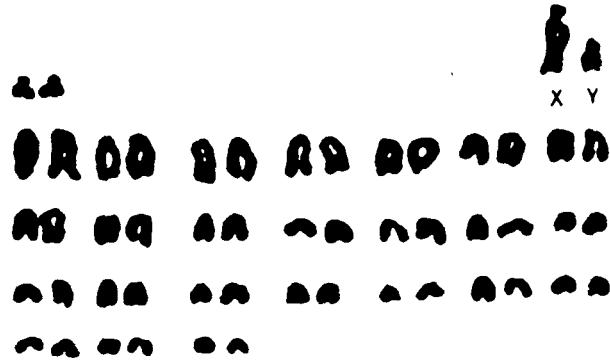


FIG. 4. Karyotype of a male *Neotoma mexicana* from the Graham Mountains, Graham Co., Arizona (after Baker and Mascarello, 1969).

In Padre Canyon east of Flagstaff, Arizona, *N. mexicana* reportedly is sympatric with both *N. albigula* and *N. stephensi* (Howe, 1976). According to Goldman (1937), the Colorado River serves as a barrier between woodrats on the North Rim of the Grand Canyon (*N. cinerea* and *N. lepida monstrabilis*) and those inhabiting the South Rim (*N. mexicana*, *N. albigula*, *N. stephensi*, and *N. lepida lepida*).

Remains of Mexican woodrats have been identified in barn owl (*Tyto alba*) pellets from Miñaca, Chihuahua (Anderson and Long, 1961), Jalisco (Twente and Baker, 1951), and Oaxaca (Mones, 1968), and a carcass was removed from the digestive tract of a black-tailed rattlesnake (*Crotalus molossus*) at Rancho Las Margaritas, Durango (Baker and Greer, 1962).

The following parasites were collected from Mexican woodrats in Colorado by Finley (1958): Taeniidae, *Taenia* sp.; Ixodidae, *Dermacentor andersoni*, *Ixodes spinipalpis*, *I. woodi*; Laelaptidae, *Eviphis* sp., *Eubrachylaelps circularis*, *Haemolaelaps glasgowi*; Macronyssidae, *Hirsionyssus* sp.; Trombiculidae, *Leeuwenhoekia americana*, *Euschogastia criceticola*, *E. lacerta*, *E. hoffmannae*, *E. finleyi*, *Trombicula alfreddugesi*, *T. hoplasi*, *T. potosina*, *T. harperi*; Haematopinidae, *Neohaematopinus inornatus*; Reduviidae, *Triatoma protaecta*; Hystrichopsyllidae, *Anomipsyllus* sp., *Megarhroglossus* sp., *Stenistomera alpina*; Ceratophyllidae, *Diamanus montanus*, *Malares* sp., *Archopeas sexdentatus*, *Peromyscopsylla* sp. Loomis (1971) reported *Euschoengastoides neotomae* from a specimen of *N. mexicana* taken in San Juan Co., New Mexico. Hoffmeister (1971) captured Mexican woodrats in Grand Canyon National Park, Arizona, that were infected with warbles (*Cuterebra* sp.). One specimen had three warbles, each nearly 2.5 cm long. Hill (1942) reported one specimen of *N. mexicana* from northeastern New Mexico had a large warble on the rump.

Finley (1958) examined two specimens of *N. mexicana* that had alveolar abscesses of the upper molars apparently caused by the lodgement of cactus glochids or other foreign material. Holdenreid and Quan (1956) reported that these rats were as susceptible to experimental infections of plague as laboratory mice. *Neotoma* is a possible reservoir for kala-azar (black disease) in Mexico (Lopez et al., 1966).

BEHAVIOR. Howe (1976, 1977, 1978) reported quantitative differences in some behavioral patterns of three species of woodrats (*N. albigula*, *N. mexicana*, *N. stephensi*) that occur sympatrically in Padre Canyon near Flagstaff, Arizona. Both scent-marking and foot-stomping were used frequently by *N. mexicana*, whereas *N. stephensi* exhibited little foot-stomping and *N. albigula* exhibited little scent-marking. Scent-marking in *N. mexicana* may be accomplished by ventral rubbing, perineal dragging, and rolling on the back. During ventral rub, a male woodrat rubs a prominent, midventral sebaceous gland against the object being marked as he slowly moves forward. Females have no midventral gland and did not exhibit ventral rub. Perineal drag, exhibited by both sexes, involved the lowering of the rump while slowly moving forward. Urine may be deposited during perineal drag (Howe, 1976, 1977; Kinsey, 1972). Rolling on the back was described as an individual wriggling on its back for some seconds while possibly depositing scent (Howe, 1976). This behavior was used less often by *N. mexicana* than by *N. albigula* or *N. stephensi*. Scent-marking occurred

during several agonistic and sexual encounters, by both dominant and submissive animals, and in both intraspecific encounters.

According to Howe (1976, 1977, 1978), *N. mexicana* was dominant over *N. albigula* and *N. stephensi* in both a large outdoor arena and a small indoor arena. During olfactory choice tests in which conspecific scent and heterospecific scent were offered as alternatives, male *N. mexicana* were attracted strongly to urine from estrous conspecifics, whereas males of the other two species paid little attention to either alternative. Female *N. mexicana* also were attracted more strongly to conspecific male glandular odor over that from heterospecifics. Females of *N. albigula* and *N. stephensi* showed strong interest in male glandular odor but no differences were apparent between species.

Howe (1976) observed that male Mexican woodrats frequently produced a low pitched, raspy vocalization in the presence of conspecific females presumed to be in estrus. This gasping sometimes became louder as the male approached the female. Males did not grasp females during mounting and copulation, but placed their forepaws lightly on the female's rump. Coquettishness (Ewer, 1968; Howe, 1976) was exhibited by females before mating. Lordosis was observed in receptive females. Copulatory lock was evident when a female attempting to move away dragged the male along. Howe (1976) noted a considerable amount of agonistic behavior interspersed with sexual behavior.

Seven Mexican woodrats that Colton (1933) observed on activity wheels averaged 14.3 to 30.8 km per night. The longest distance recorded in one night was 91.2 km. Because most of the woodrats learned to sit on the axle and rotate the wheel with one hindleg, the distances were considered to be indicative only of the general activity of the animals. These woodrats are chiefly nocturnal (Colton, 1933), but have been reported active during the day (Cary, 1911).

GENETICS. *Neotoma mexicana* has a diploid number of 52 (Baker and Mascarello, 1969; Paulete et al., 1971). Specimens from Arizona, Colorado, New Mexico, and Durango had all acrocentric autosomes (Fig. 4) except for a small pair of submetacentric elements (Baker and Mascarello, 1969). The G-banded karyotypes of *N. micropus* and *N. mexicana* differ in chromosomes 3, 17, 23, and 24 (Koop et al., 1985). In chromosome 3 only *N. micropus* had a polymorphic heterochromatic short arm. In chromosomes 17 and 24 the euchromatin distal to the centromere in the long arm appeared to be missing in *N. mexicana*. In chromosome 23 the biarm condition in *N. micropus* appeared to be rearranged to the acrocentric condition in *N. mexicana*. According to Koop et al. (1985), the standard karyotypes of the two species were identical except for the X-chromosome. Paulete et al. (1971) reported a variant karyotype for specimens of *N. m. torquata*. Zimmerman and Nejtek (1975) found a single hemoglobin pattern in all the specimens of *N. mexicana* they examined ($n = 36$). They found three patterns in *N. floridana* and eight in *N. albigula*. The pattern in *N. mexicana* was species specific with an intermediate band migrating between the first and second bands found in *N. floridana*.

Electrophoretic patterns of albumins revealed the presence of at least five different mobilities (Zimmerman and Nejtek, 1975). A definite north to south clinal increase in heterozygosity at the albumin locus was noted.

REMARKS. In spite of its wide distribution and relative abundance in North America, *N. mexicana* has not been studied extensively. The systematics of this species has not been documented fully, particularly in the southern part of the range. A number of subspecific boundaries merit further investigation. Hall (1981) suggested that *N. chrysomelas* may prove to be a subspecies of *N. mexicana*.

Neotoma is derived from the Greek words *neos*, meaning "new," and *tomos*, meaning "cut." Together they refer to a new kind of mammal with cutting teeth. The specific name, *mexicana*, is a latinized word meaning "of Mexico."

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Spermophilus variegatus.

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Spermophilus variegatus (Erxleben, 1777)

Rock Squirrel

Sciurus variegatus Erxleben, 1777:421. Type locality restricted to "Valley of Mexico, near the City of Mexico" by Nelson, (1898:898).

Sciurus grammurus Say, in James, 1823:72. Type locality Pur-gatory River, near mouth of Chacuaco Creek, Las Animas Co., Colorado.

Sciurus buccatus Lichtenstein, 1830:117. Type locality unknown. *Sciurus macrourus* Bennett, 1833:41. Type locality western Mexico.

Spermophilus couchii Baird, 1855:332. Type locality Santa Caterina, a few miles W Monterrey, Nuevo Leon.

Spermophilus buckleyi Slack, 1861:314. Type locality Packsaddle Mountain, Llano Co., Texas.

Spermophilus variegatus Nelson, 1898:898. First use of current name combination.

CONTEXT AND CONTENT. Order Rodentia, Family Sciuridae, Subfamily Sciurinae, Genus *Spermophilus*, Subgenus *Otospermophilus*. The genus *Spermophilus* contains 36 species distributed as follows: 12 Palearctic, 23 Nearctic, and 1 Holarctic (Honacki et al., 1982). There are eight subgenera of *Spermophilus*, two Palearctic, five Nearctic, and one Holarctic. *Spermophilus variegatus* is one of five species in the subgenus *Otospermophilus*; the others are *S. adocetus*, tropical ground squirrel; *S. annulatus*, ring-tailed ground squirrel; *S. atricapillus*, Baja California ground squirrel; and *S. beecheyi*, California ground squirrel (Hall, 1981). There are eight subspecies of *S. variegatus* as follows:

S. v. buckleyi Slack, 1861:314, see above.

S. v. couchii Baird, 1855:332, see above.

S. v. grammurus (Say in James, 1823:72), see above (*juglans* Bailey a synonym).

S. v. robustus (Durrant and Hansen, 1954:264). Type locality Pass Creek, Deep Creek Mountains, 8,000 ft, Juab Co., Utah.

S. v. rupestris (J. A. Allen, 1903:595). Type locality Rio Sestin, northwestern Durango.

S. v. tularosae (Benson, 1932:336). Type locality French's Ranch, 5,400 ft, 12 mi NW Carrizozo, Lincoln Co., New Mexico.

S. v. utah (Merriam, 1903:77). Type locality foot Wasatch Mountains, near Ogden, Weber Co., Utah.

S. v. variegatus (Erxleben, 1777:421), see above (*buccatus* Lichtenstein and *macrourus* Bennett are synonyms).

DIAGNOSIS. The rock squirrel is a member of the subgenus *Otospermophilus*, whose diagnostic characters include: pelage with a variegated pattern of black, white, and buff; infraorbital foramen oval with masseteric tubercle nearly ventral to foramen; width of cranium at postorbital constriction slightly greater than least interorbital breadth; fossae anterolateral to incisive foramina deep; upper cheekteeth brachyodont, M1 and M2 subquadrate in occlusal outline; metaloph of P4, M1, and M2 separated from protocone by sulcus; M3 slightly larger than M2; metaloph of M3 absent; protolophid of p4 absent and protoconid slightly larger than hypoconid; cheek pouches large; baculum with proximal end enlarged into a knob; and atlantoscapularis dorsalis muscle present (Hall, 1981).

Spermophilus variegatus (Fig. 1) is the largest member of the subgenus *Otospermophilus* and the largest ground squirrel within its geographic range. The presence of a supraorbital foramen and grayish (or mixed black and white) sides of the head in *S. variegatus*, *S. beecheyi*, and *S. atricapillus* distinguishes these three species from *S. annulatus* and *S. adocetus*, in which the supraorbital foramen is closed and the sides of the head are tawny or buffy. *S. beecheyi* and *S. atricapillus* are characterized by whitish sides

of the neck and shoulders, separated by a dark dorsal triangle, whereas *S. variegatus* lacks the whitish shoulders. *S. variegatus* is separated geographically from *S. atricapillus*, which is confined to Baja California, and from *S. beecheyi*, which, in Nevada and California, occurs west of the range of *S. variegatus* (Hall, 1981). Except for its larger size, the skull of *S. variegatus* is indistinguishable from that of *S. beecheyi* (Hall, 1981). Externally, these two ground squirrels differ in size, pelage and in relative tail length, which is greater in *S. variegatus*. In *S. variegatus* tail length is 73 to 82% of body length and usually more than 44% of total length; in *S. beecheyi*, tail length is 62 to 77% of body length and usually less than 44% of total length (Blair et al., 1968).

GENERAL CHARACTERS. In external features the rock squirrel is not modified strongly for fossorial life as are many other ground squirrels (subgenera *Xerospermophilus*, *Ictidomys*, *Spermophilus*) and their close relatives the prairie dogs (*Cynomys* sp.). Rather, *S. variegatus* more closely resembles typical tree squirrels of the genus *Sciurus* than typical ground squirrels. The head and eyes of the rock squirrel are large, and the ears extend above the top of the head and are much longer than wide. The neck is moderately long for a squirrel but stout, and the limbs are of medium length in comparison with those of other squirrels, with the forelimbs shorter than the hind limbs. The tail is long and bushy, though less so than in typical tree squirrels. Long claws are borne on all digits except the pollex, which is extremely short and carries a broad nail. Digits of the manus, ranked in order from shortest to longest, are: 1, 5, 2, 4, 3, a pattern similar to that of other ground squirrels and in contrast to that of more arboreal squirrels, in which the fourth digit is longer than the third. All five digits of the pes are long, but their relative lengths are the same as those of the manus (Bryant, 1945).

Ranges of means of standard external and selected cranial measurements (in mm) and ranges of original measurements (in parentheses) for the seven subspecies of *S. variegatus* (Howell, 1938) are as follows: total length, 466 to 503 (430 to 540); tail vertebrae, 189 to 233 (174 to 263); hind foot, 57 to 62.7 (53 to 65); and ear from notch (dry), 17 to 26.3 (15 to 29); greatest length of skull, 57.9 to 65.6 (56 to 67.7); palatilar length, 27.7 to 31.5 (26 to 32.5); zygomatic breadth, 35.6 to 40.5 (34 to 42.4); cranial breadth, 24.1 to 26.1 (23.5 to 26.6); interorbital breadth, 13.5 to 16.9 (13.2 to 18.8); postorbital constriction, 16.9 to 17.9 (16 to 19.6); length of nasals, 20.4 to 23.8 (18.5 to 24.8), and length of maxillary tooth row, 11.3 to 13.4 (10.7 to 14). Howell (1938) reported separate means for samples of adult males and females for



FIG. 1. Photograph of a rock squirrel. Photograph from a slide by J. G. Hall.

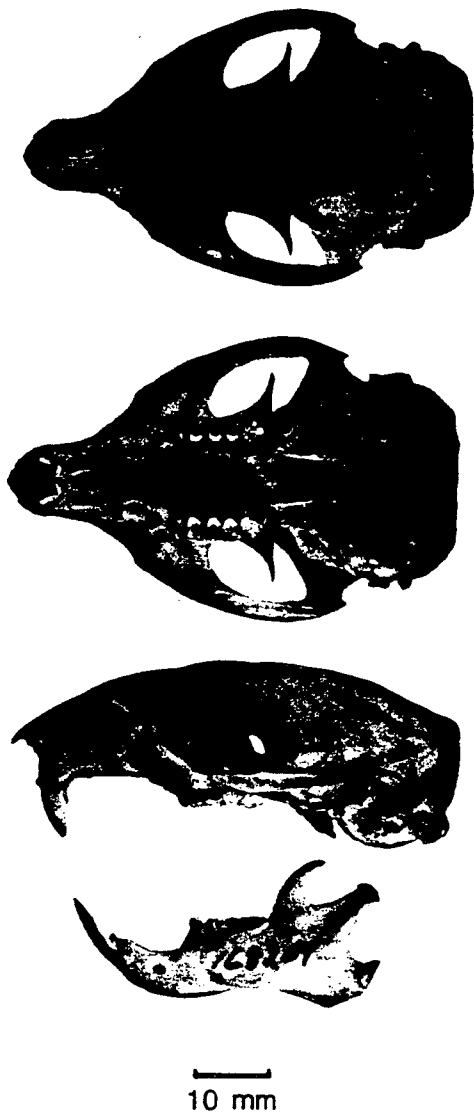


FIG. 2. Dorsal, ventral, and lateral views of the cranium and lateral view of the left mandible of *Spermophilus variegatus grammurus* (USNM 168267, adult female from 18 mi S La Junta, Otero Co., Colorado; occipitonasal length 58.0 mm). Photographs by DFS.

three subspecies (*variegatus*, *rupestris*, and *utah*) but performed no statistical comparisons between the sexes; however, in the most instances (25 of 28), means for males were larger than those for females, suggesting sexual dimorphism for size in the rock squirrel. Published data on body mass also indicate that males average larger than females. Reported mean weights (in g) of adult rock squirrels from Coahuila, Mexico (Baker, 1956) are: 4 males, 621 (range 470 to 875), 5 nonpregnant females, 546 (450 to 634); from central Texas (Johnson, 1979): 13 males, 855.4, 19 females, 734.5; from Nevada (Hall, 1946): 5 males, 684.3 (580.3 to 742.5), 3 nonpregnant females, 708.6 (643.5 to 795.5). Adult rock squirrels show substantial seasonal weight gains during preparation for hibernation (Juelson, 1970; Layton, 1973).

The skull of *S. variegatus* (Fig. 2) has a moderately convex dorsal profile, an ovate shallow braincase, and a broad interorbital region (Bryant, 1945). The parietal ridges meet near the posterior end of the cranium to form a slight crest; the rostrum is short and broad, tapering gradually; postorbital processes are long, stout and decurved, and the supraorbital borders of the frontals are slightly elevated and notched anteriorly (Howell, 1938). The infraorbital canal and foramen are narrowly oval to subtriangular with masseteric tubercle prominent at the ventrolateral margin of the foramen (Bryant, 1945; Hall, 1981). The auditory bullae are globular in shape but somewhat compressed laterally; the auditory meatal tubes are short (Howell, 1938). The body of the lower jaw is long and not deep; the diastemal part of the mandible is long and slender;

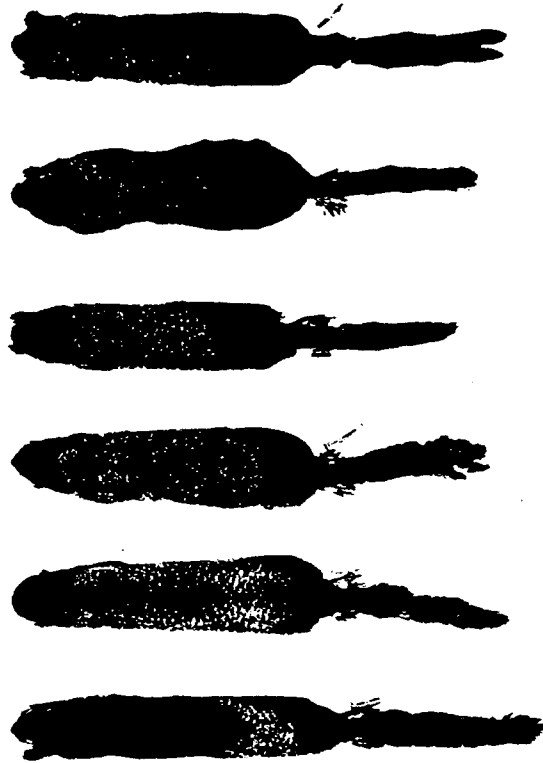


FIG. 3. Skins of *Spermophilus variegatus* illustrating range of variation in color pattern. From bottom to top, *S. v. buckleyi* (USNM 97155 female from Llano, Llano Co., Texas), *S. v. couchii* (USNM 116939 male from Saltillo, Coahuila, Mexico), *S. v. grammurus* (USNM 128541 female from Capitan Mts, Lincoln Co., New Mexico), *S. v. rupestris* (USNM 51282 male from Chihuahua Mts, Chihuahua, Mexico), *S. v. utah* (USNM 264248 female from 3 mi S Mantua, Box Elder Co., Utah), *S. v. variegatus* (USNM 34924 male from Acambaro, Michoacan, Mexico). Photographs by DFS.

the alveolar border of the mandibular body is level with the level of the anterior tip of the mandible; the coronoid process is long, narrow, and projects posteriad; and the angular process is large, extends posteriad as far as the condyloid process, and is ridged along its posterior edge (Bryant, 1945).

The dental formula is $i\ 1/1, c\ 0/0, p\ 2/1, m\ 3/3$, total 22. Upper incisors are stout and only moderately recurved; lower incisors are longer, more slender, and less curved than the upper incisors, and the lowers project forward at a moderate angle (Bryant, 1945). The anterior upper premolar (P3) is simple, peglike, and less than one-quarter the size of P4, which is molariform (Hall, 1981). Molars are subquadrate; m3 is much elongated posteriorly (Bryant, 1945). Parastylar ridges on M1 and M2 arise evenly from the protocones without abrupt change in direction (Hall, 1981). Cusps on cheek teeth are connected by crests of moderate height.

The pattern of the dorsal pelage tends to be variegated black and white, often with buff, especially over the rump. The dorsum is crossed by many indistinct wavy markings of brown and black, averaging 5 mm in width (Dalquest, 1953). Pelage coloration in rock squirrels is highly variable both within and between populations. The head varies from pinkish buff or pinkish cinnamon to seal brown and fuscous black; the back varies from grayish white mixed with cinnamon buff to snuff brown, mikado brown, bone brown, and dark blackish brown; and the tail is mixed black or brown and buffy white (Howell, 1938). In some races, the head, foreback, or entire dorsum is black (Fig. 3), although there can be considerable variation in the amount of melanin within subspecies (Baker, 1960). Color of underparts is variable, generally grayish white, buffy white, or pinkish buff to cinnamon buff (Howell, 1938).

DISTRIBUTION. In the United States, the rock squirrel occurs from the Edwards Plateau and Trans-Pecos Texas westward through much of New Mexico, Arizona, and into southeasternmost

California; northward into Colorado (primarily west of the Front Range), most of Utah, and eastern Nevada. Its range encompasses much of Mexico from Puebla, Colima, Guerrero, Mexico, and Morelos northward to the United States, although it is absent from the eastern coastal lowlands (Fig. 4). Because of its extensive latitudinal distribution, the rock squirrel's altitudinal distribution is difficult to define. It has been reported from near sea level on Tiburon Island, Sonora (Hall, 1981) to 2,900 m in Arizona (Hoffmeister, 1956).

FOSSIL RECORD. Remains of *S. variegatus* are known from a late Rancholabrean (Wisconsinan) and early Holocene site in Arizona (Mead and Phillips, 1981) and from late Rancholabrean sites in California, New Mexico, Texas, and Wyoming (Kurtén and Anderson, 1980). An extinct otospermophile, *S. wilsoni*, from early and middle Pliocene (Clarendonian and Hemphillian) of northern Oregon and southern Washington, may have been ancestral to *S. variegatus* (Black, 1963). Nothing is known of the history of the rock-squirrel lineage between midPliocene and late Pleistocene; this hiatus reflects the difficulty of interpreting the numerous but fragmentary remains of early sciurids (Bryant, 1945; Hazard, 1961; Hibbard, 1941, 1954; Kurtén and Anderson, 1980).

The geographic range of the rock squirrel has changed since the late Pleistocene. Three late Pleistocene records show that the former range was more extensive: the La Brea tar pits (Los Angeles, California); McKittrick tar seeps north of Los Angeles, about 320 km W of the present range; and Little Box Elder Cave west of Douglas, Wyoming, about 200 km N of the current range limit in Colorado (Kurtén and Anderson, 1980). Rock squirrels likely expanded their range in some areas during the so-called climatic optimum at the end of the Pleistocene but contracted it again as climates cooled (Long, 1971). Remains of rock squirrels have been found in four archeological sites in Val Verde Co., Texas. These squirrels probably have been present in Trans-Pecos Texas since late Pleistocene, but their absence from numerous other caves indicates that they moved into central Texas only about 4,000 years ago (Dalquest et al., 1969).

FORM AND FUNCTION. Cuticular scales of the hair of rock squirrels have a mosaic pattern, common in mammals, in which the visible portion of each scale is wider than long (Short, 1978). Dorsal guard hairs of rock squirrels can be distinguished from those of other mammals by a combination of other features (Mayer, 1952): simple form, compound medulla (as in sciurids generally), moderate size (more than 125 μm wide and less than 20 mm long), shaft with alternating bands of pigment (dark tip with distal and proximal light bands separated by a dark band).

Adult rock squirrels molt once a year, usually in midsummer, but later at higher altitudes and latitudes (Bradley, 1929; Davis, 1944; Hall, 1946; Juelson, 1970; Stalheim, 1965). Adult females molt while still lactating and at the same time as adult males (Johnson, 1979; Mearns, 1907). In New Mexico, molt by adults requires 5 to 6 weeks. Molts begin in a band over the neck and continue both cephalad and caudad. A definite molt line is visible as the molt progresses over the anterior part of the body, but on the rump patch several small areas of hair are replaced simultaneously (Stalheim, 1965). There may be individual or populational differences in progression of molt, for Johnson (1979) reported the molt of adult rock squirrels in central Texas to progress toward the head and in a patchy pattern. Young rock squirrels undergo both juvenile and subadult molts (Juelson, 1970).

Squirrels emit a musky scent from anal glands when disturbed (Johnson, 1979). Skin glands that secrete an oily substance with a faint musky odor occur on the dorsum immediately posterior to the shoulders. These glands are used apparently to mark objects (Juelson, 1970).

Female rock squirrels usually have five pairs of mammae, although individuals with four pairs have been reported (Hill, 1942; Mearns, 1907; Moore, 1961). Sexually mature males have large scrota (average diameter 50 mm) covered with black hair, which does not appear until the animal is about a year old (Layton, 1973).

The baculum has the same general form as those of other ground squirrels, with an enlarged, knob-like proximal end, narrow shaft, and a spoon-shaped distal end edged with spines; distally there is a midventral projection (Burt, 1960). The baculum of *S. variegatus* is indistinguishable from that of *S. beecheyi* but differs from that of other ground squirrels in being narrower, especially distally, and in having only a few (2 to 6) spines on each side of the spoon in contrast to four or more (up to 12) in other species (Burt, 1960;

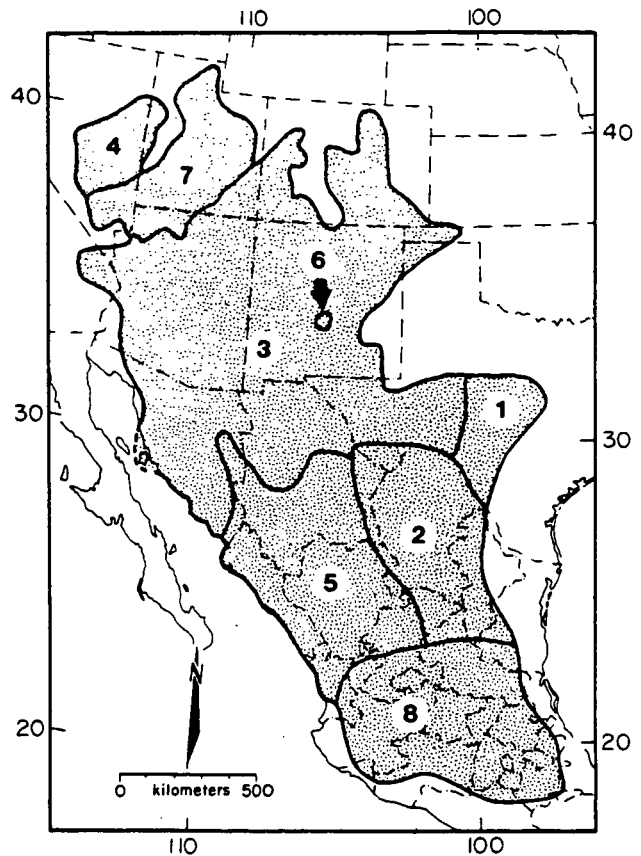


FIG. 4. Distribution of *Spermophilus variegatus*. Subspecies are: 1, *S. v. buckleyi*; 2, *S. v. couchii*; 3, *S. v. grammurus*; 4, *S. v. robustus*; 5, *S. v. rupestris*; 6, *S. v. tularosae*; 7, *S. v. utah*; 8, *S. v. variegatus*. Map redrawn by DFS after Hall (1981).

Wade and Gilbert, 1940). Burt (1960) reported means and ranges of measurements (in mm) of seven bacula (six of *variegatus* and one of *beecheyi*): length, 4.1 (4.0 to 4.5); width of base, 0.8 (0.6 to 1.1); width of distal end, 0.8 (0.6 to 1.1). The os clitoridis, as depicted and described by Layne (1954:360, Fig. 1) is rodlike, 2.0 mm long, has a dorsal sulcus distally but lacks spines characteristic of other species of ground squirrels. The absence of spines probably was an artifact of the preparation (drying) of Layne's specimen.

In many muscular and skeletal characteristics the rock squirrel appears to be intermediate between tree squirrels (for example, *Sciurus*) and more advanced ground squirrels, such as members of the subgenus *Spermophilus* (Bryant, 1945). The extensive descriptions by Bryant (1945) refer to a composite sample of rock squirrels and other members of the subgenus *Otospermophilus* that he used as a standard for comparison of sciurid genera and subgenera. Specific references to the rock squirrel consist of illustrations of the skull (Figs. 7, 21, 35), teeth (Plate 2, Fig. b; Plate 6, Figs. g to h), superficial facial musculature (Figs. 45 to 46), and extrinsic musculature of the cheek pouch (Fig. 47), and ratios between various pairs of skeletal elements (Table 2). Bryant (1945) concluded that body form, dentition, and shape of the skull of *Otospermophilus* retained more primitive characters than that of any other subgenus of *Spermophilus* with the possible exception of *Callospermophilus* (golden-mantled ground squirrels).

Auditory ossicles of the rock squirrel have the general sciurid form (Cockerell et al., 1914). The malleus has a large, high head, angled surface for articulation with the incus, straight neck, and narrow manubrium. The incus is stout and ridged, the stapes large.

Spermophilus variegatus has large internal cheek pouches, approximately 25 mm long and 15 mm high when relaxed but reaching to the sternum when stretched (Bryant, 1945; Juelson, 1970). They open slightly anterior to the cheekteeth. The pouches develop by evagination from the oral cavity into the buccinator muscles and extend posteriorly between the sphincter colli and masseter muscles. Extrinsic muscles of the pouch are modified parts of

the facial musculature. A large pit in the ventral surface of the premaxilla immediately behind the incisor marks the attachment of one of these muscles (Bryant, 1945). Intrinsic muscles of the pouches of *S. variegatus* have not been described. Juelson (1970) counted 62 acorns of Gambel's oak (*Quercus gambelii*) averaging 20 by 13 mm carried in the pouches of one squirrel. Other examples illustrating the large capacity of cheek pouches of rock squirrels include: 104 seeds of wild lupine (*Lupinus* sp.) plus parts of others (Cahalane, 1947); 360 *Purshia* seeds in one individual's pouches, in another's 234 pinyon (*Pinus edulis*) nuts (Anderson, 1961); 80 *Ephedra* fruits (Hall, 1946).

Fine structure and location of the hormone-producing cells of the adenohypophysis appear to be similar to those of other mammals (Girod and Dubois, 1976; Girod and Lhéritier, 1981).

The lens of the eye contains a large amount of yellow pigment, which has been suggested to function as a filter for light of high intensity (Dice, 1938).

Squirrels living in areas in which cadmium, copper, selenium, and zinc occur in high concentrations tend to accumulate these trace metals in their tissues (Sharma and Shupe, 1977a, 1977b).

ONTOGENY AND REPRODUCTION. Males become capable of breeding after emergence from hibernation, rather than emerging in full breeding condition as most other ground squirrels. Females attain the estrous condition about 1 week after males are ready to breed. Testes are scrotal only during the breeding season, at which time they average 32 mm in length; later they average 11 mm (Juelson, 1970). The breeding season lasts about 1 month in northern Utah, peaking in mid-March at altitudes near 1,370 m (Juelson, 1970), and about 6 weeks in March and April in central Texas (Johnson, 1979). Stalheim (1965) observed behavior he interpreted as courtship from April 23 through July 29 in central New Mexico at 1,980 m. Males with scrotal testes were observed by Young (1979) in Kimble Co., Texas from May through August. Late breeding by yearlings may lengthen the reproductive season.

The gestation period is not documented. Dates on which pregnant females have been collected range from late March through July in various parts of the range (Anderson, 1972; Baker, 1956; Bradley, 1929; Davis, 1944, 1960; Holdenried and Morlan, 1956; Hooper, 1941; Juelson, 1970; Mearns, 1907). In a particular region, squirrels breed earlier at lower altitudes than at higher ones (Davis, 1944; Juelson, 1970), at least in part because altitude affects the timing of emergence from hibernation. No latitudinal trend in the timing of reproduction is evident.

Rock squirrels reportedly have two litters per year in some southern regions with short winters (Borell and Bryant, 1942; Bradley, 1929; Dalquest, 1953). However, unequivocal data obtained by following individual females through two successful pregnancies in one season are lacking. Only one litter per season is reported for populations in northern Utah (Juelson, 1970), central Texas (Johnson, 1979), west Texas (Layton, 1973), and central New Mexico (Stalheim, 1965).

Embryo counts range from three to nine with an overall average of approximately five (Anderson, 1972; Baker, 1956; Bradley, 1929; Davis, 1944; Holdenried and Morlan, 1956; Hooper, 1941; Juelson, 1970; Mearns, 1907). Numbers of young emerging from the natal burrow range from one to seven with an average of approximately four (Dalquest, 1953; Davis, 1960; Johnson, 1979; Juelson, 1970; Layton, 1973; Long, 1940). Juelson (1970) estimated that emerged young might represent 75% of embryos implanted. Available data do not indicate geographic trends in litter size.

Rock squirrels are born hairless (except for 2 mm vibrissae), unpigmented, blind, and with closed ears. Four young born in captivity averaged 7.8 g at birth (Juelson, 1970). Neonates can crawl slowly, using primarily the forelegs. They squeak when disturbed. Pigment in the skin is first visible on the third day after birth; hair other than vibrissae appears on the seventh day, and the young are well pigmented and active at this time. On the 10th day, they can hold their heads up easily and can crawl using quadrupedal movements that resemble adult walking. The lower incisors erupt on about the 14th day. By the 17th day, the last day observations were made by Juelson (1970), the young were well haired on dorsal surfaces and well coordinated in movements.

Reported dates of first emergence of young rock squirrels range from the end of May to mid-August (Johnson, 1979; Juelson, 1970; Layton, 1973; Stalheim, 1965). Age at first emergence is

estimated to average about 8 weeks (range 6 to 10 weeks) from indirect evidence (Johnson, 1979; Juelson, 1970; Layton, 1973; Stalheim, 1965). Lactation lasts about 2 months (Johnson, 1979). Young begin to forage for themselves on the third day after emergence (Stalheim, 1965). At emergence, young rock squirrels weigh about 100 g (Johnson, 1979; Layton, 1973). One litter captured soon after emergence reached approximately 90% of adult length after about 8 weeks in captivity (Stalheim, 1965). Subsequent growth was much slower, and length did not increase significantly during the next 4 months. Johnson (1979) suggested that young squirrels continue to gain weight for more than 2 years after birth.

ECOLOGY. *Spermophilus variegatus* is primarily a species of the semiarid Upper Sonoran Zone, although it may extend upwards into the Transition Zone and descend into the Lower Sonoran Zone (Bailey, 1932; Baker, 1956). It tends to be absent from open plains, wide valleys, deserts, and the higher montane forests.

As its common name suggests, the rock squirrel is a resident of rocky habitats, and throughout its geographic range the local distribution is dictated by the presence of rocks, stones, and boulders in the form of talus slopes, rocky hillsides, canyons, arroyos, and cliffs (Bailey, 1932; Davis, 1944; Findley et al., 1975; Howell, 1938; Schmidly, 1977). In lieu of natural rocky habitats, rock squirrels exploit man-made structures such as old buildings, bridges, terraced roads, and stone walls (Bailey, 1932; Baker, 1956; Baker and Greer, 1962; Johnson, 1979).

Burrows are located under large rocks, bushes, trees, or other cover with prominent observation points nearby. Rock squirrels also occasionally den in trees (Bailey, 1905). Burrows are shallow (about 0.3 to 1 m) and usually short (to 1.5 m; Juelson, 1970; Layton, 1973), but longer ones, to 5.8 m, have been excavated (Stalheim, 1965). There is one main tunnel, 8 to 30 cm (usually 10 to 12 cm) in diameter, with one to three openings to the outside and a connecting nest chamber (Juelson, 1970; Layton, 1973; Stalheim, 1965). Feces are deposited in a side tunnel near the nest chamber (Juelson, 1970). Burrows are lined with dried grass, leaves, bark, and seed pods (Bradley, 1929; Stalheim, 1965; Steiner, 1975). Adults have a home burrow and auxiliary burrows used while foraging (Juelson, 1970; Young, 1979). Burrows are used year after year (Bailey, 1932), although there appear to be seasonal movements by individual squirrels from one burrow location to another (Layton, 1973). Deserted rock squirrel burrows are used by burrowing owls, *Speotyto cunicularia* (Martin, 1973) and probably by other animals.

Home ranges are large and overlap greatly; the size varies with season and breeding condition of the squirrels (Johnson, 1981; Juelson, 1970; Stalheim, 1965). Males often occupy areas distinct from females, except during the breeding season when the range of a resident male overlaps that of one or more females (Johnson, 1981). In central Texas in spring, means of areas (ranges in parentheses) of home ranges (in ha) were: resident male, 0.40; 11 breeding females, 0.15 (0.12 to 0.22), calculated by minimum polygon method (Johnson, 1981). During times of lactation and emergence of the young (late May-July), breeding females in Johnson's (1981) study became more territorial and excluded the resident male, and the mean size of home ranges shrank to 0.09 ha. Stalheim (1965) reported minimum home ranges (Mohr, 1947) averaged 0.43 ha for females and 0.23 ha for males, based on sightings and captures over a 2-month period during summer. Means of areas (ranges in parentheses) of minimum home ranges (in ha) for squirrels in northern Utah during the latter half of July (Juelson, 1970) were: three adult males, 0.32 (0.23 to 0.45), four adult females, 0.24 (0.11 to 0.30).

The density of a rock-squirrel population in central Texas in spring was 13 squirrels in an area of 1 ha (Johnson, 1981). Densities reported by Juelson (1970) for areas of marginal and good habitat were 2.0/ha and 5.7/ha, respectively. The sex ratio for the species as a whole probably is 1:1, but is modified locally by social structure. Males apparently move considerably during the breeding season; after that time, adult females may move into or out of a colony (Johnson, 1981). Many juveniles disperse from the maternal home range in late summer or early fall; yearlings may leave the parental range in spring (Johnson, 1979). During summer, squirrels tend to stay within 100 m of the home burrow (Juelson, 1970; Layton, 1973). Hooper (1941) found normally colored squirrels living on dark lava beds in New Mexico and concluded that significant movements occurred onto and off the areas of lava, sufficient to prevent selection for a dark population on the lava.

Rock squirrels consume a wide variety of food items, including nuts, seeds, grain, berries, fruit, roots, green vegetation, cactus, invertebrates, and fresh and dried meat (Bailey, 1905; Burt, 1934; Mearns, 1907; Young, 1979). The diet of rock squirrels changes seasonally depending upon local availability with more green material consumed in spring, berries in summer, and seeds, grains, and nuts in autumn (Bailey, 1932). Stalheim (1965) reported that rock squirrels select reproductive rather than vegetative parts of plants. He also noted that although rock squirrels in the Sandia Mountains, New Mexico, consumed a wide variety of plant foods, the following provided the bulk of the diet: berries of wild sumac (*Rhus trilobata*), blossoms and fruit of Apache plume (*Fallugia paradoxa*), heads of assorted grasses, predominantly wild rye (*Elymus* sp.), heads of ragweed (*Ambrosia* sp.), gooseberries (*Ribes* sp.), and acorns (*Quercus turbinella* and *Q. grisea*). Each of these major food items became available progressively during the summer, and rock squirrels shifted their diets accordingly (Stalheim, 1965). Other reports of plants utilized in specific areas are available for northern Utah (Juelson, 1970) and west Texas (Layton, 1973). Howell (1938) observed that nuts, including acorns, walnuts (*Juglans* sp.) and pine nuts (*Pinus edulis*) probably compose a large portion of the diet of rock squirrels but also listed seeds of the following plants among its constituents: mesquite (*Prosopis*), cactus (*Opuntia*), saltbush (*Atriplex*), wild gourd (Cucurbitaceae), wild cherries (*Prunus*), fragrant sumac (*Rhus aromatica*), Nevada jointfir (*Ephedra nevadensis*), serviceberry (*Amelanchier*), spurge (*Euphorbia*), marbleseed (*Onosmodium occidentale*), wax currants (*Ribes cereum*), cactus fruit, blossoms of mesquite (*Sophora secundiflora*), flowers and tips of *Agave*, berries of cherrystone juniper (*Juniperus pachyphloea*), and seed pods of *Yucca* and Indian breadroot (*Psoralea*). Besides feeding on native plants, rock squirrels consume the fruits or seeds of the following domesticated plants: muskmelon, watermelon, apples, cherries, apricots, blackberries, squash, peas, grains, corn, peaches, and pears. As a consequence, rock squirrels have the potential for becoming serious pests in agricultural regions (Howell, 1938). Animal foods eaten by rock squirrels include grasshoppers (Orthoptera; Layton, 1973), beetles (*Lucanus* sp.) and earthworms (Lumbricidae; Bradley, 1929), young wild turkeys (*Meleagris gallopavo*) and domestic fowl (Cook and Henry, 1940), and smaller vertebrates (Layton, 1973). A rock squirrel killed and ate part of a bannertail kangaroo rat (*Dipodomys spectabilis*) in captivity (Cahalane, 1939).

Internal parasites reported from rock squirrels include the protozoans *Babesia wrighti* (Doran, 1954), *Entamoeba citelli*, *Chilomastix magna*, *Hexamastix muris*, *Monocercomonoides pileata*, *M. robustus*, *Octomitus pulcher*, *Tritrichomonas muris*, *Sphaerita* sp. (Juelson, 1970); the trematode *Brachylaima microti*, the cestodes *Hymenolepis citelli*, *Mesocestoides corti*, and *Railletina retractilis* (Juelson, 1970); the nematodes *Capillaria hepatica*, *Citellinema bifurcatum*, *Rictularia coloradensis*, *Syphacia citelli*, *Trichuris citelli* (Juelson, 1970) and *Passalurus abditus* and *Trichuris minuta* (Doran, 1955); and the acanthocephalan *Montiliformis clarki* (Juelson, 1970). External parasites include the louse *Neohaematopinus laeviusculus*; larval dipterans belonging to the genera *Hylemya* and *Sarcophaga* and to the families Cecidomyiidae and Phoridae, genera and species undetermined (Juelson, 1970); the mites *Androlaelaps fahrenheitsi*, *Brevisterna utahensis*, *Hirstionyssus incomptis*, *Ischyropoda armatus* (Whitaker and Wilson, 1974), *Euschongastia* sp. and *Trombicula* sp. (Juelson, 1970); the ticks *Dermacentor andersoni* (Juelson, 1970), *Ixodes conepati* (Keirans and Clifford, 1974), and *Dermacentor parumapertus* (Layton, 1973); and 19 species of fleas: *Catallagia decipiens*, *Dactylopsylla (Foxella) ignota*, *Diamanus montanus*, *Echidnophaga gallinacea*, *Hoplopsyllus anomalus*, *Monopsyllus wagneri*, *M. eumolpi*, *Nosopsyllus fasciatus*, *Oropsylla idahoensis*, *Orchopeas sexdentatus*, *Opisocrotis tuberculatus*, *Thrassis pandorae*, *T. acamantis*, *T. francisi*, *T. bacchi* (Stark, 1958), *Cediopsylla inaequalis*, *Hoplopsyllus affinis*, *Thrassis gladiolus*, and *T. stanfordi* (Juelson, 1970). The rock squirrel is the definitive host for the flea *Hoplopsyllus anomalus* (Stark, 1958). This species and *Diamanus montanus* were the most common fleas on rock squirrels in northern Utah (Juelson, 1970) and New Mexico (Holdenried and Morlan, 1956). Eleven species of fleas reported from rock squirrels, including *D. montanus*, are known or potential vectors of sylvatic plague, and a few instances of rock squirrels infected with this disease have been reported (Allred, 1952; Meyer, 1939; Williams et al., 1978). Rock squirrels are susceptible to the plague

organism (*Yersinia pestis*) and apparently serve as a reservoir for this disease (Quan et al., 1985). Some ectoparasites of rock squirrels are known or implicated vectors of tularemia, brucellosis, Q-fever, and Rocky Mountain spotted fever, although the squirrels themselves are not known to be infected with any but the last (Juelson, 1970).

There is little information on longevity or on rates of mortality for rock squirrels. Three marked animals lived at least 29 months during Juelson's (1970) study; they probably were at least 1 year old when marked.

Predators on *S. variegatus* include golden eagles, *Aquila chrysaetos* (Mollhagen et al., 1972; Juelson, 1970) and probably other diurnal raptors; mammalian carnivores such as bobcats, *Lynx rufus* (Jones and Smith, 1979; Juelson, 1970), ringtails, *Bassariscus astutus* (Towell and Teer, 1977), gray foxes, *Urocyon cinereogargenteus* and raccoons, *Procyon lotor* (Layton, 1973), coyotes, *Canis latrans*, badgers, *Taxidea taxus*, and domestic cats and dogs (Juelson, 1970); rattlesnakes, *Crotalus viridis* (Juelson, 1970) and possibly bullsnakes, *Pituophis melanoleucus* (Haywood and Harris, 1971), and man (Dalquest, 1953; Davis, 1960; Gilmore, 1947) are known to prey on rock squirrels.

BEHAVIOR. Populations of rock squirrels tend to be colonial and are organized as maternal aggregations at prime denning sites with a dominant male and several subordinate males occupying peripheral locations (Johnson, 1979, 1981; Krenz, 1977; Layton, 1973). Dominant males defend a colony from other breeding males but allow females and juveniles to move about freely, and females actively defend, from other adults, the area immediately around the burrow (Johnson, 1981). Both sexes seem to maintain an area of exclusion while foraging (Young, 1979).

Agonistic behavior is highest during the breeding season when males compete for mates (Johnson, 1979). Most fights consist of a flank-to-flank shove followed by a rolling fight (Juelson, 1970; Krenz, 1977); "boxing" also is common (Juelson, 1970). Many adults are scarred on head and flanks from aggressive encounters (Johnson, 1979, 1981; Juelson, 1970; Krenz, 1977).

Courtship is initiated by the male with nasonasal contact, stroking the female's head with its paws, and nasonasal contact. The female may respond by arching her back and raising her tail. Attempts at mounting are resisted and are followed by a chase that usually leads down a burrow (Johnson, 1979; Stalheim, 1965). Copulation has not been observed in the field or laboratory and probably occurs in the burrow.

Females usually remain on the alert while newly-emerged young are above ground; they may move the denning site if disturbed (Johnson, 1979; Young, 1979). Nose-touching by female and young probably effects greeting and recognition. Juveniles appear to recognize siblings; such recognition reduces intrafamilial agonistic behavior, although dominant squirrels displace subordinate siblings from favored perches (Johnson, 1979).

Rock squirrels are diurnal, but timing of peak activity varies seasonally: in fall, winter, and spring the peak is at midday (Johnson, 1979; Juelson, 1970); in summer there may be a single peak in the morning (Johnson, 1979) or afternoon (Young, 1979), or activity in both morning and late afternoon (Bradley, 1929; Juelson, 1970; Stalheim, 1965). Ambient temperature affects activity greatly; squirrels rarely are active below 10°C in northern Utah (Juelson, 1970) or below 15°C in Texas (Johnson, 1979), and usually are not active above 27 to 30°C in northern Utah (Juelson, 1970) and 35°C in Texas (Johnson, 1979). Activity at high temperatures may be restricted to short bouts of foraging in the shade (Layton, 1973; Young, 1979). Light wind may increase activity during hot weather, whereas strong winds inhibit activity (Juelson, 1970) or restrict it to the ground (Young, 1979). Rock squirrels occasionally are active during light rain showers (Johnson, 1979; Young, 1979), but not during heavy downpours (Johnson, 1979; Juelson, 1970).

Rock squirrels communicate mainly by a combination of posture and vocalization (Johnson, 1979; Krenz, 1977). Squirrels familiar with one another usually approach head-on and may make nose contact. Unfamiliar squirrels approach and are approached obliquely and try to assert dominance (Johnson, 1979). Most encounters consist only of threat and counter-threat displays (Krenz, 1977). Vocal communication is used mostly for warning, and among free-living squirrels, only colonial females are reported to call (Krenz, 1977). Five types of calls have been reported: long and short alarm calls, composed of "chucks" and whistles, that serve to locate the

direction of the danger stimulus; whistle alarms, short ventriloquistic whistles given from the burrow; squeals, high-pitched sounds in response to pain or handling; growls, low-pitched noises used during aggressive encounters and when trapped or handled (Krenz, 1977). Rock squirrels also use tooth chattering as a warning or aggressive signal (Johnson, 1979; Krenz, 1977). There is no evidence for a repertoire of calls to distinguish different kinds of predators as reported for some other ground squirrels (Krenz, 1977). Chemical communication may be effected by means of dorsal cutaneous glands; Juelson (1970) observed males to rub their backs on rocks and stems during the breeding season. Squirrels also rub their cheeks against rocks and smell each other's cheeks and around their ears, top of head, back, and anal regions (Johnson, 1979).

Rock squirrels use a slow diagonal walk while foraging and when close to the burrow; distances greater than 1 m are covered usually by running with the bound or half-bound (al-Johny, 1983; Juelson, 1970). Speeds as great as 18 km/h have been recorded in captivity (al-Johny, 1983). In ascending trees and branches, rock squirrels use walking movements and movements that resemble the bound. Squirrels descend head first with the hind feet rotated about 120° to the body axis. The tail is used in balancing and as a prop while sitting on a branch. On small branches, rock squirrels progress cautiously and grasp twigs to maintain balance. Horizontal jumps as great as 165 cm have been recorded; squirrels land on the forefeet first or on all four feet at once (al-Johny, 1983).

King (1965) and King and Goodman (1966) used hand-reared rock squirrels as subjects to compare techniques of measuring learning ability and found these squirrels to be proficient at discrimination and at reversal learning.

Foraging and feeding compose most of the daily activity. Foraging bouts are longest in the morning (average 12 min) and become progressively shorter as ambient temperatures increase during the day (Young, 1979). Rock squirrels forage extensively in trees and on the ground (Juelson, 1970; Krenz, 1977; Mearns, 1907; Steiner, 1975; Young, 1979). Food items often are carried to a lookout point where they are consumed (Juelson, 1970; Young, 1979). Juelson (1970) observed squirrels to bury food in small pits dug outside the burrow, but food caches have not been found within excavated burrows (Layton, 1973; Stalheim, 1965).

Rock squirrels self-groom and dustbathe, possibly in response to the presence of ectoparasites, most often in early morning or late evening (Juelson, 1970; Young, 1979). No true allogrooming has been observed (Johnson, 1979). Rock squirrels sometimes defecate and urinate in small pits in cat-fashion in addition to some use of latrine chambers in the burrow (Johnson, 1979; Juelson, 1970).

All activities are interrupted by short bouts of alert behavior during which the squirrel assumes a half-crouched posture or erect (picket-pin) posture (Johnson, 1979; Juelson, 1970). Squirrels often rest, feed, and sunbathe in trees or on other high lookout points such as rocks or snags, from which alarm calls are easily heard (Bailey, 1932; Burt, 1934; Johnson, 1979; Krenz, 1977; Mearns, 1907; Young, 1979). Offensive behaviors reported include aggressive reactions toward fox squirrels, *Sciurus niger* (Young, 1979) and bullsnakes (Krenz, 1977).

Rock squirrels are shy of being observed, hence difficult to study, both in the wild and in captivity. Trap shyness usually develops after two or three captures (Juelson, 1970), and squirrels avoid burrows with traps near them (Young, 1979). Long-term movements are difficult to measure because of trap shyness.

Spermophilus variegatus is a facultative hibernator, with a circannual rhythm of winter torpor (Pengelley and Kelly, 1966). Rock squirrels store fat for hibernation; adults in northern Utah gained an average of approximately 200 gm between March and September (Juelson, 1970). Squirrels also may store food for winter use (Davis, 1960; Johnson, 1979), although not all do so, and none has been observed to store food in captivity (Pengelley, 1964).

Rock squirrels hibernate throughout much of their geographic range, but the duration of hibernation appears to vary with latitude, altitude, and severity of the winter. Reported dates of emergence and disappearance from the field vary tremendously, and animals may be seen intermittently all winter, especially in mild weather, in most parts of their range (Bailey, 1905; Davis, 1960; Dice, 1938; Krenz, 1977; Long, 1940; Mearns, 1907; Young, 1979). In northern Utah, rock squirrels may hibernate for 1 to 6 months (Juelson, 1970). In Texas, they hibernate 2 to 4 months (November–February or March; Johnson, 1979; Layton, 1973). Adults enter hibernation

earlier in the season than juveniles (Juelson, 1970). In west Texas, animals that did not become obese (both adults and young) were active in winter (19 November–15 March), whereas obese individuals were not trappable during that time (Layton, 1973). Adult females begin to store fat sooner and hibernate earlier than adult males (Juelson, 1970), in contrast to the usual pattern in ground squirrels in which males enter hibernation first (Michener, 1984). Young female and young male rock squirrels enter hibernation at the same time. Emergence is not related to age, but females emerge about 1 week before males (Juelson, 1970), again in contrast to the pattern recorded for most ground squirrels.

Rock squirrels may estivate (Juelson, 1970) but apparently not in response to lack of water. They are remarkably tolerant of water deprivation, for individuals have survived up to 100 days on dry food alone with no drop in body temperature (Pengelley, 1964). Captive squirrels from Nevada did not hibernate in October at a low ambient temperature (3°C) when supplied with food, but hibernated when food was removed (Pengelley, 1964). During torpor, rock squirrels maintain a body temperature of 5.5 to 10°C even when ambient temperature is 3°C or lower (Juelson, 1970; Pengelley, 1964). Torpid squirrels undergo periodic arousals and are active for a few hours to 2 days between bouts of torpor. Arousal takes 1.5 to 3.0 h (Juelson, 1970).

GENETICS. *Spermophilus variegatus* has a diploid number of 38 and a fundamental number of 72. There are 22 metacentric and 14 submetacentric autosomes; the X is metacentric and the Y acrocentric. There are no observable karyotypic differences from *S. beecheyi* (Nadler, 1966). Other species of *Spermophilus*, including *S. (Otospermophilus) adocetus*, differ from these two (Birney and Genoways, 1973; Nadler, 1966).

The genus *Spermophilus* first appears in deposits of mid-Miocene age, and most Tertiary specimens have been assigned to the subgenus *Otospermophilus* by Black (1963), who considered *Otospermophilus* to be an early, generalized ground-squirrel lineage that gave rise to the other living subgenera. Immunological comparisons of *S. variegatus* with *S. (Callospermophilus) lateralis*, *S. (Spermophilus) richardsonii*, and *S. (Ictidomys) tridecemlineatus* indicate that *S. lateralis* is closest of these to the rock squirrel, although still a considerable distance from it (Gerber and Birney, 1968). Likewise, Hafner (1984:13, Fig. 1.3) indicated that the subgenera *Callospermophilus* and *Otospermophilus* are closer genetically to each other than either is to any other subgenus in *Spermophilus*. This relationship had been suggested earlier on morphological grounds by Bryant (1945), although Black (1963) placed *S. lateralis* farther from the Recent rock-squirrel lineage. Of living otospermophilines, *S. beecheyi* is closest to *S. variegatus* in many features. However, Black (1963:237, Fig. 8) showed these two species were separate since the early Pliocene, suggesting a long period of evolution of *S. variegatus* independent from other living members of the genus *Spermophilus*.

Populations of rock squirrels in New Mexico and Colorado exhibit polymorphism in serum proteins; two or three separate albumin fractions are present in individual squirrels, and significant variation in concentration and relative mobilities of transferrins exists (Seaman and Nash, 1977).

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LEAST SHREW

Cryptotis parva

Distribution.--The least shrew generally occurs in the eastern half of the United States and is common in Mexico and Central America. In Colorado, the species is found in the drainages of the South Platte and Republican rivers. There is evidence that the habitat created by extensive irrigation has allowed the animal to extend its range westward in the last two decades. In Boulder County the species occurs in wetlands to the base of the foothills; it was first traced here in 1966, near Boulder Reservoir.

Description.--The least shrew is small, with inconspicuous ears, minute black eyes, and a long pointed snout. Brownish gray in color, the pelage is fine, dense, short and almost velvety. Its extremely short tail is less than one-third the total body length, and that distinguishes it from other shrews.

Measurements of a male and a female from Yuma County were: total length, 81, 85; tail, 18, 18; hindfoot, 11, 11; weight 5.2, 4.7 gr; condylobasal length, 15.5, 15.2; cranial breadth, 7.7, 7.9.

Natural History.--In the northern part of its range, the least shrew inhabits grassy, weedy and brushy fields. It is often associated with dense herbaceous cover. Burrows may be of several forms but are generally simple, small, and terminate in a nest. Nests are also found on the surface under logs or human artifacts. Approximately 100 cm. in diameter, the nests are usually constructed of dried grasses and/or leaves. The species may be colonial or at least social. This is unusual behavior for a shrew. Large numbers of the animal often are found together in the same nest. The species is active at all hours of the day but is most active at night. The least shrew is active throughout the year.

Food consists almost entirely of insects, earthworms, and spiders. Food habits in Colorado have not been studied, but in Indiana, the larva of moth beetles, earthworms, spiders and the internal organs of crickets and grasshoppers made up the bulk of the animal's diet.

Females give birth to litters of three to seven young from March to November in the northern part of the range. The young are altricial but development is fairly rapid. Adult weight is reached in about 30 days.

Owls are known to prey heavily on the least shrew. Other predators include hawks, skunks and falcons. Very little is actually known about this species. Thorough studies of the animal's population ecology, genetics, and social behavior remain to be done.

Selected References.--Whitaker (1974); Williams and McArthur (1972).

S.M.A.

EASTERN COTTONTAIL

Sylvilagus floridanus

Distribution.--The eastern cottontail is a species of the Great Plains and eastward, and has a wider distribution than other species of cottontails. It has a range from southern Canada to Venezuela and from the eastern seaboard of the United States to the base of the Rocky Mountains. In Colorado, the species occurs in the northeastern corner of the state. It has yet to be documented in Boulder County but doubtless occurs here.

Description.--In Colorado, S. floridanus may be distinguished by much darker pelage and larger size from S. audubonii, with which it is sympatric. The animals are brownish to grayish on the upper parts and white on the underside of the body and tail. There is no real pattern except a distinct rusty patch on the nap of the neck.

External measurements of ten animals from Cherry County, Nebraska were: total length, 420.3 (400-452); tail, 50.5 (41-71); hindfoot, 97.5 (83-104); ear, 55.9 (52-61); weight, 2 to 3 lbs. Greatest length of skull, averages 72.6 (70.8-75.3); zygomatic breadth is 36.0 (35.6-36).

Natural History.--Eastern cottontails prefer riparian communities along major streams of the eastern plains or adjacent agricultural situations where dense plant growth provides good cover. This species feeds upon a wide variety of plant species. In summer the diet is chiefly herbaceous plants with a preference for legumes and grasses. They also utilize stems and shoots of shrubs and woody vegetation, especially in winter when preferred foods are dormant.

Females bear two to six litters per season with a litter size of four to seven. Breeding periods are of one week duration separated by intervals of about two weeks. Gestation last twenty six to twenty seven days and in Missouri post-partum breeding was measured at almost one hundred percent. As time of parturition approaches, the female digs an elliptical nest lined with vegetation and wads of soft fur pulled from her shoulders, flanks, and legs. The young are nursed at dawn and dusk by the female who also defends the nest from intruders. The young are altricial but show rapid growth in the first two weeks then leveling off. Mortality rate is extremely high with seventy percent of the individuals dying before the age of five months.

Coyotes, foxes, weasels, hawks, owls, rattlesnakes, and numerous other carnivores prey on these cottontails. Home ranges have been estimated in Colorado to be from one to five acres for females although it may be as large as fifteen. Adult males may range as far as one hundred acres.

Eastern Cottontails are important game animals and it is not uncommon for the kill in the U. S. to exceed one million animals. However, general knowledge of the biology of this species in Colorado is poor.

Selected References.--Chapman et al. (1980); Jones et al. (in press).

NUTTALL'S COTTONTAIL

Sylvilagus nuttallii

Distribution.--The range of Nuttall's cottontail extends from the Canadian border south to Arizona and New Mexico, and from the eastern slopes of the Rocky Mountains west to the eastern slopes of the Cascade-Sierra Nevada Range. It is found in suitable habitat throughout most of the mountainous areas of Colorado from foothills to medium elevations. Individuals have been documented throughout higher parts of Boulder County.

Description.--Sylvilagus nuttallii is relatively large for a cottontail with long hind legs, comparatively short, round-tipped ears, a long rostrum, and a large tail. It is dark pinkish and buffy above, with a grayer, paler pelage on the sides and white underparts. Nuttall's cottontail is sympatric with S. audubonii and is distinguished by its darker colored pelage with more dorsal black hairs; smaller ears with a thin black line on the margin; a bright rusty nape; smaller hind feet, and long dense hair covering the hind feet. Locally, S. nuttallii may also be found in close proximity to S. floridanus and is separated (with difficulty) by slightly paler dorsal pelage, duller brownish throat patch, and more densely furred ears.

External measurements of four females from Garfield County were: total length, 377 (367-397); tail, 40.2 (36-42); hindfoot, 97.2 (90-104); ear, 64.0 (60-68). Greatest length of skull is around 70; zygomatic breadth about 35. Average weight of six males from South Dakota was 809.5 g.

Natural History.--The species occurs at the edge of coniferous forests and in dense stands of sagebrush or other brushy areas. It ranges in elevation from 6000 feet (1800 m.) to 11,500 ft. (3500 m.) in the Pikes Peak region. Forms are used for cover. These are cup-like cavities lined and covered with fur, grass, and small sticks. The cottontail is known to inhabit the abandoned burrows of other animals, but burrowing behavior has not been well documented.

Foraging activity usually occurs in early morning, late afternoon and evening, though this species may be active any time of the day or night. Diet consists of sagebrush, juniper, and other shrubs. Grasses are a preferred food in spring and summer.

Reproduction has not been detailed in Colorado, but in Oregon, the breeding season was reported from late February to late July. Gestation is 28 to 30 days and females bear four or five litters per season. Litter size may vary from one to eight.

Cottontails are poorly known in Colorado, despite their abundance. Perhaps this is partly because the species are so difficult to identify. Nonetheless the Boulder Mountain Parks and adjacent greenbelt lands would be an excellent place to study habitat relationships among these three closely related species.

Selected References.--Chapman et al. (1980); Jones et al. (in press).

DESERT COTTONTAIL

Sylvilagus audubonii

Distribution.--The desert cottontail occurs throughout the west from the Canadian border to central Mexico and from central Nebraska to the Pacific Coast. Locally, the species ranges through the plains of eastern Colorado, including eastern Boulder County. The cottontail may be found in the foothills or on arid mesas and creekbeds.

Description.--The coat of the desert cottontail is short with sparsely furred ears and slender hindfeet. The color is a pale grayish wash which gets paler on the sides to a whitish belly. They also have an orangish-brown throat and chest patch. S. floridanus and S. nuttallii are both close relatives, both are darker dorsally.

External measurements of two males and mean (and extreme) of nine females from Larimer County are: total length, 431, 448, 410.5 (392-438); length of tail, 44, 46, 46.8 (35-56); hindfoot, 86, 98, 89.9 (83-100); ear, 65, 75, 69.7 (59-88); weight, 1125, 985, 952.0 gr. (609-1139); greatest length of skull, 72.3, 68.6, 69.66 (67.9-74.1); zygomatic breadth, 34.8, 34.6, 35.23 (33.3-36.5).

Natural History.--The habitat of desert cottontails is low elevation deserts and semiarid grasslands. They prefer heavy brush and weedy field margins. These cottontails do not normally burrow as they prefer protection of thickets and rest in small, shallow, pear-shaped "forms". The animals avoid the hot sun and feed in early morning and evening. The species is active throughout the year and is generally solitary.

Grasses, forbs, and shrubs especially succulent terminal shoots, comprise the diet of desert cottontails.

Breeding patterns vary greatly depending on the warmth of the climate. In Colorado, breeding can start as late as April and extend through August. Females may have between one and five litters per year with an average of three. Litter size is generally three to four; embryos are reabsorbed if the mother is frightened or if there are food shortages. The gestation period is 28 days. The young are very altricial and about 90 mm long at birth. Growth and development are very rapid, however, and the animals are able to reproduce at about 90 days of age. Cottontails in the wild usually live to be only about a year old.

Cottontails are common prey for many aerial and terrestrial predators, such as hawks, large owls, coyotes, fox, badger, bobcats, large snakes, dogs, and cats. They also carry many parasites and are prone to rabies and tularemia. They are also hunted extensively by man. In Colorado, about 250,000 cottontails are harvested annually, of which some 2000 are taken in Boulder County.

Selected References.--Chapman and Willner (1978); Jones et al. (in press).

K. M. K.

LEAST CHIPMUNK

Eutamius minimus

Distribution.--The least chipmunk is a species of the western United States, ranging east to Wisconsin, Nebraska, Colorado, and New Mexico. In central Colorado, this is a species of the mountains, and the animals occur throughout much of the Boulder Mountain Park system.

Description.--A distinct pattern of four pale stripes and five blackish stripes, and two pale stripes on the face, characterize this animal. It is very difficult to distinguish this species from E. quadrivittatus or E. umbrinus in the field. Color and size, cranial details, and baculum are often good characters (depending on geographical location) to distinguish museum specimens.

Mean (and extreme) measurements of four females from Boulder County were: total length, 203.0 (200-208); tail, 86.0 (79-93); hind-foot, 31.7 (31-33); ear, 16.3 (15-18); weights range from 35 to 60 gr. Cranial measurements include: greatest length of skull, 32.20 (31.9-32.7); zygomatic breadth, 17.60 (17.2-17.9).

Natural History.--Least chipmunks are found almost anywhere but wholly open ground including sagebrush, pine and spruce forests, in brush along streams, and areas of brush and rocks. The animals use both ground and tree nests, and also may have underground burrows at the end of a somewhat intricate tunnel system. The chipmunk's peak activity is in the morning, only a few hours are spent above ground each day. There has been disagreement as to whether or not they hibernate during the colder months, but most probably go into torpor and remain underground most of the winter. Occasionally they surface to forage for food or to sun themselves.

Food consists of a variety of vegetation, with dandelions being the preferred source of food in west-central Colorado, and comprising over 80 percent of the diet during the summer. When readily available, fruits, nuts, berries, stems, seeds, and occasional insects are eaten.

Females are monoestrous, giving birth to five to eight altricial young. The chipmunk's breeding season is in late spring and early summer. By two weeks of age, the young are covered with a pale, silky fur, and the eyes are open. Based on tooth eruption patterns, ages are: juveniles, birth to 60 days; subadults, 60-90 to 100 days; adult, older than 100 days. Longevity is unknown.

Coyotes prey upon chipmunks as do weasels and diurnal raptors. More study is needed on their ecology, as well as other aspects of their biology. Difficulties in identification have led to neglect of these conspicuous little squirrels.

Selected References.--Carleton (1966); Telleen (1976, 1978); Skryja (1974).

B.S.S.

THIRTEEN-LINED GROUND SQUIRREL

Spermophilus tridecemlineatus

Distribution.--The thirteen-lined ground squirrel ranges from south-central Canada southward to Texas and from the Rocky Mountains to the northern Lake States. They occur throughout eastern Boulder County, extending in suitable habitat to the base of the foothills.

Description.--S. tridecemlineatus is similar in size to the sympatric spotted ground squirrel. The pelage is moderately bushy with a pattern consisting of a series of alternating brownish or blackish and light longitudinal stripes with a row of almost square white spots in each dark dorsal stripe.

Mean (and extreme) external measurements of eight males and of five females from Larimer County are: total length, 244.6 (212-260), 248.6 (228-260); tail, 84.2 (78-104), 89.2 (76-98); length hindfoot, 32.4 (30-35), 33.2 (31-35); weights of five males, 158.30 (125.0-193.5). Greatest length of skull of seven males, 40.33 (38.4-41.0), zygomatic breadth, 23.63 (23.0-24.1).

Natural History.--The thirteen-lined ground squirrel inhabits dry grasslands ranging from sea level to 2740 m. They prefer short grass such as grazed pastures, golf courses, and highway borders and commonly are found in farmland.

Home ranges of males are approximately 11.5 acres, largest during the breeding season. Home ranges of females are approximately 3.5 acres, largest during pregnancy and lactation. These animals are burrowers. Burrow openings are not marked by a mound of soil. Vocalization is a twittering or whistling alarm call.

Hibernation is preceded by weight gain, aggressiveness, a reduction in home range and reduced activity. Males may enter hibernation in July, females in late July and early August, and most young by early September. Emergence occurs about mid-April, males emerging a week earlier than females. Periodic arousals, occurring every 10-26 days, interrupt hibernation. During summer the animals are diurnal and mostly solitary. Diet consists of insects and larvae, grass, seeds, and flower and fruit heads in summer.

In Colorado, mating occurs the first two weeks after emergence. After a 28-day gestation period, females bear an average of eight to ten young. The young are weaned at 28 days and reach reproductive capacity at nine months. Females bear one litter annually. Survivorship of young is 16 percent compared to 29 percent for adults. Longevity is 4 to 5 years.

Badgers, coyotes, skunks, foxes, weasels, hawks, and snakes are known to prey on these squirrels, which are beneficial economically due to their insect consumption and soil-building. However, they are also injurious to crops such as peas, beans, cucumbers, squash, wheat, and oats.

Selected References.--McCartey (1966); Streubel and Fitzgerald (1978b).

ROCK SQUIRREL

Spermophilus variegatus

Distribution.--The rock squirrel is found from southern Mexico to northern Utah and Colorado and is locally abundant in rocky habitats. In Colorado it is found in Front Range canyons and quarries north to the Cache la Poudre drainage. In the course of this study the rock squirrel was observed in a wall at the south end of the Mesa Trail.

Description.--The rock squirrel is distinguished from other ground squirrels by its large size and long tail. The tail is not as bushy as the tail of a tree squirrel. The color is grayish black mixed with cinnamon brown, sometimes with the head and face blackish. There is a slightly mottled effect over the whole body.

Mean (and extreme) external measurements of five females from southern Colorado were: total length, 470 (440-498); length of tail, 197.2 (176-223); hindfoot, 59.2 (58-60); ear, 30 (29-31). Mean weight of females in Utah was 550 grams in the spring and 750 grams in the autumn. Greatest length of skull varies from 57.6 to 63.5 (mean, 60.56); zygomatic breadth varies from 35.6 to 39.1 (mean, 37.38).

Natural History.--The rock squirrel occurs over a remarkably wide climatic range. Everywhere it is found it is restricted to rocky habitat. nests are constructed of dry leaves, grass, bark, and pine needles in burrows under rocks. The animals hibernate from one to six months per year, depending on elevation and food availability.

There are two breeding periods. In Utah average litter size was 6.1 (three to nine). Young emerge from the nest at about 56 days of age. Rock squirrels are not particularly social. There is no dominance hierarchy and communication is poorly developed. Mean home range is about 0.7 acres, larger for males than for females. Densities in Utah ranged from 2.3 per acre in spring to 6.1 per acre in fall.

Seeds, nuts, berries, insects, and carrion make up the diet. The squirrels are sometimes pests in orchards. Bobcats and badgers are known to prey on them. This is one of our least-studied ground squirrels. There have been no studies of the species in Colorado. Further study would be interesting, because the rock squirrel has traits not common in northern ground squirrels; such as two litters per year and short hibernation.

Selected References.--Johnson (1981); Juelson (1970); Steiner (1975).

J. I. K.

BLACK-TAILED PRAIRIE DOG

Cynomys ludovicianus

Distribution.--An early traveler through Texas reported seeing 400 million prairie dogs in a town that covered 25 thousand acres. Though their numbers have decreased, prairie dogs still inhabit much of the western Great Plains. They range from the Rockies eastward to the Dakotas, central Kansas and Nebraska, and parts of Texas and Oklahoma. They are found across the plains of eastern Colorado, in places extending into lower, open areas of the foothills, such as the swale behind Red Rocks, above Settlers' Park.

Description.--Prairie dogs are medium-sized ground squirrel with short tails, short legs, and small ears. They have a larger body and shorter tail than the rock squirrel. The body is tan or yellowish above, whitish below. Mean (and extreme) size of 10 males and of eight females, from Larimer County are: total length, 378.7 (358-400), 371.4 (340-400); length of tail, 82.2 (71-95), 75.0 (60-84); hindfoot, 60.5 (57-63), 61.0 (55-63); ear, 14.2 (12-17), 14.5 (11-18); greatest length of skull, 64.02 (62.0-67.8), 63.09 (60.5-66.0); zygomatic breadth, 45.20 (43.6-48.5), 44.71 (42.6-48.0); weights range from 500 to 1000 gr.

Natural History.--Sitting erect atop earthen mounds, barking shrilly, these rodents are a common sight in mixed-grass prairie country. Mounds mark the entrances to complex burrow systems. They are constructed such that a convection current circulates air through the burrows. They also provide a vantage point from which to watch for predators such as coyotes, foxes, badgers and hawks. Different two-syllable calls convey different messages.

Social organization has been studied extensively. Towns are divided into smaller "wards" by geographic features and these are composed of several "coterie" or territories. A "coterie" usually consists of one or two adult males and two to eight females and young.

Prairie dogs feed on the "best of the season." In spring and summer they eat seeds, leaves, and stolons of grasses and forbs. In fall and winter, dried forbs, roots and occasional insects make up the diet. Grazing changes the plant community from perennials to the more productive annuals favored by prairie dogs. Once this grazing was by bison; now it is by cattle. Prairie dogs are more symptom than cause of overgrazing.

Active during the day, this species may reduce its activities during cold weather, but does not actually hibernate in our area. In March or April they give birth to two to eight young. In the seventh or eighth week they are weaned and come above ground. By their first winter, young will be almost full grown, and reproduce as yearlings. Average longevity is three years.

Selected References.--King (1955); Koford (1958); Lechleitner (1969) Smith (1967).

PINE SQUIRREL, OR CHICKAREE

Tamiasciurus hudsonicus

Distribution.--The pine squirrel is a species of coniferous forests, ranging throughout much of Canada and Alaska, the Rocky Mountain states, and the northeastern United States, southward along the Appalachians. In Colorado, the species occurs in the mountains, high plateaus, and mesas of the western part of the state, including the Boulder Mountain Parks.

Description.--T. hudsonicus is the smallest tree squirrel in its range. It is rust to grayish-red above and white below. The tail is outlined with a broad black band edged with white and there is a prominent white eyering.

Average (and extreme) external measurements of 13 males and 12 females from Lake and Chaffee counties are: total length, 320.0 (302-343), 319.9 (300-352); length of tail, 125.2 (116-135), 124.1 (117-132); hindfoot, 49.2 (46-51), 48.9 (46-52); ear, 24.6 (19-27), 25.3 (21-29); weights, 227.8 (202.5-252.0), 222.7 (193.7-238.6) gr.; greatest length of skull, 47.09 (46.0-48.1), 46.93 (46.1-47.8).

Natural History.--The pine squirrel inhabits denser forests of cooler zones and is restricted only by availability of food and nesting sites. They have been observed at elevations of 12,000 ft. A certain sign of their presence is middens (or caches) of cones and cone remnants. Nests are built in trees out of grass and shredded bark. Pine squirrels move about on the ground and may burrow a little in earth or snow. They are active morning and evening. They do not hibernate, and are solitary.

Food consists mainly of tree seeds, although some dry and cache fungi. Seeds of spruce and lodgepole pine make up the bulk of the diet.

Females bear a single litter each year, with two to five young born after a gestation period of 40 days in early to mid-summer. The female alone cares for the young; lactation lasts seven weeks. Longevity is 5 to 9 years.

T. hudsonicus has few competitors, although deer mice and red-backed voles may raid their cone caches. They harbor fleas and ticks and they are potential prey for a number of carnivores, especially pine martens, hawks, and owls.

A general survey of the biology of the pine squirrel in the Boulder Mountain Parks would be of interest. The area may be unique in supporting sympatric populations of three species of tree squirrels: Abert's squirrel, the fox squirrel, and the chickaree.

Selected References.--Dolbeer (1973); Finley (1969); Smith (1978).

NORTHERN POCKET GOPHER

Thomomys talpoides

Distribution.—The northern pocket gopher is a mammal of western North America, ranging from New Mexico northward to central Canada. Mostly it occurs in mountainous areas; other kinds of pocket gophers occupy adjacent valleys and plains. However, the northern pocket gopher occurs away from the mountains in Boulder County, at Rocky Flats, for example, and near Eldorado Springs. Sign of these animals is abundant in suitable habitat throughout the study area.

Description.—These are relatively small pocket gophers, being adapted to rough upland soils. In our area, the animals are dark in color, deep brown washed with blackish; often there are small white spots about the head. The tail is nearly naked, brownish to silvery gray. With their short ears, short tail, external fur-lined cheek pouches, tiny eyes, and fossorial habit, these animals can be confused with no other local mammals except plains pocket gophers, which are larger in size and occupy mostly irrigated agricultural lands on the plains.

Mean (and extreme) external measurements of 25 males, followed by those of 21 females, all from northern Larimer County, are: total length, 226.9 (211-244), 228.7 (210-255); length of tail, 69.6 (58-79), 68.3 (60-83); length of hindfoot, 28.7 (27-31), 28.7 (26-31); length of ear, about 7 mm; weights range from 110 to 150 gr.; condylobasal length of those animals was 39.62 (37.1-42.2), 38.32 (36.7-40.7); zygomatic breadth was 23.72 (21.7-25.1), 22.91 (21.4-24.5).

Natural History.—Northern pocket gophers are strongly fossorial, coming to the surface only rarely to forage. Mostly, they meet all of their needs below ground, feeding on roots and tubers of a wide variety of plants, including forbs, grasses, and shrubs. Burrow systems may be 150 to 200 m in length, with several entrances (actually exits for excess soil) which typically are plugged. The burrow system may represent the movement of three tons of soil. Side tunnels are used as storerooms or latrines. The animals are active year round and evidence of their winter activity is in the form of ridges of earth ("gopher eskers") festooning the vegetation of mountain meadows and woodlands. Those ribbons of soil actually represent the contents of tunnels in snow. The tunnels are filled with excess soil and as the snow melts, the eskers are left behind.

Pocket gophers may be serious pests on rangelands or about irrigated fields, because their burrows can injure livestock or damage ditchworks. However, they are very important agents in the soil-forming process, aerating the soil and mixing it with organic matter.

Predators of pocket gophers include badgers, snakes, coyotes, and weasels. Owls take a few pocket gophers as well, particularly young that are dispersing above ground. The breeding season is in April or May and three to 10 (mean four to six) young are born after a gestation period of about 19 days.

Selected References.—Hansen (1960); Hansen and Ward (1966).

HISPID POCKET MOUSE

Perognathus hispidus

Distribution.—The hispid pocket mouse is a species of the Great Plains, ranging from southern North Dakota southward to central Mexico and from the Missouri River to the Rockies. In Colorado, the species occurs throughout the eastern plains, including eastern Boulder County. During the course of the present study, the species was captured on piedmont grassland at the south end of Mesa Trail.

Description.—Large size and spiny, harsh fur distinguish this from other pocket mice, and external, fur-lined cheek pouches, grooved incisors, and short ears distinguish it from the deer mouse, the only large-sized, long-tailed mouse with which it is sympatric. The animals are buffy above, white below, and have a fairly prominent yellowish lateral line.

External measurements of two females from Larimer County were: total length, 200, 220 mm.; tail, 98, 108; hindfoot, 25, 27; ear, 9, 8; weight, 39.1, 43.0 gr. Greatest length of skull ranges from about 30 to 35 mm., zygomatic breadth is 15 to 18.

Natural History.—Hispid pocket mice inhabit semi-arid grasslands. They are less restricted to areas of sandy soil than some other pocket mice are, and often they are found in areas of gravelly or rocky loam, typically with vegetation of bunchgrasses, low shrubs, yucca, and cacti. The animals are active burrowers. Burrows may have two or three entrances, which may be marked with small mounds of earth, rather like those of pocket gophers but smaller. They also may burrow into roadcuts, cutbanks, or beneath shrubs, as kangaroo rats do. Burrows are plugged during the day. The animals are nocturnal and active throughout the year. Mostly they are solitary.

Food consists almost entirely of seeds, including those of grasses, forbs, and shrubs. Diets in Colorado have not been detailed, but in West Texas, seeds of sunflower, sagebrush, cacti, Gaillardia, and bluestem were prominent in the diet, along with cultivated grains (sorghum, millet). Some insects were eaten, especially in spring.

Females bear two or more litters of young annually, giving birth to litters of two to nine young from April or May to September. The young are altricial, but development has not been studied, and longevity is unknown.

Owls are known to prey on these pocket mice, and other prairie predators do as well. No studies of the population ecology of this species have been done; indeed, its biology generally is poorly known.

Selected References.—Alcoze and Zimmerman (1973); Jones et al. (in press); Maxell and Brown (1968); Turner (1974).

D.M.A.

WESTERN HARVEST MOUSE

Reithrodontomys megalotis

Distribution--The western harvest mouse has a wide distribution, from California to recently invaded Indiana. The species occurs at lower elevations throughout Colorado, on both sides of the Divide. It occurs in suitable habitat throughout the Boulder Mountain Parks; museum specimens are available from Gregory Canyon.

Description--Harvest mice are distinguished from other mice by the presence of grooved upper incisors. The animals are buffy above and vary from dark buff to white beneath, with prominent ears and a tail that is as long as the head and body. They are distinguished from the plains harvest mice by their externally larger size, a wider dorsal caudal stripe, and larger cranial size.

Mean (and extreme) measurements of nine males and five females, respectively, from the Big Thompson and South Platte river valleys were: total length, 139.5 (136-143), 144.8 (141-152); tail, 66.7 (63-70), 70.2 (65-74); hindfoot, 17.7 (17-21), 16.5 (16-17); ear, 15.0 (13-17), 14.4 (13-16); weight, 14.19 (12.9-15.9), 16.08 (12-21); greatest length of skull, 21.96 (21.7-22.5), 21.73 (21.1-22.4); zygomatic breadth, 10.89 (10.7-11.1), 10.92 (10.7-11.2).

Natural History--Harvest mice are commonly associated with tall vegetation and are very resilient to perturbation of their habitat. They are found in rank vegetation of flood plains in disturbed situations. They were found to be the most abundant small mammals in ungrazed sand sage, grazed riparian, and ungrazed riparian ecosystems in revegetated agricultural land in eastern Colorado. The animals build grass nests, with one or more openings near the base on the surface of the ground, in holes, on grass stems, or in small shrubs.

The diet consists of seeds, green plant parts, and some insects. The animals are nocturnal and active year round. There are spring and autumn molts.

Females are polyestrous, with occasional postpartum estrus known. Reproductive activity commences in early spring and extends to late autumn, with reduced activity during mid-summer. There are one to seven young per litter, and there have been several litters per year when bred in captivity. The young are altricial, and are weaned at 24 days. The animals live about one year.

Owls, foxes, weasels, hawks, jays, skunks, and badgers are known to prey upon harvest mice. They have numerous parasites, including ticks, mites, chiggers, lice, and fleas. The animals are commonly associated with the house mouse, the meadow vole, and the prairie vole.

Selected References--Webster and Jones (1982).

B.S.S.

DEER MOUSE

Peromyscus maniculatus

Distribution-- The deer mouse ranges across most of North America. In Colorado, the species occurs statewide. This is doubtless the most abundant mammalian species in the Boulder Mountain arks. In live trapping studies, it was taken at all localities.

Description--Medium in size, short ears and short tail distinguish the deer mouse from the rock mouse. Smooth incisors and larger size distinguish it from the harvest mice. The animals are brownish to reddish above and white below, including their feet.

Average (and extreme) external measurements of eleven males from Larimer County were: total length, 152.9 (142-161); length of tail, 64.5 (58-78); length of hindfoot, 19.8 (18-21); length of ear, 17.3 (15-19). The weights range from 19 to 24 gr. for a full grown adult. Greatest length of skull ranges from 24.9 to 25.9, and zygomatic breadth is 12.7 to 13.7.

Natural History--Deer mice range from above timberline down to the lowest elevations. They live in all types of topographic settings, from plains to rocky, broken surroundings. Vegetation may range from virtually none, to grass, to brush, to woodland. The animals are not active burrowers. They do remodel small burrows of other species by accumulating dirt under the body and then depositing it in front of the hole. Materials such as feathers, hair, plants, and dry grass may be accumulated to form comfortable living quarters. These animals tend to be most active at night.

Food consists of seeds, insects, and fungi. Food habits seem to shift through the season.

Average number of litters per year is about 3.5. Litter size was determined to be about 5.7 (range 2-10, n=4) in Coloradan subalpine forest. The breeding season is initiated during or after snowmelt and lasts for 5.5 months. Young deer mice may associate with their mothers past the age of weaning.

P. maniculatus has many natural predators. There are many birds of prey (owls, shrikes, hawks) that make these mice a part of their diet. Mammalian and reptilian predators also feed on them. Probably, deer mice are the most important prey base for the smaller carnivores of the Mountain Parks.

Selected References--Halfpenny (1980); King (1968); Merritt and Merritt (1980); and Stinson (1977).

M.S.T.

MEXICAN WOODRAT

Neotoma mexicana

Distribution--The Mexican woodrat is a species of the Mexican Plateau and southwestern United States. It reaches its northern limits in Larimer County, Colorado. In the Boulder area it occurs in the foothills, in suitable habitat throughout the Boulder Mountain Parks. Specimens have been reported from the following localities: Skunk Canyon; base of Flagstaff Mountain; Gregory Canyon; Boulder Canyon; Bluebell Canyon. The type locality of the local subspecies, Neotoma mexicana fallax, is Gold Hill.

Description--Mexican woodrats are dirty grayish brown above and whitish below. The long, slender tail is obviously bicolored. They are smaller in size than the bushy-tailed woodrat, and the tail is not so fully haired.

Mean (and extreme) external measurements of eight males, followed by those of six females, from Larimer and Boulder counties, are: total length, 337.9 (313-361), 321.4 (303-334); length of tail, 153.8 (144-167), 141.7 (132-150); length of hind foot, 34.2 (33-36), 32 (20-24). A male weighed about 150 gr. Condylbasal length of 10 males and eight females was 42.68 (41.7-45.3), 41.83 (40.5-43.6); zygomatic breadth was 23.42 (22.3-24.6), 22.67 (21.8-23.5).

Natural History--The Mexican woodrat is a fairly common resident of the broken, rocky areas of the foothills. The character of the rock outcrops is a more important feature of habitat than is vegetation. Mostly these rats live in and among boulders and beneath shelves of sedimentary rock. There they build characteristic stick dens, festooned with whatever other material is at hand, including castoffs from civilization: paper, woodscraps, tin cans, bottle caps, and so forth. Within the den is a nest, usually lined with soft plant fibers, and nearby there will be a food supply.

The diet consists mostly of foliage of forbs and shrubs. Vegetation is stored in and around the den. Some cactus is eaten, although less in this species than some more southern kinds. Typical food plants in our area are skunkbush and mountain mahogany, although needles of conifers may be eaten. The animals are active throughout the year, feeding on food stored up in autumn.

The breeding season begins in March. Two to five young are born in April after a gestation period of about 30 days. Apparently, there is a postpartum estrus. Most females produce two litters per year. By autumn the young disperse to set up housekeeping on their own. Probably, most individuals are able to take over and renovate some abandoned den. Woodrats without proper den sites are vulnerable to both predators and to physical extremes.

Predators include coyotes, bobcats, snakes and owls. Woodrats harbor a variety of parasites, including fleas and parasitic worms of various kinds.

Selected references--Armstrong (1982); Brown (1969); Finley (1958).

D.M.A.

MEADOW VOLE

Micotus pennsylvanicus

Distribution--The meadow vole has the most extensive range of any North American microtine, except the muskrat, occurring throughout Canada, the northern and eastern United States, and southward into Mexico. In Colorado, the species occurs in the valley of the South Platte River and in the mountains on the Eastern Slope, eastward on the Platte-Arkansas Divide at least to Ramah. On the Mountain arks, it has been captured at the foot of the First Flatiron and in Skunk Canyon.

Description--The meadow vole is a medium-sized, robust-bodied mouse with small eyes and ears and short legs. It is distinguishable from other voles by its larger size and relatively short tail. Its fur is long and soft, the summer pelage being sparser and coarser than winter, and the color varies from gray faintly washed with brown to dark brown, the belly being silvery to slightly buffy or dark gray. The tail is bicolored.

Measurements of three males and two females from Larimer County were: total length, 192, 180, 185, 187, 178; tail, 54, 44, 67, 56, 50; hindfoot, 23, 21, 22, 23, 22; ear, 15, --, 13, 15, 14; weight, 73.61, --, 68.49 gr. Condylbasal length ranges from 29.4 to 30.2, zygomatic breadth from 16.3 to 17.7.

Natural History--Meadow voles seem to prefer moist grasslands or wetlands, but are occasionally found in orchards or wooded areas with little ground cover. Choice of habitat seems to be related to the presence of sympatric species. The meadow vole is reported to be subordinate to other Microtus species. Voles are inclined to make surface runways in dense grass or sedge cover, and may burrow if the soil is not too waterlogged. They are good swimmers. Spherical nests are constructed of leaves and coarse grasses with softer vegetation as lining, and are usually found on the ground surface. The animals may be active both day or night, depending on temperature and ground cover; they do not hibernate. Meadow voles tend to be solitary, and breeding is promiscuous.

Voles are said to eat their own weight in food each day. Diet consists primarily of grasses, Poa, Panicum, and Muhlenbergia being prominent, but the voles will also eat grain, seeds, bark, roots, fruits, flowers, fungi, and sometimes insects. The animals may store food against thin seasons.

Mating in meadow voles occurs throughout the year, with up to 17 litters of one to nine young being born per year. Young are altricial, are weaned in about two weeks, and are independent soon after. Females begin reproducing in about a month, and males about two weeks later.

This vole is said to have more species of predators than any other North American mammal. Owls, hawks, snakes, weasels, foxes, and most other carnivores will prey on them. Densities of vole populations tend to run in cycles of two to five years. At high densities, this may cause serious damage, especially in orchards, due to girdling.

Selected References--Brown (1977), Jones et al. (in press); Reich (1981).

PRAIRIE VOLE

Microtus ochrogaster

Distribution-- Prairie voles are found across central North America from Alberta to Ohio and Oklahoma, and west to the base of the Rocky Mountains. They occur in Colorado along the drainages of the South Platte and Republican rivers, westward to mesas and grassy canyon bottoms of the lower foothills.

Description--The species has a dark grayish to dark brown dorsum with coarse, tawny-tipped hair, giving it a grizzled appearance. The venter is pale and buffy and the tail is short, distinguishing it from the meadow vole which has a finer pelage, grayer belly, and slightly longer tail.

Average and extreme measurements of six males and of five females from Larimer County were: total length, 175.6 (162-188), 175.2 (168-182); tail, 45.2 (41-53), 45.0 (41-50); hindfoot, 21.5 (20-23), 21.5 (20.22); ear, 12.8 (12-15), 12.8 (12-14); weights, 60.0 (54-71), 59.2 (58-68); condylobasal length, 29.45 (28.2-30.5), 29.34 (28.9-30.1); zygomatic breadth, 16.55 (15.8-17.4), 16.72 (16.5-16.8).

Natural History--Prairie voles have been found in both dry and wet grasslands but tend to live in the drier areas when sympatric with meadow voles. Dominant plant cover consists of grasses and clover through which they have extensive runway systems. Burrows lead to nests and food chambers 6 to 18 inches below ground surface.

Diets locally are not documented but studies at Lawrence, Kansas, showed a preference to dicotyledons, although grasses dominated the vegetation. Grasses, seeds, and some insects supplement the diet.

Reproduction occurs year-round with no distinct season but reaching a height around March and a drop in winter dependant upon the percentage of adults in the population. Litter sizes tend to vary seasonally, averaging about 3.9 young. Females mature at 4 to 6 weeks. They have three or four litters per year. The gestation period is 21 days.

Predators include coyotes, raccoons, owls, and hawks, but predation does not seem to affect population densities strongly. Populations fluctuate in two- to six-year cycles, dependant on available adults, due to causes which are unknown but which may be related to aggressive behavior, immigration, and abundance of vegetation.

Selected References--Choate and Williams (1978); Cruzan (1968); Fitch (1957); Jameson (1947); Martin (1956).

M.J.W.

MEADOW JUMPING MOUSE

Zapus hudsonius

Distribution--The meadow jumping mouse is a species of northeastern and central United States and southern Canada. Populations in Colorado are scarce, and they may be local relict populations. Museum specimens are available from a variety of localities about Boulder and may occur (or have occurred) on the lowest parts of the Mountain Parks.

Description--The animals are ochraceous to dark brown above and pale on the sides. The lateral line is ochraceous-buff. The belly is white or sometimes suffused with ochraceous. Hind legs are longer than fore legs; tails are longer than their bodies. The meadow jumping mouse is smaller in size and paler in color (with less black on the back and a less prominent lateral line) than the western jumping mouse.

External measurements of three males from Boulder County were: total length, 202, 211, 219; tail, 123, 125.6, 127; hind foot, 29, 30, 31. Skull measurements were: zygomatic breadth, 11, 11, 11.2; length of maxillary toothrow, 3.9, 3.9, 4.0, and interorbital constriction, 4.0, 3.7, 3.9.

Natural History--Meadow jumping mice live in a variety of habitats. In our area, they occur mostly about prairie wetlands. Such areas have been much modified by humans, and this species may be threatened. The animals hibernate throughout the winter, remaining in hibernation an average of six months. They have poor metabolic activity and cannot adjust to cold temperatures. A nest may be a hollow log or tree, under some protecting object, or underground. Grass is the usual bedding material.

Jumping mice do not normally jump from one place to another. They frequently crawl through the grass or under the grass. If they do hop, leaps will only be 3 to 15 cm. long. If startled, however, a jumping mouse will often take several leaps of up to a meter long, then stop and remain motionless or proceed by shorter hops.

Food consists of insects, seeds, and fruit. Seeds are the main source in their diet. Water may be supplied from vegetation or dew, or both.

Females may bear two to three litters per year. Litter size may range from three to seven pups (average 5.1). The young are born naked and helpless, but by the third week are able to walk and make short hops. By their fourth week, the young look like adults and can fend for themselves. At birth, the young make a high-pitched squeaking sound and "sucking note." Few sounds are recorded in adults.

Red-tailed hawks, barnowls, and long-eared owls are known to prey on jumping mice. Population studies on this species are few in this area due to the low abundance of the species.

Selected References--Kruttsch (1954); Whitaker (1972).

M.S.T.

COYOTE

Canis latrans

Distribution--The coyote is one of the most wide-ranging carnivorous mammals of North America. It occurs from northern Alaska to Costa Rica and from the Pacific Coast eastward across the Great Plains to New England. It is found throughout Colorado, and its presence on the Mountain Parks was confirmed by numerous scats and tracks observed in the course of our field work.

Description--Coyotes are similar in size and shape to a moderately large dog. Coyotes generally appear gray with a red or brown hue to their fur. The venter is paler than the rest of the body, and it can vary from tawny to white. The ears are also tawny. Coyotes have thick fur, and the tail is long and bushy.

Males usually are larger than females. Average weights of males vary from 11.2 to 14.1 kg., and female average weights range from 9.8 to 11.8 kg. Morphological measurements of the coyote include: total length, 1,000 to 1,500; tail, 300 to 500; condylobasal length, 165 to 185; zygomatic breadth, 85 to 100.

Coyotes can be confused with several other members of the Canidae. Several cranial measurements differentiate coyotes from the gray wolf and from domestic dogs. The coyote's nose is also more pointed than a dog's nose. All fox species are smaller than the coyote.

Natural History--The coyote occupies an extremely wide variety of habitats over almost any kind of topography from sea level to montane regions. These habitats include open grasslands, sagebrush grasslands, sagebrush deserts, oak woodland, grasslands, coniferous forests, riparian deciduous forests, and even large cities. Much of their present range extension is probably due to the extermination and withdrawal of other larger carnivores such as the gray wolf and the mountain lion.

Coyotes are omnivorous. Their diet includes everything from blueberries, pricklypear, grasshoppers, rodents, and lagomorphs to the large ruminants. The diet is seasonal. In winter, small rodents (voles) or large carrion (mule deer or elk) contribute much of the diet. In spring and summer, larger rodents (ground squirrels and rabbits) are eaten. Insects are taken most often in the spring, and fruit intake increases in summer and fall.

Coyotes mate from January to April. Gestation is 63 days, and pups are born during April or May. Average litter size varies from four to seven, and one litter occurs per season. Pups remain in the den until three weeks old, and they are weaned at five to seven weeks.

Undoubtedly, a few coyotes take domestic prey; however, the actual extent of economic losses by ranchers due to coyotes is not clear. This is an area sorely in need of scientific research. The coyote's diet of small rodents, rabbits, and carrion makes this much-maligned carnivore a very important and integral part of the ecosystems of the Boulder Mountain Parks.

Selected References--Bekoff (1977, 1978, 1982); Bekoff and Wells (1980, in press).

STRIPED SKUNK

Mephitis mephitis

Distribution--The range of the striped skunk extends from southern Canada to northern Mexico and through most of the United States, except for the most arid regions. Coloradan skunks occupy most of the state, especially wooded urban areas and heavily cultivated areas. In Boulder County, skunks are most common in woodland and riparian ecosystems, but may be encountered anywhere.

Description--The characteristic color pattern of these skunks makes them easily distinguishable from other mammals. Skunks are most commonly black with a white dorsal stripe, but there are color morphs of seal brown and yellow. Another common trait is a white tuft at the end of the tail. Two males and a female from eastern Colorado showed the following external measurements: total length, 640, 745, 640; tail, 285, 320, 285; hindfoot, 75, 75, 75. Condylbasal length of 16 males averaged 77.38 (73.4-82.9), of all females, 69.96 (68.3-71.7); zygomatic breadth, 50.19 (44.8-52.6), 44.44 (43.2-46.2). Females average about 2.5 kg., males perhaps 5 kg.

Natural History--The habitats of skunks vary greatly from woodlands to cultivated fields to urban areas. Although skunks themselves normally do not burrow, they inhabit single-entranced burrows abandoned by badgers and woodchucks. They use these burrows as shelter in the winter and females communally occupy them throughout the year to protect their young. Skunks do not hibernate and are mostly nocturnal.

Skunks are opportunistic feeders. They eat insects, especially grasshoppers, fallen fruit and foliage, small mammals, birds' eggs, and nestlings, and carrion.

The breeding season is in February and March and the young are born 60 to 77 days later. The females have one litter of two to ten young which are altricial and remain in or near the nest for at least two months.

Flying predators, such as eagles and owls, often prey on striped skunks, as do terrestrial predators, including coyotes, badgers, and foxes. Skunks have a unique and well known defense mechanism of spraying musk from their anal canal up to 6 meters. This foul smell repels many predators. Their distinctive coloration provides added protection by warning would-be predators of their potential. These defenses are not effective against vehicles, of course, and hence, skunks become traffic fatalities to a disproportionate extent. Striped skunks carry numerous parasites and diseases of which rabies causes the most concern.

Selected References--Verts (1967); Wade-Smith and Verts (1982).

K. M. K.

Odocoileus hemionus

Distribution--The mule deer is a western species, ranging from the Pacific Coast eastward to the Great Plains and from southern Alaska to central Mexico. In Colorado it occurs statewide, wherever suitable forest edge, woodland, or brush habitat occurs. It is a common species throughout the Boulder Mountain Parks.

Description--Mule deer are of moderate size, standing 1 meter tall at the shoulder. They have a coarse pelage that is reddish to yellowish brown in summer and dark brown to gray speckled with white in winter. The large ears are black on their front borders, and there is a white rump patch, a narrow, black-tipped tail, and males have dichotomous antlers. Average weights of bucks are about 120 kg., and of does 60 to 70 kg. Total length is 1,200 to 1,800, and the tail is 100 to 230 mm. long. Basilar length of skull ranges from 200 to 290, and zygomatic breadth is 90 to 135.

Antlers grow on males and are a rare freak on females. Mature deer normally have five tines on each side. Fewer tines indicate youth, disease, or old age, and more indicate parasite damage or injury. Most mature racks measure 60 to 90 cm. across and are shed in February or March of each year; replacement begins immediately.

Natural History--Mule deer are browsers, feeding on the terminal shoots of a variety of shrubs. The most important foods in summer are aspen, willow, and vaccinium, and winter foods are skunkbush, sagebrush, bitterbrush, and mountain mahogany, with a preference for recent growth. No one browse species furnishes all needed nutrients at a given season. A variety of browse species is essential to a healthy population.

Mule deer migrate between summer and winter range. Summer range for bucks may extend above timberline, but does and fawns remain somewhat lower. Deer are driven to winter range by snows in about October and move back up with the melt in spring. Deer typically concentrate on winter range, but the high year-round populations on the Boulder Mountain Parks are atypical. That herd very much deserves the studies now planned and in progress.

Rut begins in November; bucks' necks swell and sparring begins. Breeding is polygamous. The peak of the breeding season is mid- to late November. Both bucks and does begin breeding at about 18 months. Gestation is about 200 days, with peak of fawning in mid-June. Birth weights are 4 to 5 kg. The precocial fawns are covered with spots which disappear at the end of the first summer. Fawns are kept kidden; mothers return to them only to feed them. After a few weeks, fawns follow the mother as she feeds. Does usually are mutually intolerant when with fawns, but there are reports of does cooperating to defend fawns from coyotes. Fawns are weaned in autumn and are independent of their mother at 12 months.

Predators of the mule deer include coyotes, bobcats, mountain lions, black bear, golden eagles, and dogs. Deer serve as host to a variety of parasites. Hunting is now the principal check on populations. In 1975, nearly 128,000 deer were harvested in Colorado, most of them mule deer; of those, only 128 were taken from Boulder County.

Selected References--Anderson and Medin (1979); Loveless (1967); Taylor (1956); Wallmo (1982).

APPENDIX C

LIST OF AMPHIBIANS AND REPTILES

Common Name	Scientific Name	Habitat Preference
COLUBRIDS	COLUBRIDAE	
E. Racer	<i>Coluber constrictor flaviventris</i>	Grasslands & foothills below 6,000 ft.
W. Milk Snake	<i>Lampropeltis triangulum gentilis</i>	Eastern plains & foothills below 8,000 ft.
Northern Water Snake	<i>Nerodia sipedon sipedon</i>	Permanent streams and marshes below 5,500 ft.
* W. Smooth Green Snake	<i>Opheodrys vernalis blanchardi</i>	Riparian vegetation between 5,500-9,000 ft. Stengle I July 1989
* Bullsnake	<i>Pituophis melanoleucus sayi</i>	Most habitats below 8,500 ft. BVR June 1989
Plains Blackhead Snake	<i>Tantilla nigriceps nigriceps</i>	Grasslands & rocky canyons to 7,000 ft.
Western Terrestrial Garter Snake	<i>Thamnophis elegans vagrans</i>	Most habitats below 11,000 ft. except plains
Plains Garter Snake	<i>Thamnophis radix haydenii</i>	Most habitats below 7,000 ft.
Common Garter Snake	<i>Thamnophis sirtalis parietalis</i>	Riparian habitat below 6,000 ft.
Lined Snake	<i>Tropidoclonion lineatum lineatum</i>	Grasslands below 6,000 ft.
VIPERS	VIPERIDAE	
Prairie Rattlesnake	<i>Crotalus viridis viridis</i>	All habitats up to about 8,000 ft.

MOLE SALAMANDERS Barred Tiger Salamander	AMBYSTOMATIDAE <i>Ambystoma tigrinum mauortium</i>	Small ponds and lakes in most habitats up to 12,000 ft.
ARCHAIC TOADS Plains Spadefoot	PELOBATIDAE <i>Scaphiopus bombifrons</i>	Grasslands and sandhills below 6,000 ft.
TRUE TOADS Western Toad	BUFONIDAE <i>Bufo boreas boreas</i>	Wet areas in subalpine, 8500-11,000 ft.
Great Plains Toad	<i>Bufo cognatus</i>	Grasslands & floodplains below 6,000 ft.
Woodhouse's Toad	<i>Bufo woodhousii woodhousii</i>	Irrigate ag land & deep floodplain soils below 7,000 ft.
TREEFROGS Striped Chorus Frog	HYLIDAE <i>Pseudacris triseriata</i>	Wet meadow & marshy ponds to 12,000 ft.
TRUE FROGS Bullfrog Northern Leopard Frog	RANIDAE <i>Rana catebeiana</i> <i>Rana pipiens</i>	Permanent water on plains Banks, shallow permanent water up to 10,000 ft.
SNAPPING TURTLES Common Snapping Turtle	CHELYDRIDAE <i>Chelydra serpentina serpentina</i>	Permanent water on plains below 5,500 ft.
* POND AND BOX TURTLES W. Painted turtle	EMYDIDAE <i>Chrysemys picta bellii</i>	Tracy Collins May 1989 Permanent water below 6,000 ft.
SOFTSHELL TURTLES W. Spiny Softshell	TRIONYCHIDAE <i>Trionyx spiniferus hartwegi</i>	Large rivers & pools along streams on plains below 5,500 ft.
IGUANIDS Short-horned Lizard Eastern Fence Lizard	IGUANIDAE <i>Phrynosoma douglassii</i> <i>Sceloporus undulatus erythrocheilus</i>	Most habitats below 5,700 ft. Rocky terrain in foothills and mountains up to 9,200 ft.