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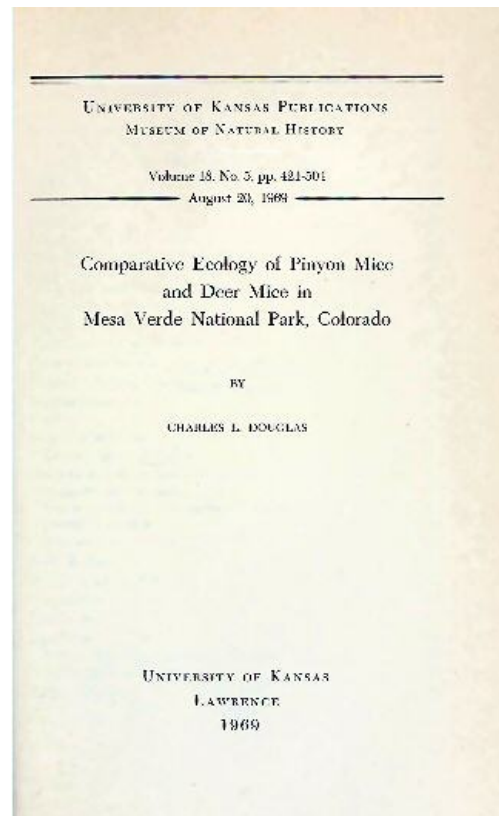
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[421]

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Comparative Ecology of Pinyon Mice and Deer Mice in Mesa Verde National Park, Colorado

BY

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INTRODUCTION

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Centuries ago in southwestern Colorado the prehistoric Pueblo inhabitants of the Mesa Verde region expressed their interest in mammals by painting silhouettes of them on pottery and on the walls of kivas. Pottery occasionally was made in the stylized form of animals such as the mountain sheep. The silhouettes of sheep and deer persist as pictographs or petroglyphs on walls of kivas and on rocks near prehistoric dwellings. Mammalian bones from archeological sites reveal that the fauna of Mesa Verde was much the same in A. D. 1200, when the Pueblo Indians were building their magnificent cliff dwellings, as it is today. One of the native mammals is the ubiquitous deer mouse, *Peromyscus maniculatus*. The geographic range of this species includes most of the United States, and large parts of Mexico and Canada.

Another species of the same genus, the pinyon mouse, *P. truei*, also lives on the Mesa Verde. The pinyon mouse lives mostly in southwestern North America, occurring from central Oregon and southern Wyoming to northern Oaxaca. This species generally is associated with pinyon pine trees, or with juniper trees, and where the pinyon-juniper woodland is associated with rocky ground (Hoffmeister, 1951:vii).

P. maniculatus rufinus of Mesa Verde was considered to be a mountain subspecies by Osgood (1909:73). The center of dispersion for *P. truei* was in the southwestern United States, and particularly in the Colorado Plateau area (Hoffmeister, 1951:vii). The subspecies *P. truei truei* occurs mainly in the Upper Sonoran life-zone, and according to Hoffmeister (1951:30) rarely enters the Lower Sonoran or Transition life-zones. *P. maniculatus* and *P. truei* are the most abundant of the small mammals in Mesa Verde National Park, which comprises about one-third of the Mesa Verde land mass.

Under the auspices of the Wetherill Mesa Archeological Project, the flora of the park recently was studied by Erdman (1962), and by Welsh and Erdman (1964). These studies have revealed stands of several distinct types of vegetation in the park and where each type occurs. This information greatly facilitated my study of the mammals inhabiting each type of association. The flora and fauna within the park are protected, in keeping with the policies of the National Park Service, and mammals, therefore, could be studied in a relatively undisturbed setting.

Thus, the abundance of these two species of *Peromyscus*, the botanical studies that preceded and accompanied my study, the relatively undisturbed nature of the park, and the availability of a large area in which extended studies could be carried on, all contributed to the desirability of Mesa Verde as a study area.

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My primary purpose in undertaking a study of the two species of *Peromyscus* was to analyze a number of ecological factors influencing each species—their habitat preferences, how the mice lived within their habitats, what they ate, where they nested, what preyed on them, and how one species influenced the distribution of the other. In general, my interest was in how the lives of the two species impinge upon each other in Mesa Verde.

Physiography

The Mesa Verde consists of about 200 square miles of plateau country in southwestern Colorado, just northeast of Four Corners, where Colorado, New Mexico, Arizona and Utah meet. In 1906, more than 51,000 acres of the Mesa Verde were set aside, as Mesa Verde National Park, in order to protect the cliff dwellings for which the area is famous.

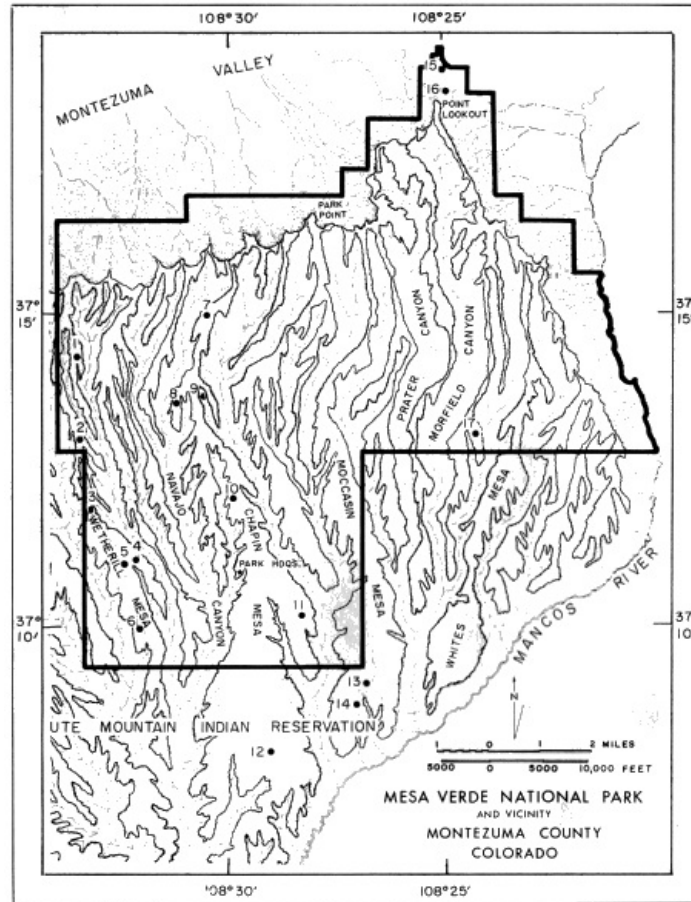
The Mesa Verde land mass is composed of cross-bedded sandstone strata laid down by Upper Cretaceous seas. These strata are known locally as the Mesaverde group, and are composed, from top to bottom, of Cliff House sandstone, the Menefee formation, the Point Lookout sandstone, the well known Mancos shale, and the Dakota sandstone, the lowest member of the Cretaceous strata. The Menefee formation is 340 to 800 feet thick, and contains carbonaceous shale and beds of coal.

There are surface deposits of Pleistocene and Recent age, with gravel and boulders of alluvial origin; colluvium composed of heterogeneous rock detritus such as talus and landslide material; and alluvium composed of soil, sand, and gravel. A layer of loess overlays the bedrock of the flat mesa tops in the Four Corners area. The earliest preserved loess is probably pre-Wisconsin, possibly Sangamon in age (Arrhenius and Bonatti, 1965:99).

The North Rim of Mesa Verde rises majestically, 1,500 feet above the surrounding Montezuma Valley. Elevations in the park range from 8,500 feet at Park Point to about 6,500 feet at the southern ends of the mesas. The Mesa Verde land mass is the remnant of a plateau that erosion has dissected into a series of long, narrow mesas, joined at their northern ends, but otherwise

separated by deep canyons. The bottoms of these canyons are from 600 to 900 feet below the tops of the mesas.

The entire Mesa Verde land mass tilts southward; Park Headquarters, in the middle of Chapin Mesa (Fig. 1), is at about the same elevation as is the entrance of the park, 20 miles by road to the north.



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Click on image to view larger sized.

FIG. 1: Map of Mesa Verde National Park and vicinity, showing major trapping localities from 1961-1964. Trapping localities are designated in the text as follows: 1) North End Wetherill Mesa 2) Rock Springs 3) Mug House 4) Bobcat Canyon Drainage 5) North of Long House 6) Juniper-Pinyon-Bitterbrush Site 7) Navajo Hill 8) West of Far View Ruins 9) South of Far View Ruins, also general location of trapping grid 10) M-2 Weather Station 11) East Loop Road Site 12) Big Sagebrush Stand, Southern end Chapin Mesa 13) Grassy Meadow, Southern end Moccasin Mesa 14) Bedrock Outcroppings, Southern end Moccasin Mesa 15) $\frac{1}{4}$ mi. SE Park Entrance 16) Meadow, 1 mi. SE Park Entrance 17) Morfield Ridge.

Vegetation and Climate

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Mesa Verde is characterized by pinyon-juniper woodlands that extend throughout much of the West and Southwest. Although the pinyon-juniper woodland dominates the mesa tops, stands of Douglas fir occur in some sheltered canyons and on north-facing slopes. Thickets of Gambel oak and Utah serviceberry cover many hillsides and form a zone of brush at higher elevations in the park. Aspens grow in small groups at the base of the Point Lookout sandstone and at a few other sheltered places where the supply of moisture suffices. Individual ponderosa pine are scattered through the park, and stands of this species occur on some slopes and in the bottoms of some sheltered canyons.

Tall sagebrush grows in deep soils of canyon bottoms, and in some burned areas, and was found to be a good indicator of prehistoric occupation sites.

The climate of Mesa Verde is semi-arid, and most months are dry and pleasant. Annual precipitation has averaged about 18.5 inches for the last 40 years. July and August are the months having the most rainfall. Snow falls intermittently in winter, and may persist all winter on north-facing slopes and in valleys. In most years, snow is melting and the kinds of animals that hibernate are emerging by the first of April.

Because of the great differences in elevation between the northern and southern ends of the mesas, differences in climate are appreciable at these locations. Winter always is the more severe on the northern end of the park, owing to persistent winds, lower temperatures, and more snow. The northern end of the park is closer to the nearby La Platta Mountains where ephemeral storms of summer originate. They reach the higher elevations of the park first, but such storms dissipate rapidly and are highly localized. The northern end of the park therefore receives much more precipitation in summer and winter than does the southern end.

The difference in precipitation and the extremes in weather between the northern and southern ends of the mesas affect the distribution of plants and animals. Species of mammals, plants, and reptiles are most numerous on the middle parts of the mesas, as also are cliff-dwellings, surface sites, and farming terraces of the prehistoric Indians.

Anderson (1961) reported on the mammals of Mesa Verde National Park, and Douglas (1966) reported on the amphibians and reptiles. In each of these reports, earlier collections are listed and earlier reports are summarized.

I lived in Mesa Verde National Park for 28 months in the period July 1961 to September 1964, while working as Biologist for the Wetherill Mesa Archeological Project, and the study here reported on is one of the faunal studies that I undertook.

ACKNOWLEDGMENTS

This study could not have been completed without the assistance and encouragement of numerous persons. I am grateful to Dr. Olwen Williams, of the University of Colorado, for suggesting this study and helping me plan the early phases of it.

Mr. Chester A. Thomas, formerly Superintendent, and Mrs. Jean Pinkley, formerly Chief of Interpretation at Mesa Verde National Park, permitted me to use the park's facilities for research, issued collecting permits, and in 1965 appointed me as a research collaborator in order that I might complete my studies.

Dr. H. Douglas Osborne, California State College, Long Beach, formerly Supervisory Archeologist of the Wetherill Mesa Project, took an active interest in my research and provided supplies, transportation and laboratory and field assistance under the auspices of the Wetherill Project. His assistance and encouragement are gratefully acknowledged. [428]

Mrs. Marilyn A. Colyer of Mancos, Colorado, ably assisted in analyzing vegetation in the trapping grid; Mr. Robert R. Patterson, the University of Kansas, assisted me in the field in October of 1963 and in August of 1965. Mr. James A. Erdman, United States Geological Survey, Denver, formerly Botanist for the Wetherill Mesa Project, and Dr. Stanley L. Welsh, Brigham Young University, identified plants for me in the field, and checked my identifications of herbarium specimens. I owe my knowledge of the flora in the park to my association with these two capable botanists.

I am grateful to the following persons for identification of invertebrates: D. Eldon Beck, fleas and ticks; Paul Winston, mites; V. Eugene Nelson, mites; William Wrenn, mites; Wayne W. Moss, mites; William B. Nutting, mites (*Desmodex*); Marilyn A. Colyer, insects; John E. Ubelaker, endoparasites; Veryl F. Keen, botflies. George A. King, Architect, of Durango, Colorado, prepared the original map for [Figure 1](#).

Mr. Harold Shepherd of Mancos, Colorado, Senior Game Biologist, Colorado Department of Fish, Game and Parks, obtained permission for me to use the department's trapping grid near Far View Ruins, and provided me with preserved specimens of mice.

Mr. Fred E. Mang Jr., Photographer, National Park Service, processed large numbers of photomicrographs of plant epidermis. Dr. Kenneth B. Armitage, The University of Kansas, offered valuable suggestions for the study of water consumption in the two species of *Peromyscus*, and permitted me to use facilities of the Zoological Research Laboratories at The University of Kansas. Dr. Richard F. Johnston, The University of Kansas, permitted me to house mice in his controlled-temperature room at the Zoological Research Laboratories. I am grateful to all of the above mentioned persons for their aid.

I acknowledge with gratitude the guidance, encouragement, and critical assistance of Professor E. Raymond Hall throughout the course of the study and preparation of the manuscript. I also extend my sincere thanks to Professors Henry S. Fitch, Robert W. Baxter, and William A. Clemens for their helpful suggestions and assistance.

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Travel funds provided by the Kansas Academy of Science permitted me to work in the park in August, 1965. The Wetherill Mesa Project was an interdisciplinary program of the National Park Service to which the National Geographic Society contributed generously. I am indebted to the Society for a major share of the support that resulted in this report. This is contribution No. 44 of

DESCRIPTIONS OF MAJOR TRAPPING LOCALITIES

Trapping was begun in September of 1961 in order to analyze the composition of rodent populations within the park. I used the method of trapping employed by Calhoun (1948) in making the Census of North American Small Mammals (N. A. C. S. M.). It consisted of two lines of traps, each 1,000 feet long having 20 trapping stations that were 50 feet apart. The lines were either parallel at a distance of 400 feet from each other, or were joined to form a line 2,000 feet long. Three snap traps were placed within a five-foot radius of each station, and were set for three consecutive nights. More than a dozen areas were selected for extensive trapping (Fig. 1). Some of these were retrapped in consecutive years in order to measure changes in populations.

One circular trapline of 159.5 feet radius was established in November 1961, and was tended for 30 consecutive days to observe the effect of removing the more dominant species (Calhoun, 1959).

Other mouse traps and rat traps were set in suitable places on talus slopes, rocky cliffs, and in cliff dwellings. Most of these traps were operated for three consecutive nights. [429]

In order to test hypotheses concerning habitat preferences of each of the species of *Peromyscus*, several previously untrapped areas that appeared to be ideal habitat for one species, but not for the other, were selected for sampling. In the summers of 1963 and 1964 snap traps were set along an arbitrary line through each of these areas. Traps were placed in pairs; each pair was 20 feet from the adjacent pairs.

A mixture of equal parts of peanut butter, bacon grease, raisins, roman meal and rolled oats was used as bait. Rolled oats or coarsely ground scratch feed was used in areas where insects removed the mixture from the traps.

Rodents trapped by me were variously prepared as study skins with skulls, as flat skins with skulls, as skeletons, as skulls only, or as alcoholics. Representative specimens were deposited in The University of Kansas Museum of Natural History. In the course of my study, traps were set in the following areas:

Morfield Ridge

In July 1959 a fire destroyed more than 2,000 acres of pinyon-juniper forest (*Pinus edulis* and *Juniperus osteosperma*) in the eastern part of the park. The burned area extends from Morfield Canyon to Waters Canyon, encompassing several canyons, Whites Mesa, and a ridge between Morfield Canyon and Waters Canyon that is known locally as Morfield Ridge (Fig. 1). Beginning on September 4, 1961, three pairs of traplines were run on this ridge at elevations of 7,300 to 7,600 feet.

Vegetation in the trapping area consisted of dense growths of grasses and herbaceous plants, which had covered the ground with seeds. In this and in the following accounts, the generic and specific names of plants are those used by Welsh and Erdman (1964). The following plants were identified from the trapping area on Morfield Ridge:

Lithospermum ruderale
Chenopodium
pratericola
Achillea millefolium
Artemisia tridentata
Aster bigelovii
Chrysothamnus
depressus
Chrysothamnus
nauseosus
Helianthus annuus
Helianthella sp.
Lactuca sp.
Lepidium montanum
Quercus gambelii
Agropyron smithii
Bromus inermis
Bromus japonicus
Oryzopsis hymenoides
Calochortus nuttallii
Linum perenne
Sphaeralcea coccinea
Polygonum
sawatchense
Solidago petradoria

Wyethia arizonica
Nicotiana attenuata
Fendlera rupicola
Penstemon linarioides

Only *Peromyscus maniculatus*, *Perognathus apache* and *Reithrodontomys megalotis* were taken in this area (Table 1). Many birds inhabit this area, including hawks, ravens, towhees, jays, juncos, woodpeckers, doves, sparrows and titmice. Rabbits, badgers and mule deer also live in the area. Only two reptiles, a horned lizard and a collared lizard, were seen.

South of Far View Ruins

Two parallel trap lines were established on October 4, 1961, in the area immediately south of Far View Ruins (Fig. 1). In altitude, latitude and geographical configuration the area is similar to that trapped in the Morfield burn, but the Chapin Mesa site had not been burned.

Canopy vegetation is pinyon-juniper forest. A dense understory was made up of *Amelanchier utahensis* (serviceberry), *Cercocarpus montanus* (mountain mahogany), *Purshia tridentata* (bitterbrush), and *Quercus gambelii* (Gambel oak). The ground cover consisted of small clumps of *Poa fendleriana* (muttongrass), and *Koeleria cristata* (Junegrass), intermingled with growths of one or more of the following:

[430]

Artemisia nova
Solidago petradoria
Sitanion hystrix
Astragalus scopulorum
Lupinus caudatus
Eriogonum alatum
Penstemon linarioides
Eriogonum racemosum
Eriogonum umbellatum
Polygonum
sawatchense
Amelanchier utahensis
Purshia tridentata
Comandra umbellata

Seeds of *Cercocarpus montanus* covered the ground under the bushes in much of the trapping area, and large numbers of juniper berries were on the ground beneath the trees. Individuals of *P. truei* and *P. maniculatus* were caught in this area (Table 1).

Several deer, rabbits, one coyote, and numerous birds were seen in the area. No reptiles were noticed, but they were not searched for. A mountain lion was seen in this general area two weeks after trapping was completed.

West of Far View Ruins

Three pairs of traplines were run west of Far View Ruins in an area comparable in vegetation, altitude, general topography, and configuration to the area previously described. The elevations concerned are typical of the middle parts of mesas throughout the park. This area differs from the trapping area south of Far View Ruins and the one on Morfield Ridge in being wider and on the western side of the mesa.

The woody understory was sparse in most places, and where present was composed of *Cercocarpus montanus*, *Purshia tridentata*, *Fendlera rupicola* (fendlerbush), *Amelanchier utahensis*, *Quercus gambelii*, and *Artemisia tridentata* (sagebrush). The herbaceous ground cover was dominated by *Solidago petradoria* (rock goldenrod), and grasses—including *Poa fendleriana*, *Oryzopsis hymenoides*, and *Sitanion hystrix*. Other herbaceous species were as follows:

Echinocercus coccineus
Achillea millefolium
Aster bigelovii
Wyethia arizonica
Lepidium montanum
Lupinus caudatus
Yucca baccata
Linum perenne
Eriogonum racemosum
Eriogonum umbellatum
Polygonum
sawatchense
Delphinium nelsonii
Penstemon linarioides

Fresh diggings of pocket gophers were observed along the trap lines. Badger tunnels were noted in numerous surface mounds that are remnants of prehistoric Indian dwellings, but no

badgers were seen. Numerous deer and several rabbits were present. Juncos, two species of jays, and woodpeckers were seen daily. No reptiles were observed.

Both *Peromyscus maniculatus* and *P. truei* were caught in this area ([Table 1](#)).

Big Sagebrush Stand, South Chapin Mesa

A circular trapline, 1,000 feet in circumference, was established on November 16, 1961, in a stand of big sagebrush, and was operated for 30 consecutive nights.

The vegetation of the trapping area was predominantly *Artemisia tridentata* (big sagebrush), interspersed with a few scattered seedlings of pinyon and juniper. This stand was burned in 1858 (tree-ring date by David Smith) and some charred juniper snags still stood. The deep sandy soil also supported a variety of grasses and a few other small plants. The following species were common in this area:

Bromus inermis
Oryzopsis hymenoides
Poa fendleriana
Sitanion hystrix
Solidago petradoria
Orthocarpus purpureo-
albus

The 15 to 20 acres of sagebrush were surrounded by pinyon-juniper forest. The trapping station closest to the forest was approximately 100 feet from the edge of the woodland. More *P. truei* than *P. maniculatus* were caught here ([Table 1](#)). [431]

East Loop Road, Chapin Mesa

The trapping area lies north of Cliff Palace, eastward of the loop road, at elevations of 6,875 to 6,925 feet. Two pairs of traplines were run from January 9, 1962, to January 12, 1962, and from February 13 to 15, 1962.

Vegetation was pinyon-juniper woodland with an understory of mixed shrubs. One to four inches of old snow covered the ground during most of the trapping period, but the ground beneath trees and shrubs was generally clear, providing suitable location for traps.

Numerous juncos and jays were seen in this area; deer and rabbits also were present.

Individuals of *P. truei* and of *P. maniculatus* were taken ([Table 1](#)).

Navajo Hill, Chapin Mesa

Navajo Hill is the highest point (8,140 feet) on Chapin Mesa. The top of the hill is rounded and the sides slope gently southward and westward until they level out into mesa-top terrain at elevations of 7,950 to 8,000 feet. The northern and eastern slopes of the hill drop abruptly into the respective canyon slopes of the East Fork of Navajo Canyon and the West Fork of Little Soda Canyon. The gradually tapering southwestern slope of the hill extends southward for one mile and is bisected by the main highway, which runs the length of the mesa top.

Heavy growths of grasses cover the ground; *Amelanchier utahensis*, *Cercocarpus montanus*, and *Fendlera rupicola* comprise the only tall vegetation. Trees are lacking on this part of the mesa, except on the canyon slopes, where *Quercus gambelii* forms an almost impenetrable barrier.

Four traplines were run from May 4-7, 1962, and from May 9-12, 1962. *P. maniculatus* was taken but *P. truei* was not present here in 1962, or in 1964 or 1965 when additional trapping was performed as a check on populations ([Table 1](#)).

Other species trapped include the montane vole, long-tailed vole, and Colorado chipmunk. Mule deer and coyotes were abundant in the area. Striped whipsnakes, rattlesnakes and gopher snakes are known to occur in this vicinity (Douglas, 1966).

North End Wetherill Mesa

In 1934 a widespread fire deforested large areas of pinyon-juniper woodland on the northern end of Wetherill Mesa. The current vegetation consists of shrubs with a dense ground cover of grasses. Many dead trees still remain on the ground, providing additional cover for wildlife.

The trapping area was a wide, grassy meadow, three and a half miles south of the northern end of the mesa. A pronounced drainage runs through this area and empties into Rock Canyon. Four traplines were run parallel to each other. The first lines were established on May 23, 1962, and the second pair on June 3, 1962.

Another pair of lines was run in a grassy area two miles south of the northern escarpment of

Wetherill Mesa. This area was one and a half miles north of the above-mentioned area. These lines ran along the eastern side of a drainage leading into Long Canyon. The vegetation was essentially the same in both areas, and they will be considered together.

The vegetation was composed predominantly of grasses. *Quercus gambelii* and *Amelanchier utahensis* were the codominant shrubs. *Artemisia tridentata* and *Chrysothamnus depressus* (dwarf rabbitbrush), were common. Plants in the two areas included the following:

- Juniperus scopulorum*
- Symphoricarpos oreophilus*
- Artemisia ludoviciana*
- Sitanion hystrix*
- Stipa comata*
- Astragalus scopulorum*
- Artemisia tridentata*
- Chrysothamnus depressus*
- Helianthus annuus*
- Tetradymia canescens*
- Quercus gambelii*
- Bromus tectorum*
- Poa fendleriana*
- Lupinus caudatus*
- Yucca baccata*
- Sphaeralcea coccinea*
- Eriogonum umbellatum*
- Amelanchier utahensis*
- Fendlera rupicola*
- Lomatium pinatasectum*

[432]

Individuals of *P. maniculatus* and of *Reithrodontomys megalotis* were caught ([Table 1](#)).

TABLE 1—Major Trapping Localities in Mesa Verde National Park, Colorado. Vegetational Key as Follows: 1) Pinyon-Juniper-Muttongrass 2) Pinyon-Juniper-Mixed Shrubs 3) Juniper-Pinyon-Bitterbrush 4) Juniper-Pinyon-Mountain Mahogany 5) Grassland with Mixed Shrubs 6) Big Sagebrush 7) Pinyon-Juniper-Big Sagebrush 8) Grassland.

Locality	Date	No. trap nights	<i>P. truei</i>	<i>P. man.</i>	Type of vegetation
Morfield Ridge	Sept. 1961	1080	0	83	5
	Oct. 1963	360	0	13	5
S. of Far View	Oct. 1961	360	10	13	2
W. of Far View	Oct. 1961	1080	22	17	2
South Chapin Mesa	Nov.-Dec. 1961	3600	16	9	6
East Loop Road	Jan. 1962	720	6	2	2
Navajo Hill	May 1962	720	0	18	5
	Aug. 1964	20	0	2	5
	Aug. 1965	50	0	8	5
N. Wetherill Mesa	May-June 1962	1080	0	57	5
Bobcat Canyon Drainage	June 1962	360	0	0	6
N. of Long House	June 1962	1080	3	4	1
Mug House—Rock Springs	Aug. 1962	720	8	14	4
	Aug. 1963	720	9	7	4
S. Wetherill Mesa	Aug. 1962	720	0	5	3
1 mi. SE Park Entr.	June 1963	50	0	16	7
1/4 mi. SE Park Entr.	July 1963	100	0	7	8
M-2 Weather Sta.	May 1964	25	2	0	1
8 mi. S North Rim	Aug. 1964	100	0	3	8
Moccasin Mesa					
10 mi. S North Rim	Aug. 1964	25	2	0	2
Moccasin Mesa					

Bobcat Canyon Drainage

[433]

Bobcat Canyon, a large secondary canyon on the eastern side of Wetherill Mesa, is a major

drainage for much of the mesa at its widest part. The mesa top drains southeast into a pour-off at the head of Bobcat Canyon. A stand of big sagebrush, *Artemisia tridentata*, grows in the sandy soil of the drainage, and extends northwest for several hundred yards from the pour-off. The sagebrush invades the pinyon-juniper forest at the periphery of the area.

Two traplines were set in the drainage, with trapping stations at intervals of 25 feet. The lines traversed elevations of 7,000 to 7,100 feet, and were run from June 26 to 29, 1962.

Grasses are the most abundant plants in the ground cover. *Artemisia dracunculus* is common in the drainage, and *A. nova* grows around the periphery of the drainage. Other species occurring in this stand include:

Aster bigelovii
Tetradymia canescens
Tragopogon pratensis
Bromus tectorum
Poa fendleriana
Sitanion hystrix
Stipa comata
Lupinus argenteus
Calochortus gunnisonii
Sphaeralcea coccinea
Phlox hoodii
Eriogonum umbellatum
Peraphyllum
ramosissimum
Purshia tridentata
Penstemon linarioides

No mice were caught in three nights of trapping (360 trap nights), and only one mammal, a *Spermophilus variegatus*, was seen.

North of Long House, Wetherill Mesa

Pinyon-juniper forest with a dominant ground cover of *Poa fendleriana* was described by Erdman (1962) as one of the three distinct types of pinyon-juniper woodland on Wetherill Mesa. Such a woodland occurs adjacent to the Bobcat Canyon drainage, and is continuous across the Mesa from above Long House to the area near Step House. Plants in the ground cover include:

Cryptantha bakeri
Opuntia rhodantha
Chrysothamnus
depressus
Solidago petradoria
Koeleria cristata
Lupinus argenteus
Yucca baccata
Phlox hoodii
Eriogonum racemosum
Eriogonum umbellatum
Cordylanthus wrightii
Pedicularis
centranthera
Penstemon linarioides
Penstemon strictus

Two traplines were run from July 9 to 12, 1962, in the area south of the Bobcat Canyon drainage at an elevation of 7,100 feet. No mice were caught in three nights of trapping. Four additional lines were established on July 24, 1962, and were run for three nights, in the area north of the Bobcat Canyon drainage at elevations of 7,100 to 7,150 feet.

P. maniculatus and *P. truei* were caught here (Table 1). This vegetational association may have few rodents because there is a shortage of places where they can hide. Although *Poa fendleriana* is abundant, the lack of shrubs leaves little protective cover for mammals.

Mug House—Rock Springs

A juniper-pinyon-mountain mahogany association extends from the area of Mug House to Rock Springs, on Wetherill Mesa. On that part of the ridge just above Mug House, the understory is predominantly *Cercocarpus montanus* (mountain mahogany), but northward toward Rock Springs the understory changes to *Fendlera rupicola*, *Amelanchier utahensis*, *Cercocarpus*, and *Purshia tridentata*. The ground cover is essentially the same as that in the pinyon-juniper-muttongrass association described previously.

Four traplines were run from July 31 to August 2, 1962, and from August 13 to 15, 1963. These lines ran northwest-southeast, starting 1,000 feet southeast of, and ending 3,000 feet

northwest of, Mug House. The lines traversed elevations of 7,225 to 7,325 feet. Individuals of *P. maniculatus* and *P. truei* were caught here ([Table 1](#)).

Deer and rabbits inhabit the trapping area. Bobcats have been seen, by myself and by others, near Rock Springs. Lizards of the genera *Cnemidophorus* and *Sceloporus*, as well as gopher snakes were seen in this area.

Juniper–Pinyon–Bitterbrush

Three pairs of traplines were run from August 7-9, 1962, in a juniper-pinyon-bitterbrush stand on the southern end of Wetherill Mesa, starting 200 yards southwest of Double House ([Fig. 1](#)).

The forest on the southern end of the mesas consists of widely-spaced trees, which reflect the low amounts of precipitation at these lower elevations. Juniper trees are more numerous than pinyons, and both species are stunted in comparison to trees farther north on the mesa. *Purshia tridentata* (bitterbrush) is the understory codominant. *Artemisia nova* (black sagebrush) is present and grasses are the most abundant plants in the ground cover. Herbaceous species in the sparse ground cover include the following:

Opuntia polyacantha
Solidago petradoria
Lathyrus pauciflorus
Penstemon linarioides
Lupinus caudatus
Yucca baccata
Phlox hoodii

Only *P. maniculatus* was caught in this stand; all mice were caught in the first night of trapping.

Five areas were selected for trapping in the summers of 1963 or 1964, in order to test hypotheses concerning habitat preferences of each of the species of *Peromyscus*. Four of these areas appeared to be ideal habitat for one species, but not for the other. The fifth area was expected to produce both species of *Peromyscus*. Each of these areas is discussed below.

One Mile Southeast of Park's Entrance

A small stand of *Artemisia tridentata*, occurring one mile southeast of the entrance to the park, is bordered to the north and northeast by a grassy meadow, discussed in the following account. Kangaroo rats have been reported in this general area, and I wanted to determine whether *P. maniculatus* and *Dipodomys* occurred together there. Fifty trap nights in this sagebrush, on June 20, 1963, yielded only *P. maniculatus* ([Table 1](#)).

Meadow, One-Quarter Mile Southeast of Park's Entrance

A grassy meadow lies just to the east of the highway into the park, one-quarter of a mile southeast of the park's entrance. On July 30, 1963, one hundred traps were placed in two lines through the meadow, and were run for one night. Only individuals of *P. maniculatus* were caught ([Table 1](#)).

M-2 Weather Station, Chapin Mesa

The M-2 weather station of the Wetherill Mesa Archeological Project was on the middle of Chapin Mesa at an elevation of 7,200 feet. This site was in an old C. C. C. area, about one mile north of the park's U. S. Weather Bureau station. The vegetation surrounding the M-2 site was a pinyon-juniper-muttongrass association. It was thought that both species of *Peromyscus* would occur in this habitat.

On May 10, 1964, 25 traps were placed in this area and were run for one night. Only individuals of *P. truei* were caught ([Table 1](#)).

Grassy Meadow, Southern End Moccasin Mesa

This large meadow is located eight miles south of the northern rim of Moccasin Mesa. The meadow lies in a broad, shallow depression that forms the head of a large drainage ([Fig. 1](#)). To the south of the meadow the drainage deepens, then reaches bedrock as it approaches the pour-off.

On August 23, 1964, one hundred traps were set in pairs in a line through the middle of the meadow; adjacent pairs were 20 feet from each other. Only individuals of *P. maniculatus* were caught ([Table 1](#)).

Grasses are dominant in the ground cover, and *Sphaeralcea coccinea* (globe mallow) is codominant. The abundance of globe mallow is due to the present and past disturbance of this meadow by a colony of pocket gophers. Trees are absent in the meadow. Species of plants include the following:

Opuntia polyacantha
Chenopodium sp.
Artemisia ludoviciana
Chrysothamnus
nauseosus
Koeleria cristata
Poa pratensis
Lupinus ammophilus
Calochortus gunnisonii
Erigeron speciosus
Gutierrezia sarothrae
Tetradymia canescens
Tragopogon pratensis
Bromus tectorum
Sphaeralcea coccinea
Eriogonum racemosum
Polygonum
sawatchense
Comandra umbellata
Penstemon strictus

Bedrock Outcroppings, Southern End Moccasin Mesa

Two miles south of the preceding site, much of the mesa is a wide expanse of exposed bedrock, which extends approximately 100 feet inward from the edges of the mesa. Pinyon-juniper-mixed shrub woodland adjoins the bedrock.

On August 23, 1964, 25 traps were placed along the bedrock, near the edge of the forest. Only two mice, both *P. truei*, were caught. ([Table 1](#)).

HOME RANGE

In order to learn how extensively mice of different ages travel within their habitats, whether their home ranges overlap, and how many animals live within an area, it was necessary to determine home ranges for as many mice, of each species, as possible (Hayne, 1949; Mohr and Stumpf, 1966; Sanderson, 1966).

In 1961, the Colorado Department of Fish, Game and Parks established a permanent trapping grid in the area south of Far View Ruins ([Fig. 1](#)). The grid was constructed and used by Mr. Harold R. Shepherd, Senior Game Biologist, and his assistant, in the summers of 1961 and 1962, in a study concerning the effect of rodents on browse plants used by deer. The Department of Fish, Game and Parks allowed me to use the grid during 1963 and 1964, and also permitted me to use its Sherman live traps.

The grid is divided into 16 units, each with 28 stations ([Fig. 2](#)). Traps at four stations (1a, 1b, 1c, 1d) are operated in each unit at the same time, with two traps being set at each station. The traps are moved each day in a counter-clockwise rotation to the next block of four stations (2a, 2b, 2c, 2d) within each unit. The stations are arranged so that on any given night, traps in adjacent units are separated by at least 200 feet. As a result, animals are less inclined to become addicted to traps, for even within one unit they must move at least 50 feet to be caught on consecutive nights.

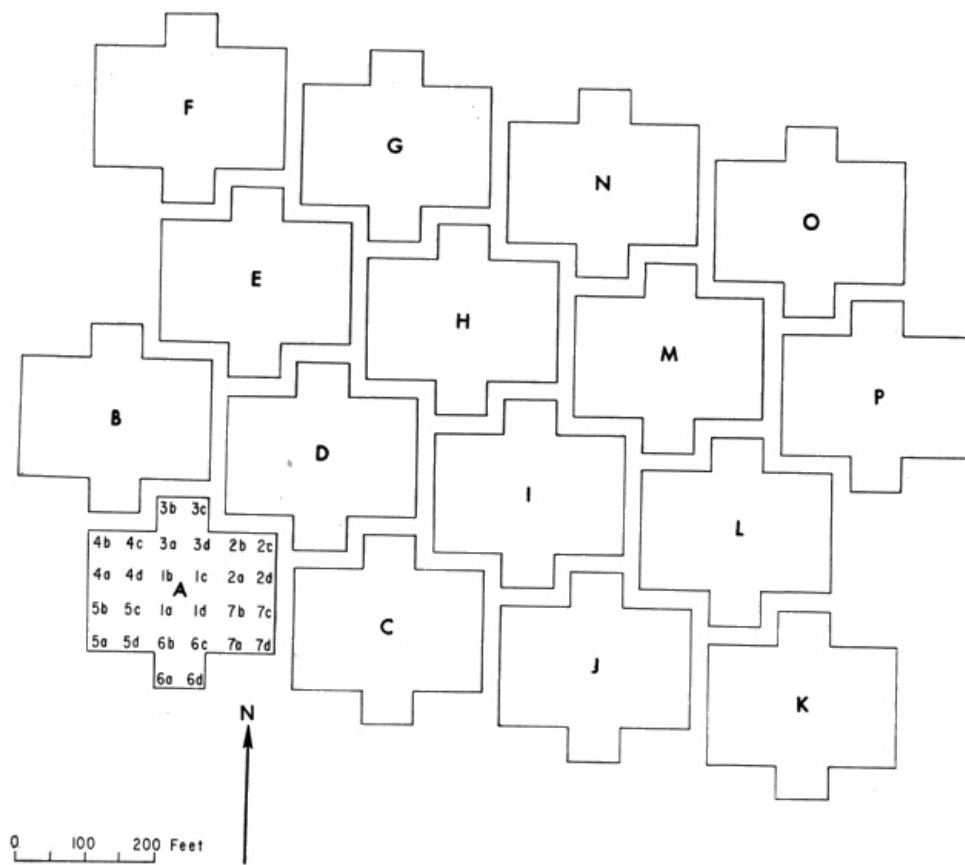


FIG. 2: Diagram of trapping grid for small mammals, showing units of subdivision. Trapping stations were numbered in each unit as shown in unit A.

Traps were carefully shaded and a ball of kapok was placed in each trap to provide protection against the killing temperatures that can develop inside. In spite of these precautions, mice occasionally succumbed from heat or cold. The traps were baited with coarsely-ground scratch feed.

Mammals trapped in the grid were inspected for molt, sexual maturity, larvae of botflies, anomalies, and other pertinent data. Each animal was marked by toe- and ear-clipping and then released. Four toes were used on each front foot, and all five toes were used on each hind foot; two toes were clipped on the right front foot to signify number nine. The tip of the left ear was clipped to signify number 100, and the tip of the right ear was clipped to signify 200. If 300 or more animals had been captured, the tip of the tail would have been clipped to represent number 300. A maximum of 799 animals could have been marked with this system, which was used by Shepherd. I continued with it, starting my listings with number one.

Only two mice were caught that had been marked in the previous season by Shepherd.

Live traps were operated in the trapping grid from July 9 through October 25, 1963, and from June 25 through August 21, 1964. Traps were rotated through all stations five different times (35 days) in 1963, and twice (14 days) in 1964. Approximately three man hours were required each day to service and rotate the traps to the next group of stations. By the autumn of 1964, a total of 282 mice had been captured, marked and released; these were handled 817 times. In 1963, 235 mice were caught for an average of 20 captures per day; in 1964, 47 mice were caught for an average of 9 captures per day.

[437]

Calculations of Home Range

A diagrammatic map of the trapping grid was drawn to scale with one centimeter equal to 100 linear feet. Trapping stations were numbered on the diagram to correspond with stations in the field. An outline of this drawing also was prepared to the same scale, but station numbers were omitted. Mimeographed copies of such a form could be placed over the diagrammatic map and marks made at each station where an animal was caught. A separate form was kept for each animal that was caught four or more times.

In calculating home range, it was assumed that animals would venture half-way from the peripheral stations, at which they were caught, to the next station outside the range. A circle having a scaled radius of 25 feet (half the distance between stations) was inscribed around each station on the periphery of the home range by means of a drafting compass. The estimated range for each animal was then outlined on the form by connecting peripheries of the circles. Both the inclusive boundary-strip method and the exclusive boundary-strip method (Stickel, 1954:3) were used to estimate the ranges. The area encompassed within the home ranges was measured by planimetry of the outline of the drawing. At least two such readings were taken for each home range; then these planimeter values were converted into square feet.

The customary practice in delimiting home ranges on a scaled map of a grid is to inscribe squares around the peripheral stations at which the animal was trapped, and then to connect the exterior corners of these squares (Stickel, 1954:3). If the distance between stations was 50 feet, such squares would have sides 50 feet long. An easier method is to inscribe a circle having a scaled radius of 25 feet around the peripheral stations by means of a drafting compass. To my knowledge this method has not been used previously and consequently has not been tested by experiments with artificial populations.

To test the accuracy of this method, a "grid of traps" was constructed by using 8 1/2 by 11 inch sheets of graph paper with heavy lines each centimeter. The intersects of the heavier lines were considered as trap stations. A "home range" of circular shape, 200 feet (4 cm.) in diameter, with an area of 31,146 square feet (0.71 acre), was cut from a sheet of transparent plastic. Another "home range" was made in an oblong shape with rounded ends. This range measured 2 by 65 centimeters (100 by 325 feet) and had an area of 32,102 square feet (0.74 acre). Each plastic range was tossed at random on sheets of graph paper for fifty trials each. The range was outlined on the graph paper, then circles having a scaled radius of 25 feet were inscribed around each "trap station" within the range. The peripheries of the inscribed circles were then connected and the estimated home range was delimited by the exclusive boundary-strip method. The estimated range was measured by planimetry, and the data were compared with the known home range (Table 2).

It was found that when calculated by the exclusive boundary-strip method, the circular home range was overestimated by 2.22 per cent. The oblong home range was overestimated by only 1.50 per cent. Stickel (1954:4) has shown that the exclusive boundary-strip method is the most accurate of several methods of estimating home ranges, and in her experiments this method gave an overestimate of two per cent of the known range. Thus, my method of encircling the peripheral stations yields results that are, on the average, as accurate as the more involved method of inscribing squares about the trap stations, and saves a great deal of time as well. My method probably yields better accuracy; a perfect circle is easily drawn by means of a compass, whereas a perfect square is more difficult to construct without a template.

[438]

It is generally understood that the estimated home range of an animal tends to increase in size with each additional capture; this increase is rapid at first, then slows. Theoretically, the more often an animal is captured, the more reliable is the estimate of its home range. Most animals, however, rarely are captured more than a few times. The investigator must decide how many captures are necessary before the data seem to be valid for estimating home ranges.

An animal must be trapped at a minimum of three stations before its home range can be estimated, and even then the area enclosed in the triangle will be much less than the actual home range. Some investigators have plotted home ranges from only three captures (Redman and Selander, 1958:391), whereas others consider that far more captures are needed to make a valid estimate of range (Stickel, 1954:5).

TABLE 2—Summary of Data from Experiments in Calculating Home Ranges for an Artificial Population.

Series	No. of trials	Trap spacing in ft.	Shape of range	Actual area of range in ft.	Calculated area of range by exclusive boundary-strip method	± S. D.
A	50	50	Circular	31,146	31,782	9,600
B	50	50	Oblong	32,102	32,583	9,466

In my study, 161 individuals of *P. truei* were caught from one to 13 times each. The estimated home ranges of 10 individuals of *P. truei*, each caught from eight to 13 times, were plotted and measured after each capture from the fourth to the last. The percentage of the total estimated range represented by the fourth through tenth captures was, respectively, 52, 65, 73, 85, 88, 93, and 96 per cent.

Ninety-seven individuals of *P. maniculatus* were caught from one to 10 times each. For five individuals that were each caught from seven to 10 times, the percentage of total estimated range represented by the fourth through seventh captures was, respectively, 59, 69, 85, and 93 per cent.

The above percentages do not imply that the true home range of individuals of these species can be reliably estimated after seven or 10 captures; the average percentages do, however, indicate a fairly rapid increase in known size of home ranges between the fourth and tenth captures. The estimated home ranges of *P. maniculatus* tended to reach maximum known size at about seven captures, whereas the estimated ranges of *P. truei* tended to attain maximum known size after nine or more captures. The controversy over the number of captures of an individual animal required for a reliable estimate of its home range was not settled by my data.

[439]

I initially decided to estimate home ranges for animals caught five or more times and at three

or more stations. Of the 282 animals caught and marked, only 48 were caught five or more times. Because of the small numbers of *P. maniculatus* that were caught five or more times, I wanted to determine whether mice caught four times had an estimated range that was significantly smaller than that of mice caught five times. Eight individuals of *P. maniculatus* were caught four times each, and it seemed desirable to use the data from these mice if such use was justified. Data from the 48 mice caught five or more times were used for this testing.

By means of a T-test, I compared the estimated ranges of those 48 mice following their fourth capture with ranges estimated after the fifth capture. The results did not demonstrate significant differences between the two sets of estimates; therefore, I decided to use data resulting from four or more captures, and at three or more stations.

[Table 3](#) shows estimations of the home ranges of males and females of each species of *Peromyscus*. When the inclusive boundary-strip method is used, the area encompassed by the range tends to be larger than the area of the same range when estimated by the exclusive boundary-strip method. Stickel (1954:4) has shown that the inclusive boundary-strip method overestimates the home range by about 17 percent.

Analysis of Home Range by Inclusive Boundary-Strip Method

When all age groups were considered, the ranges of 16 males of *P. truei* averaged 20,000 to 80,000 square feet (ave. 47,333; S. D. 19,286). The sizes of home ranges were not significantly different ($P > 0.05$) between adult and subadult (including juveniles and young) males.

All females of *P. truei* (22) had ranges encompassing 16,666 to 83,333 square feet (ave. 40,666; S. D. 17,566). Sizes of home ranges between adult and non-adult females did not differ significantly. The mean range of adult males of *P. truei* did not differ from that of adult females ($P > 0.05$).

Fifteen males of *P. maniculatus* had ranges of 16,666 to 66,666 square feet (ave. 34,222; S. D. 16,000); six adult males had ranges of 33,333 to 53,333 square feet (ave. 38,666). Sizes of home ranges of adult and non-adult males of this species did not differ significantly.

Five females of *P. maniculatus* had ranges of 33,333 to 76,666 square feet (ave. 51,333; S. D. 15,913); of these, four adults had ranges of 33,333 to 53,333 square feet (ave. 45,000). Sizes of home ranges of adult males of this species did not differ ($P > 0.05$) from those of adult females.

The ranges of adult males of *P. truei* were compared with ranges of adult male of *P. maniculatus*; likewise the ranges of adult females of each species were compared. In each case no difference was demonstrable in sizes of ranges between the species.

The largest home range of any *P. truei* was that of animal number 18, a young male with an estimated home range of 133,333 square feet. This animal was caught only five times, and his home range appeared unusually large in relation to that of other young males of this species; hence some of the widely-spaced sites of capture probably represent excursions from the animal's center of activity, rather than the true periphery of his range. These data were, therefore, not used in further computations. Stickel (1954:13) pointed out the advisability of removing such records from data to be used in calculations of home range.

[440]

Number eight had the largest home range of any female of *P. truei*; she was captured ten times, and had a range of 83,333 square feet. The vegetation within her range was pinyon-juniper woodland with understories of *Amelanchier*, *Artemisia nova* and *Purshia*. Most of her home range was in the western half of unit H, but extended into parts of units D, I, G and N.

The largest home range for adult males of either species was number three of *P. truei*; he had a range of 80,000 square feet. The largest range for an adult of *P. maniculatus* was 66,666 square feet ([Table 3](#)).

Analysis of Home Range by Exclusive Boundary-Strip Method

Stickel (1954:4) has shown that under theoretical conditions the exclusive boundary-strip method is the most accurate of several methods of estimating home range. This method overestimates the known range by only two percent.

[Table 3](#) shows a comparison of home range calculations obtained for each species, when calculated by inclusive and exclusive boundary-strip methods.

The data for males and for females of each species were compared in the same manner as in the inclusive boundary-strip method. The ranges of 16 male individuals of *P. truei* encompassed 14,000 to 56,666 square feet (ave. 34,333; S. D. 13,266); of these, the ranges of 10 adult males were from 23,333 to 53,333 square feet (ave. 39,733). Twenty-two females of this species had ranges of 13,333 to 50,000 square feet (ave. 27,199; S. D. 8,820). Eighteen adult females had the same extremes, but the average size of range, 28,000 square feet, was larger. Sizes of home ranges of males and females did not differ significantly.

The ranges of fifteen males of *P. maniculatus* encompassed 13,333 to 46,666 square feet (ave. 26,666; S. D. 10,180). Of these, six adults had the same extremes in range, but an average size of

31,440 square feet.

The ranges of five females of *P. maniculatus* varied from 28,000 to 53,333 square feet (ave. 37,199; S. D. 10,140). All but one of these females were adults. The sizes of home ranges of males and females did not differ significantly. No differences were found when ranges of adult males, or adult females, of both species were compared.

Adjusted Length of Home Range

The adjusted length of the range also can be used as an expression of home range. In this method, one-half the distance to the next trapping station is added to each end of the line drawn between stations at either end of the long axis of the range (Stickel, 1954:2).

The average length of home range for 15 males of *P. truei* was 363 feet (S. D. 105 ft.); for 22 females of this species 326 feet (S. D. 94 ft.); for 14 males of *P. maniculatus* 286 feet long (S. D. 94 ft.); and for four females of this species 347 feet (S. D. 83 ft.). The mean lengths of range of males and females differed significantly in *P. maniculatus*, but not in *P. truei*. However, no difference was demonstrable in mean sizes of ranges between males, or between females, of the two species. [441]

Distance Between Captures

The distance between captures has been used by several investigators as an index of the extent of home range. More short than long distances tend to be recorded when traps are visited at random, and when inner traps of the range are more strongly favored (Stickel, 1954:10).

TABLE 3—Summary of Data for Estimated Home Ranges of Mice from a Wild Population.

Type of Estimate	Species	Sex	No.	Estimated home range in sq. ft.	± S. D.
Inclusive boundary-strip	<i>P. truei</i>	M	16	47,333	19,286
	" "	F	22	40,666	17,566
	<i>P. maniculatus</i>	M	15	34,222	16,000
	" "	F	5	51,333	15,913
Exclusive boundary-strip	<i>P. truei</i>	M	16	34,333	13,266
	" "	F	22	27,199	8,820
	<i>P. maniculatus</i>	M	15	26,666	10,180
	" "	F	5	37,199	10,140
Adjusted Length	<i>P. truei</i>	M	16	363	105
	" "	F	22	326	94
	<i>P. maniculatus</i>	M	14	286	94
	" "	F	4	347	83

It is important to know approximately how far mice travel in one night. The distances traveled between captures on successive nights were calculated for all mice. Even animals caught most frequently usually were caught only once or twice on successive nights. Data from animals caught less than four times, and hence not usable for calculations of home range, could be used in calculating the distance between captures on successive nights. Thus the data were sampled in a more or less random manner for each species.

The mean distance traveled between captures on successive nights was determined for adult and non-adult animals (juvenile, young and subadult) of both sexes. Adult males of *P. maniculatus* traveled an average of 151.66 feet (n = 24); young males of this species traveled an average of 134.28 feet (n = 7). Adult females of *P. maniculatus* traveled 170.00 feet (n = 4); no data were available for young females.

Adult males of *P. truei* traveled an average of 169.47 feet (n = 38); and young males traveled 159.44 feet (n = 18). Adult females of this species traveled 155.71 feet between captures (n = 35), while young females traveled 140.66 feet (n = 15). [442]

The means were tested for differences in the distances traveled between young and adult males and between young and adult females of each species, as well as between males and between females of opposite species. In all cases, there were no demonstrable differences in the distance traveled between captures.

One of the more striking journeys between captures was that of number 59, a juvenal male of *P. maniculatus*, which traveled 1,070 feet between captures on July 16 and 17, 1963. The route between the two capture sites was over the most rugged part of the trapping grid. This datum was excluded from further calculations. The only other animal that approached this distance was

a young female *P. truei* that traveled 750 feet between captures.

[Figure 3](#) shows the distribution of distances traveled by mice of each species between successive captures. Since there were no demonstrable differences between age groups or sexes in the distances traveled, these data represent a composite of the ages and sexes of each species. They show 101-125 feet to be the most prevalent of the distances traveled by both species, and 51-75 feet to have a higher percentage of occurrence among *P. maniculatus*. These distances indicate that if an animal was trapped on successive nights, it tended to be trapped within the same unit of the grid. It would have been necessary for an animal to travel 200 feet or more in order to be caught in traps in an adjoining unit of the grid.

The distance between captures also was calculated by the more customary method of averaging the distances between sites of capture, regardless of the time intervening between captures.

Only data from mice caught four or more times were used because these individuals probably had home ranges in the study area, whereas those caught fewer than four times may have been migrants.

The mean distance between captures ($n = 95$) for 15 males and five females of *P. maniculatus* was 161 feet. Sixteen males and 22 females of *P. truei* traveled an average of 143 feet between captures ($n = 248$). For purposes of comparison, these average distances between captures could be considered as radii of the estimated home ranges. When the range for each species is calculated by considering average distance between captures as the radius of the estimated home range, the average range of *P. truei* is 64,210 square feet, and that of *P. maniculatus* is 81,392 square feet. Both of these estimations are larger than those made by the inclusive and exclusive boundary-strip method ([Table 3](#)), and smaller than those calculated by using adjusted length of range as the radius.

Since it is known that ranges of some animals tend to be longer than wide (Mohr and Stumpf, 1966), calculations of estimated range based on average distance between captures probably are more accurate than those based on adjusted length of range.

Usually the estimated home ranges were not symmetrical, and did not resemble oblongs or circles in outline. Rather, the ranges tended to follow parts of vegetational zones. Since trapping grids are geometrical in form, there is a tendency among investigators to consider home ranges of animals as conforming to geometrical design. This may or may not be the true situation; telemetric studies on larger animals indicate that home ranges do not conform to geometrical design. At present there is a poverty of knowledge concerning methods for determining the precise home ranges of small mammals. Telemetry appears to offer an unlimited potential for studies of this kind.

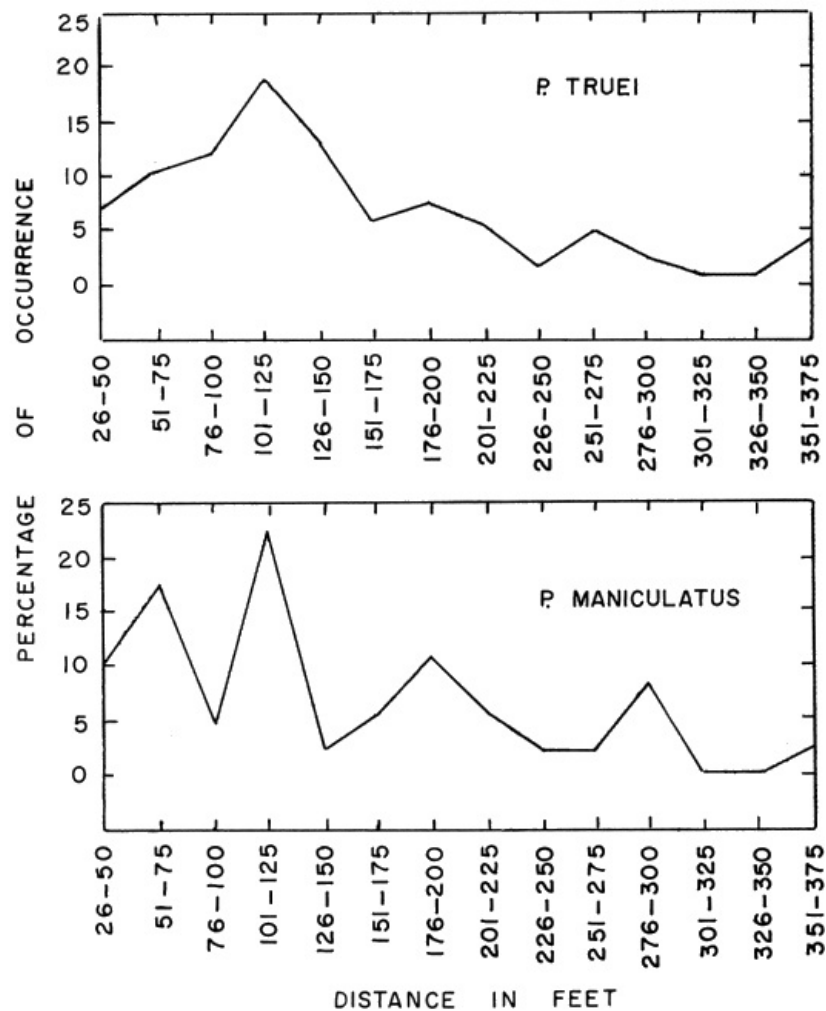


FIG. 3: Graphs showing the distribution of distances between stations at which mice were captured on successive nights in Mesa Verde National Park. Graphs for each species represent records of both males and females.

Individuals of *P. truei* and *P. maniculatus* usually do not have mutually exclusive home ranges. When the home ranges for all females or males of one species are drawn on a single map of the trapping grid, almost every one of their ranges overlaps with the range of at least one other mouse. In some instances, the home range of an individual overlaps ranges of several other individuals. In extreme cases an animal's range lies completely within the estimated boundaries of another individual's range. Such an enclosed range was always that of a juvenile or of a young animal. However, an adult may have more than half of its range overlapping with that of another adult of the same sex and of the same, or different, species.

[444]

In general, the two species tended to be restricted to certain areas of the trapping grid where the respective habitats were more favorable for their needs. Figure 4 shows the parts of the trapping grid utilized by each species. Of course there is overlap in the areas utilized by each species; a few individuals of *P. maniculatus* may be found in what appears to be *P. truei* habitat, and *vice versa*. In such cases, an inspection of the vegetation usually reveals an intermediate type of habitat—for example, an open sagebrush area in pinyon-juniper woodland—that is habitable for either or both species.

The ranges of *P. truei* tend to be clustered in the western half of the trapping grid, where ranges of *P. maniculatus* are clustered in the eastern half of the grid (Fig. 4). The vegetation of the grid and the preferred habitats of each species are discussed in following chapters.

On the basis of the sizes of estimated home ranges, it is possible to compute the approximate number of individuals of each species that occur in each acre of appropriate habitat.

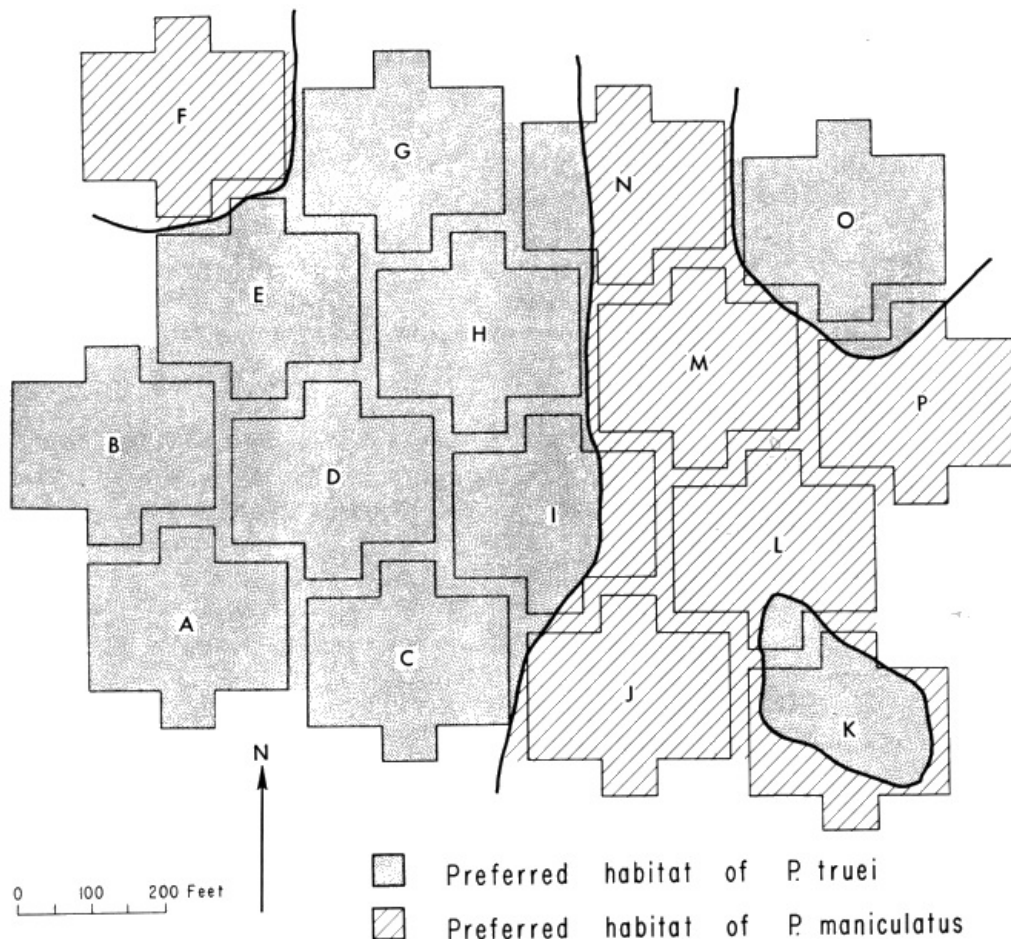


FIG. 4: Diagram of trapping grid south of Far View Ruins, showing the preferred habitats of *P. truei* and *P. maniculatus*.

On the basis of an average home range of $30,206 \pm 25,545$ square feet (one standard deviation) for both male and female individuals of *P. truei*, there should be approximately 0.781 to 9.345 individuals of this species per acre of pinyon-juniper woodland. An average home range of $29,400 \pm 24,570$ square feet for males and females of *P. maniculatus* indicates that the density of this species is between 0.807 and 9.018 animals per acre in mixed shrub or shrub and sagebrush types of vegetation.

[445]

Figure 4 shows that approximately 10 of the 16 units of the trapping grid are suitable habitat for *P. truei*; the remaining six units are habitat of *P. maniculatus*. From the preceding calculations of density one could expect to find between seven and 90 individuals of *P. truei*, and between five and 54 individuals of *P. maniculatus* as residents within the 22.95 acres of the trapping grid. The higher estimates of density appear to be large enough to compensate for any overlapping of home ranges.

The calculation of density of each species within the trapping grid is dependent upon the precision with which the home ranges of individuals can be estimated. At this time, home ranges of small rodents can not be measured with great precision, therefore any such calculations are, at best, only approximations. This does not imply that estimations of home range are of little value; however, calculations of density, using home ranges as a basis, tend to amplify the variance inherent in the data. This amplification is reflected in the wide range between low and high limits of the densities for each species within the trapping grid.

In order to check on the accuracy of the above calculations, an estimate of density was made for each species on the basis of trapping data. Trapping records kept for each animal were checked for the year 1963. More data on home ranges were obtained in that year due to higher population densities than in 1964. If an animal was caught four or more times in 1963, it was considered to be a resident; animals caught in both 1963 and 1964 were considered to be residents even if caught fewer than four times. Mice caught three times, with at least a month elapsing between the first and third captures, were considered to be probable residents. Other animals caught three or fewer times were considered to be migrants.

In 1963, 15 individuals of *P. truei* were caught four or more times, or in both years, and considered to be residents; six other mice were classed as probable residents. Of *P. maniculatus*, 18 individuals were classed as residents, and two as probable residents. Thus the trapping data for 1963 indicate that 21 individuals of *P. truei* and 20 of *P. maniculatus* were residents of the trapping grid. These estimates lie well within the estimated limits of density of each species, as calculated from data on home range while taking into account the relative proportions of available habitat for each species within the trapping grid. Analyses of trapping data indicate that the density of each species probably is overestimated by calculations of density based on home range data.

Males and females of both species of *Peromyscus* appeared to be highly individualistic in the amount of area they utilized. Some adult males of *P. truei* covered large areas, whereas others were relatively sedentary. The same was true of young males of *P. truei*, although the younger males tended to have smaller ranges than adult males. Most pregnant or lactating females, of both species, tended to use smaller areas for their daily activities than did non-pregnant or non-lactating females. There were notable exceptions to this generality, for some lactating females had exceptionally large home ranges.

Size of home range apparently was not influenced by the location of an animal's range within the grid. Far more data would be needed to correlate minor differences in vegetational associations with sizes of ranges in different parts of the grid. [446]

It is surprising that adults of *P. truei* do not have larger home ranges than adults of *P. maniculatus*. *P. truei* is the larger, more robust animal, capable of rapid running and occasional saltatorial bounding; individuals of this species can traverse large areas with ease. The semi-arboreal nature of *P. truei* may explain why individuals of this species do not have larger ranges than individuals of *P. maniculatus*. *P. truei* has a three-dimensional home range, whereas *P. maniculatus* has a range that is two-dimensional only (excluding the relatively minor amount of burrowing done by each species).

VEGETATIONAL ANALYSIS OF HABITATS

Detailed maps of vegetation within the trapping grid were needed to aid in analyzing distribution of mice within the grid. In preparing such maps, I recorded all plants within a 25 foot radius of each trapping station. The dominant and codominant plants in the overstory (trees or shrubs) were noted at each station. Next the three most abundant plants other than the dominant and codominants were rated for each station, where possible. Finally a listing was made of all remaining species of plants.

On the basis of this analysis, four vegetational maps were prepared. One shows associations of dominant overstory and understory plants. Individual maps are devoted to the first, second and third most abundant plants in the ground cover within the trapping grid (Figs. 5-8). Approximately seven man-hours were required to analyze each trapping unit, and 112 man-hours to analyze the entire grid.

The home range grid encompasses approximately one million square feet. At least four different vegetational stands occur within the grid: 1) pinyon-juniper woodland with various associations in the understory; 2) *Artemisia tridentata* (big sagebrush), or *A. nova* (black sagebrush); 3) *Quercus gambelii* (Gambel oak); and 4) mixed shrubs—*Fendlera rupicola* (fendlerbush), *Amelanchier utahensis* (Utah serviceberry), and *Cercocarpus montanus* (mountain mahogany).

Flora in the ground cover is regulated, at least in part, by the canopy cover; hence different associations of pinyon-juniper woodland and each of the stands mentioned above have different plants, or a different distribution of the same kinds of plants, in their ground cover.

Units A, B, E, and parts of D and G in the western third of the grid are in pinyon-juniper woodland (Fig. 5). A relatively pure understory of *Poa fendleriana* (muttongrass), is typical of such woodland on the middle parts of the mesas. Woodland on the western third of the grid differs somewhat in that, when the area occupied by each plant is considered, *Artemisia tridentata* is codominant there with *Poa fendleriana*. As far as individual plants are concerned, *Poa* far outnumbers *Artemisia*. The next most abundant plants in the ground cover are *Solidago petradoria* (rock goldenrod), *Chrysothamnus depressus* (dwarf rabbitbrush), and *Penstemon linarioides* (penstemon), in that order.

In unit E there is a large depression, about 200 by 60 feet, created by removal of soil (Fig. 8). *Artemisia nova* grows there, and pioneering plants adapted to early stages of succession are present.

A zone of woodland, where *Artemisia nova* replaces *A. tridentata* as an understory codominant with *Poa fendleriana*, borders the pinyon-juniper-muttongrass community to the east. The next most abundant plants in the ground cover are *Solidago petradoria*, *Penstemon linarioides* and *Comandra umbellata* (bastard toadflax). *Koeleria cristata* (Junegrass) is as abundant as *Comandra*, but probably is less important as a source of food for mice. [447]

A small strip of the pinyon-juniper-muttongrass community with an understory of *Artemisia nova* and *Purshia tridentata* (bitterbrush) adjoins the above area to the east (Figs. 5-8). *Solidago petradoria*, *Balsamorhiza sagittata* (balsamroot), and *Comandra umbellata* are the three most abundant plants in the ground cover. The terrain slopes eastward from this zone into a large drainage.

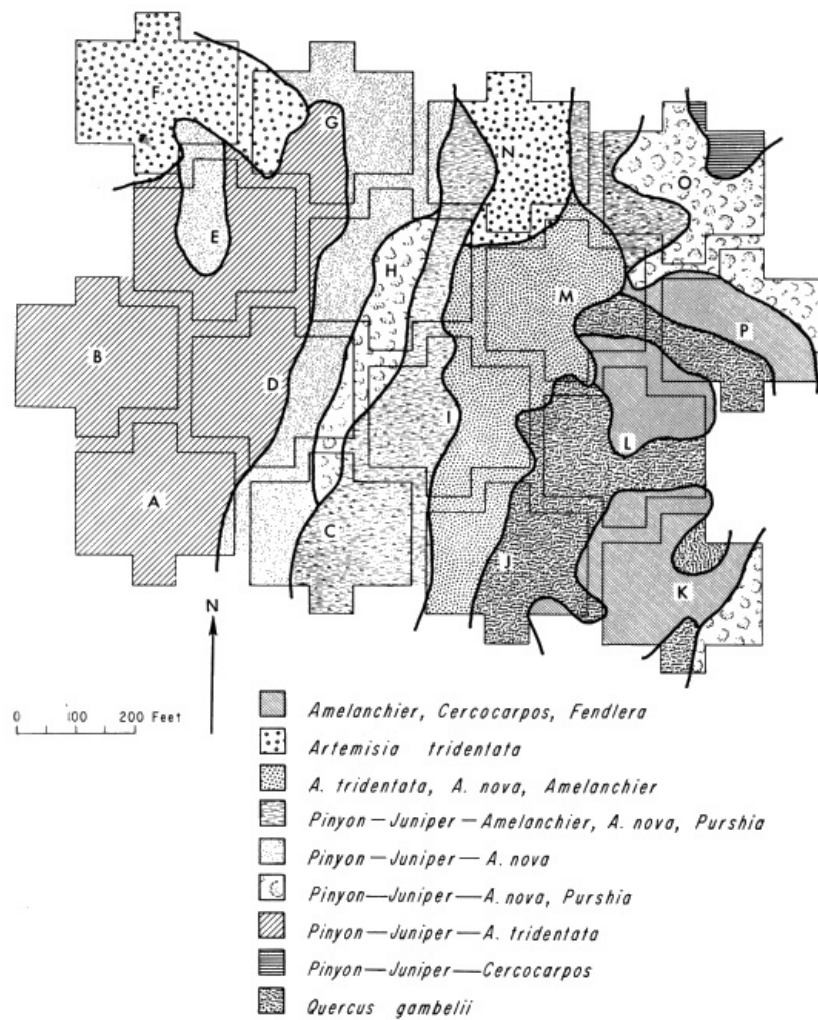


FIG. 5: Diagram showing the major associations of understory and overstory vegetation in a trapping grid located south of Far View Ruins, Mesa Verde National Park, Colorado.

As the forest floor begins to slope into the drainage, the ground becomes rocky and shrubs assume more importance in the understory. Most of this shrubby zone is on the slope; on the western side this zone abuts pinyon-juniper woodland, and on the eastern side is bordered by *Artemisia tridentata* in the sandy bottom of the drainage. Shrubs become more abundant and pinyon and juniper trees become less abundant as one approaches the drainage. In the vegetation maps, this brushy zone is delimited on the east by a heavy line passing vertically through the middle of the grid (Figs. 5-8). The codominant shrubs in the understory of this zone are *Amelanchier utahensis*, *Artemisia nova* and *Purshia tridentata*. The three most abundant plants on the ground are *Artemisia ludoviciana*, *Chrysothamnus depressus* and *Penstemon linarioides*.

[448]

The drainage occupies most of unit N and parts of Units I, J and M. Unit N is at the head of the drainage; the ground slopes rapidly southward and the bottom of the drainage in unit J is approximately 50 feet lower than in unit N. The canopy cover of the drainage is *Artemisia tridentata* (Fig. 5). The same three plants that are most abundant in the ground cover of the slope are also most abundant in the drainage.

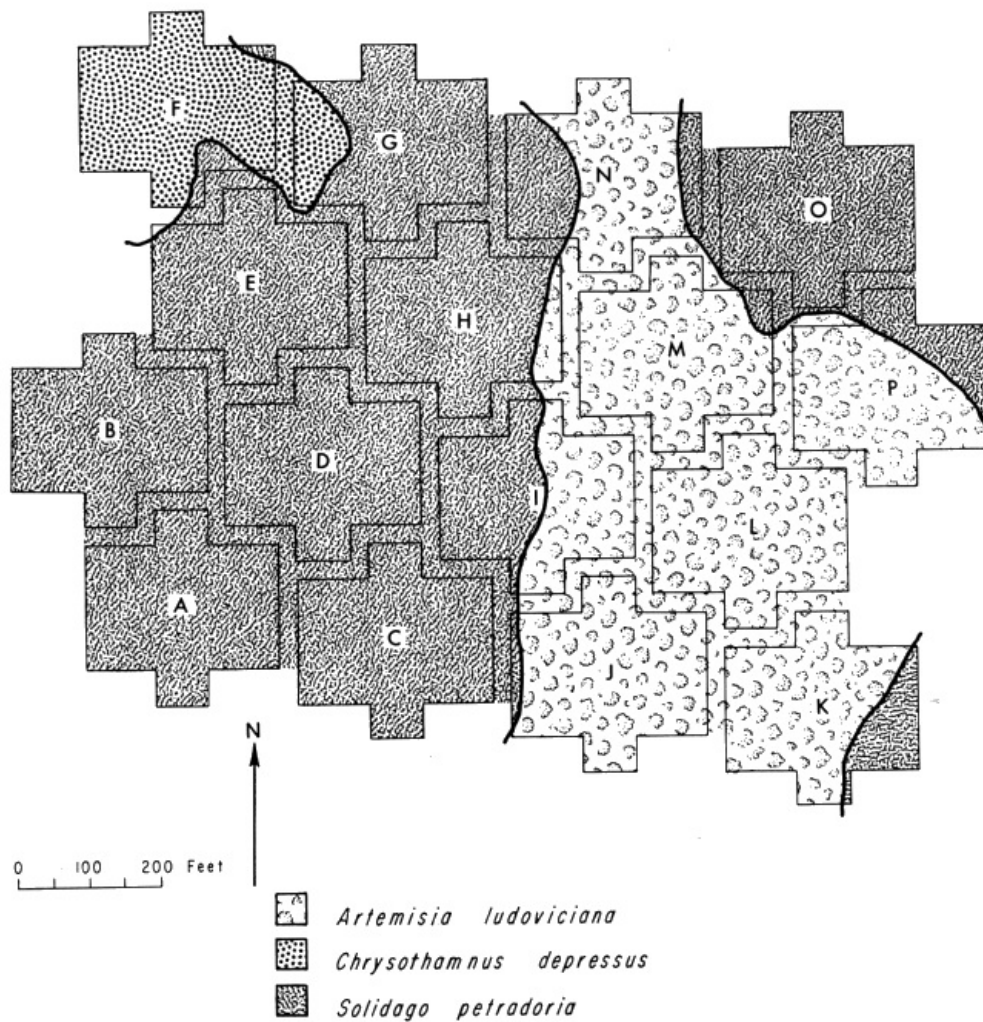


FIG. 6: Diagram showing the most abundant species of plants in the ground cover of the trapping grid south of Far View Ruins.

The eastern slope of the drainage is covered with oak chaparral (*Quercus gambelii*); this zone occupies parts of units J, L, M, and P. *Artemisia ludoviciana*, *Solidago petradoria*, and *Viguiera multiflora* (goldeneye), are the most abundant plants of the ground cover. [449]

Mixed shrubs (*Amelanchier*, *Cercocarpos*, and *Fendlera*) form large islands in the oak chaparral, in units K, L and P. The brushy areas of oak and mixed shrub give way at the top of the slope to pinyon-juniper forest with an understory of *Artemisia nova* and *Purshia tridentata*. The three most abundant plants in the ground cover of the shrub zones are *Solidago petradoria*, *Balsamorhiza sagittata*, and *Comandra umbellata*. The eastern part of unit O has *Amelanchier utahensis* in the understory, in addition to *Artemisia nova* and *Purshia tridentata* (Fig. 5). The northeastern corner of unit O is in pinyon-juniper woodland with an understory of *Cercocarpos montanus*.

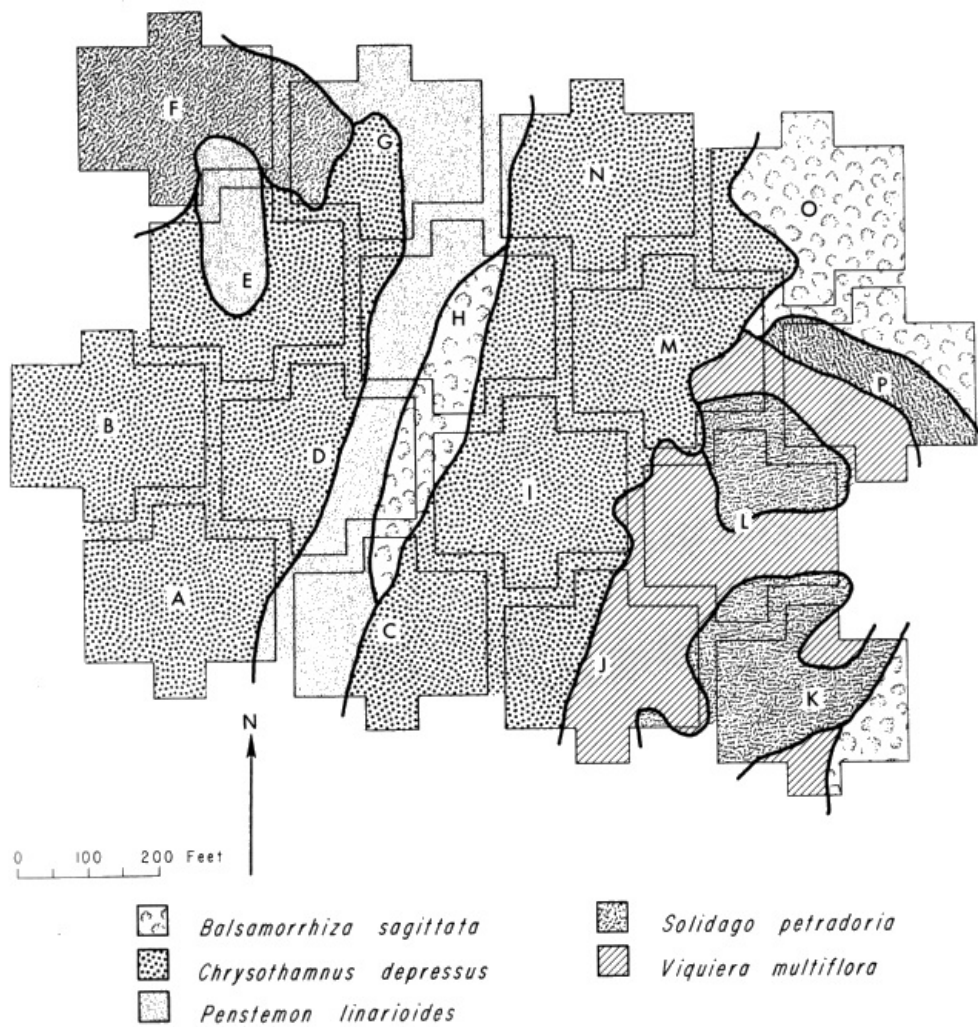


FIG. 7: Diagram showing the second most abundant species of plants in the ground cover of the trapping grid south of Far View Ruins.

There are two relatively pure stands of sagebrush in the grid: one is in unit N, and the other in unit F and part of unit G. As figures 5 to 8 show, unit N has a relatively pure stand of *Artemisia tridentata* (big sagebrush), with *Artemisia ludoviciana*, *Agropyron smithii* (western wheatgrass), and *Koeleria cristata* (Junegrass), being most abundant in the ground cover. *Artemisia tridentata* and *Artemisia nova* form the overstory in unit F and part of G. The three most abundant plants in the ground cover there are *Chrysothamnus depressus*, *Solidago petradoria*, and *Penstemon linarioides* (Figs. 6-8).

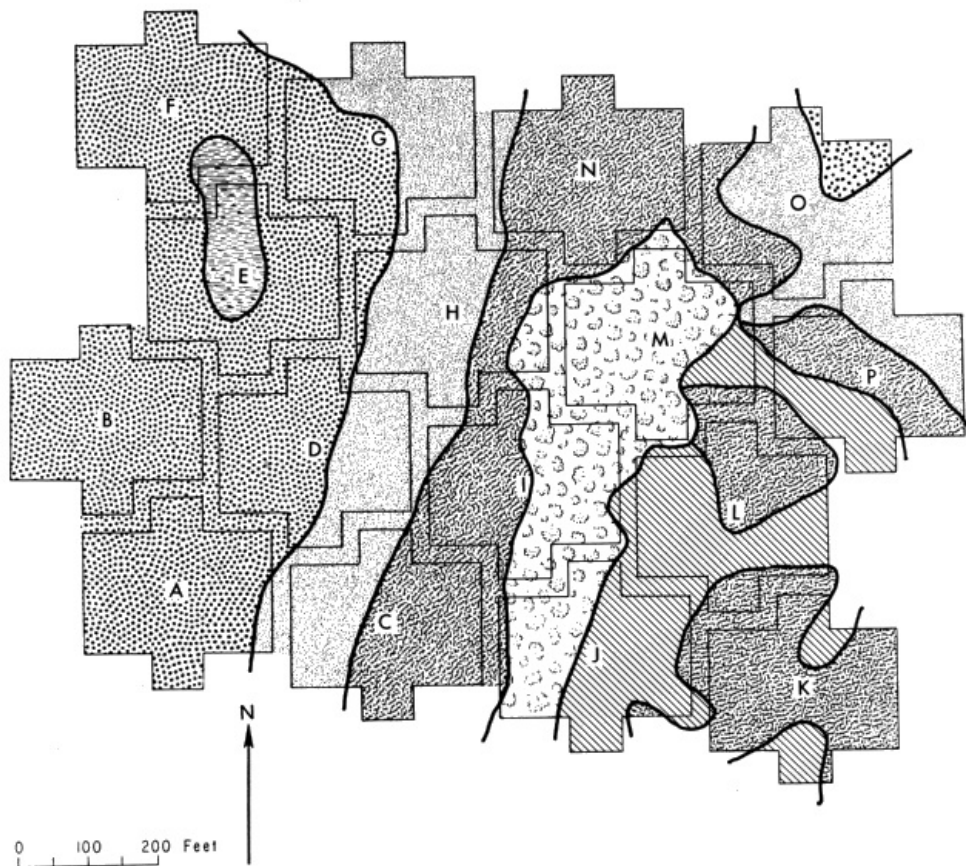


FIG. 8: Diagram showing the third most abundant species of plants in the ground cover of the trapping grid south of Far View Ruins.

MICROCLIMATES OF DIFFERENT HABITATS

Four microclimatic stations were established in units D, F, L and M of the trapping grid to record air temperatures and relative humidities at ground level. These sites were chosen as being representative of larger topographic or vegetational areas within the grid. Belfort hygrothermographs were installed on June 10, 1964, and were serviced once each week through October 31, 1964, at which time the stations were dismantled. Each station consisted of a shelter 18 by 9 by 11.5 inches, having a false top to minimize heating (Fig. 9). The shelters were painted white. Several rows of holes, each one inch in diameter, were drilled in all four sides of each shelter, to provide circulation of air. The holes were covered by brass window screening to prevent entry of insects and rodents. Preliminary tests with several U. S. Weather Bureau maximum and minimum thermometers, suspended one above the other, from the top to the bottom of the shelter, revealed that there was no stratification of air within the shelters. Nevertheless, each shelter was placed so that the sun did not strike the sensing elements of the hygrothermograph inside it.

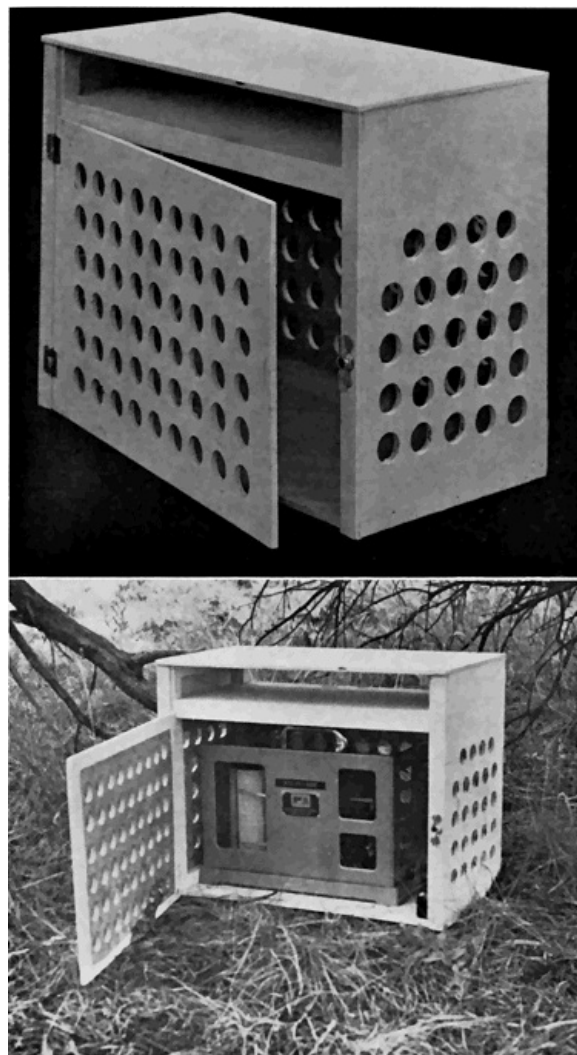


FIG. 9: (above) Photograph of microclimatic shelter built to house hygrothermograph. False top minimizes heating, and ventilation holes are covered with screening. (below) Photograph showing shelter in use.

Accuracy of the hair elements was checked by means of a Bendix-Friez battery driven psychrometer, in periods when humidity conditions were stable (on clear days the relative humidity is at its lowest limits and is "stable" for several hours during early afternoon).

[452]

The four microclimatic stations were in the following places: 1) a stand of big sagebrush near Far View Ruins; 2) a pinyon-juniper-muttongrass association; 3) a stand of big sagebrush at the head of a drainage; and 4) a stand of Gambel oak on a southwest-facing slope of the drainage. [Table 4](#) shows monthly averages of maximum and minimum air temperatures and relative humidities at each of the four sites. Vegetation and microclimates of the sites are discussed below.

Far View Sagebrush Site, 7,650 feet elevation

The shelter housing the hygrothermograph was next to the stake of station F4a in the trapping grid ([Fig. 10](#)), in a stand of big sagebrush on the flat, middle part of the mesa top, approximately 100 yards southwest of Far View Ruins. The sagebrush extends approximately 200 feet in all directions from the station ([Fig. 5](#)). Pinyon pine and Utah juniper trees are encroaching upon this area, and scattered trees are present throughout the sagebrush. This area is one of the habitats of *P. maniculatus*.

Sagebrush tends to provide less shade for the ground than pinyon-juniper woodland, and therefore the surface temperatures of the soil rise rapidly to their daily maximum. In mid-June, air temperatures rise rapidly from 6 A. M. until they reach the daily maximum between 2 and 4 P. M. Shortly after 4 P. M. the air temperatures decrease rapidly and reach the daily low by about 5 A. M.

Relative humidities follow an inverse relationship to air temperatures; when air temperatures are highest, relative humidities approach their lowest values. Thus, on clear days, humidities decrease during the day, reaching a minimum slightly later than air temperatures attain their maximum. Unless it rains, the highest humidities of the day occur between midnight and 6 A. M.

Drainage Site, 7,625 feet elevation

This site was in the bottom of the drainage that runs through the eastern side of the trapping grid, and through parts of units M, N, I, and J. The site was at station M4d on a level bench at the head of the drainage (Fig. 11). Southward from the station the drainage deepens rapidly, and the bottom loses approximately 25 feet in elevation for every 200 feet of linear distance. *P. maniculatus* lives here.

The microclimate of the drainage differs markedly from that of other stations. The major difference is attributable to the topography of the drainage itself. Nocturnal cold air flows from the surrounding mesa top to lower elevations. A lake of cold air forms in the bottom of the drainage; the depth of the lake depends in part upon the depth of the drainage. The same phenomenon occurs in canyons and causes cooler night time temperatures on the floor of canyons than on adjacent mesa tops (Erdman, Douglas, and Marr, in press). Drainage of cold air into lower elevations affects both nocturnal air temperatures and relative humidities. Table 4 shows that maximum air temperatures in the drainage did not differ appreciably from those at other stations. Mean minimum temperatures, however, were considerably lower in the drainage than at the other sites. This phenomenon is reflected also in the mean air temperatures at this station.



[453]

FIG. 10: (above) Photograph of microclimatic station at the Far View Sagebrush Site, at trapping station F4a in the grid south of Far View Ruins. Dominant vegetation is *Artemisia tridentata*.

FIG. 11: (below) Photograph of microclimatic station at the Drainage Site, in the bottom of a shallow drainage at trapping station M4d of the grid south of Far View Ruins.

The drainage site had the highest humidities of all stations each month in which data were collected (Table 4). Relative humidities of 90 to 100 per cent were common in the drainage, but occurred at other stations only in rainy periods. For example, in the month of August, 26 of the daily maximum readings were between 95 and 100 per cent at the drainage site, but at the other stations relative humidities were above 95 per cent for an average of only nine nights. Minimum humidities were about the same for all stations, since they are affected by insolation received during the day, and not by the drainage of cold air at night.

[454]

Oak Brush Site, 7,640 feet elevation

The station was in an oak thicket at trapping station L4a, 250 feet south and 50 feet east of the drainage site on a southwest-facing slope of about 30 degrees (Fig. 12). The station was on

the lower third of the slope, approximately 15 feet higher than M4d, the station in the bottom of the drainage. *P. truei* and *P. maniculatus* occur together in this area.

Air temperatures and relative humidities at this station did not differ appreciably from mean temperatures and humidities at the other stations. The unusual feature is the lack of evidence of cold air drainage. The lake of cold air in the bottom of the drainage apparently is too shallow to reach this station. This site is near the head of the drainage, and the cold, nocturnal air probably moves rapidly down slope into the deeper parts of the canyon, rather than piling up at the shallow head of the drainage.

In spite of the shade afforded the ground by the oak brush, temperatures reached the same maximum values as at the drainage site, owing to the orientation of the slope. South-facing slopes receive more direct insolation throughout the day and throughout the year than north-facing slopes and mesa tops (Geiger, 1965:374). In Mesa Verde, south-facing slopes tend to be more arid; snow melts rapidly, and most of this moisture evaporates. As a consequence, south-facing slopes have less soil moisture and more widely-distributed vegetation than north-facing slopes where snows often persist all winter and melt in spring. (For a detailed discussion of climates on northeast-versus-southwest-facing slopes in Mesa Verde, see Erdman, Douglas, and Marr, in press.)

Pinyon-Juniper-Muttongrass Site, 7,600 feet elevation

The station was in the trapping grid at D5b (Fig. 13). The pinyon-juniper woodland surrounding this site resembles much of the woodland on the middle part of the mesa. The forest floor is well shaded by the coniferous canopy, and muttongrass is the dominant plant in the ground cover. *P. truei* lives in this habitat.

The climate at this site is moderate. Shade from the canopy greatly moderates the maximum air temperatures during the day; minimum air temperatures, however, are about the same as at the other stations (Table 4). Mean temperatures are somewhat lower at this site than at the others because of the lower maximum temperatures. Relative humidities do not differ markedly from those at other stations.

Figure 14 shows hygrothermograph traces at all stations for a typical week. An interesting phenomenon is illustrated by several of these traces. By about midnight, air temperatures have cooled to within a few degrees of their nightly low. At this time, heat is given up by the surface of the ground in sufficient quantities to elevate the air temperature at ground level. This release of reradiated energy lasts from one to several hours, then air temperatures drop to the nightly low just before sunrise. A depression in the percentage of relative humidity accompanies this surge of warmer air. On some nights winds apparently disturb, or mix, the layers of air at ground level. On such nights the reradiation of energy is not apparent in the traces of the thermographs. Reradiation of energy is restricted to ground level, and traces of hygrothermographs in standard Weather Bureau shelters, approximately four feet above the ground surface, at other sites on the mesa top did not record it.

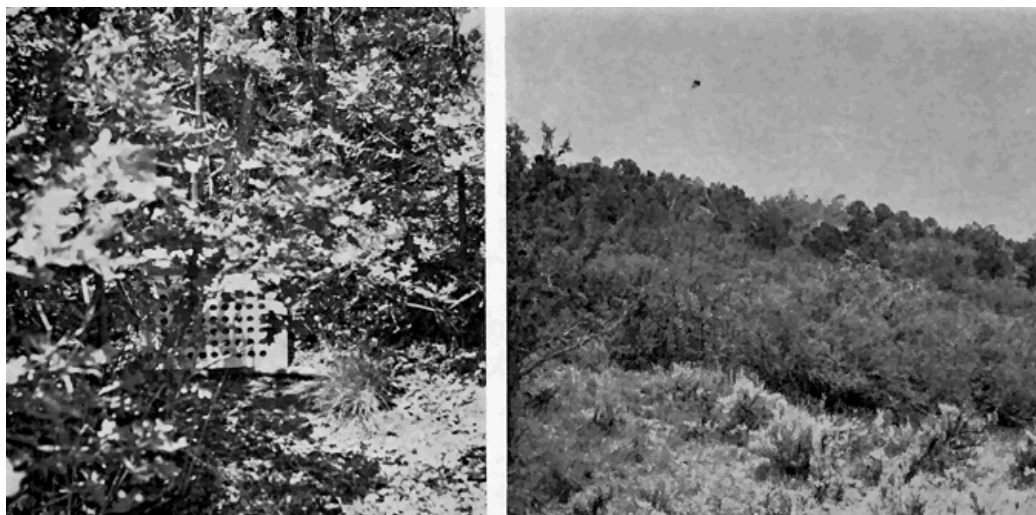


FIG. 12: (left) Photograph of microclimatic station at the Oak Brush Site, at trapping station L4a of the grid south of Far View Ruins. (right) General view of the stand of Gambel oak in unit L of the trapping grid.

[455]

[456]



FIG. 13: Photograph of microclimatic station at the Pinyon-Juniper-Muttongrass Site, at trapping station D5b of the grid south of Far View Ruins. Grass in the foreground is muttongrass, *Poa fendleriana*.

The instruments used in this study were unmodified Belfort hygrothermographs containing as sensing units a hair element for relative humidity and a Bourdon tube for air temperatures. The hair element, especially, does not register changes in humidity at precisely ground level; rather, it reflects changes in the layer of air from about ground level to about a foot above. Thus data from these instruments give only approximations of the conditions under which mice live while they are on the ground.

Climatic conditions greatly influence trapping success. Larger numbers of mice generally were caught on nights when humidities were higher than average. Rain in part of the evening almost invariably resulted in more mice of each species being caught. This was probably due to increased metabolism, by the mice, to keep warm. Apparently the mice began foraging as soon as the rains subsided; mice were always dry when caught after a rain. Few mice were caught if rains continued throughout the night and into the daylight hours.

TABLE 4—Monthly Averages of Daily Means for Maximum, Minimum, and Mean Air Temperatures and Relative Humidities at Four Sites in Mesa Verde National Park, Colorado.

[457]

Site	Maximum Temps.					Maximum R. H.				
	J	J	A	S	O	J	J	A	S	O
Far View Sagebrush Drainage	89	91	86	77	74	68	84	82	88	71
Oak Brush	86	91	85	78	78	87	94	93	96	84
Pinyon-Juniper-Poa	75	80	74	66	64	59	83	82	88	58
Site	Minimum Temps.					Minimum R. H.				
	J	J	A	S	O	J	J	A	S	O
Far View Sagebrush Drainage	42	53	50	42	31	18	24	25	29	21
Oak Brush	36	48	45	38	26	21	26	27	29	30
Pinyon-Juniper-Poa	42	52	50	42	32	19	25	30	31	21
Pinyon-Juniper-Poa	44	54	50	42	34	22	30	29	32	25
Site	Mean Temps.					Mean R. H.				
	J	J	A	S	O	J	J	A	S	O
Far View Sagebrush Drainage	66	72	68	60	52	43	54	54	48	46
Oak Brush	61	70	65	58	52	54	60	60	62	52
Pinyon-Juniper-Poa	64	70	66	59	56	38	51	55	56	44
Pinyon-Juniper-Poa	60	67	62	54	49	41	56	55	60	42

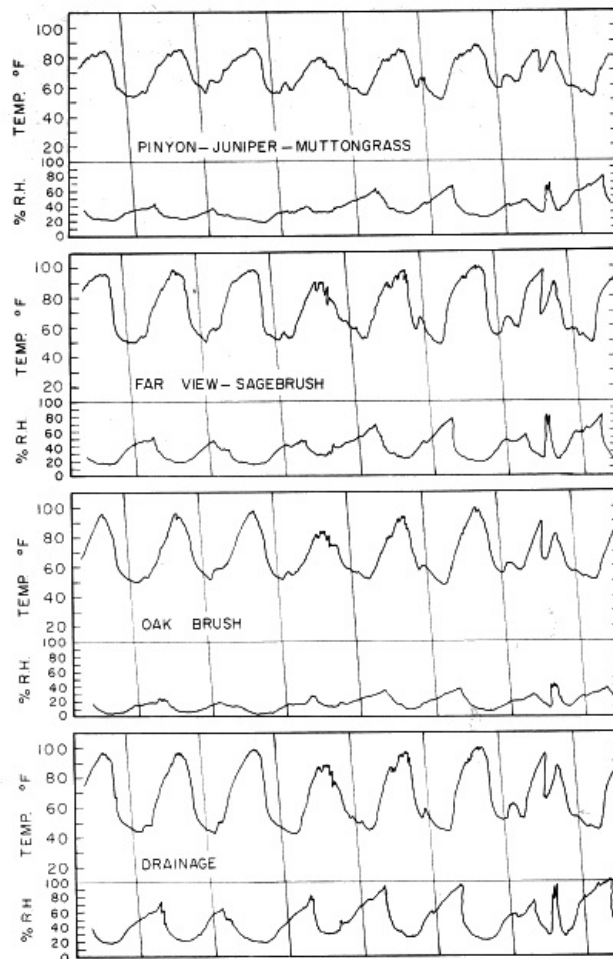


FIG. 14: Diagram of hygrothermograph traces showing daily progressions of air temperatures and relative humidities at each of four microclimatic stations, from the morning of July 1 through the morning of July 8, 1964. Slanting vertical lines on each chart designate midnight (2400 Hrs.) of each day.

Nights of high trapping success usually were associated with days having solar insolation below the average. Insolation was measured with a recording pyrliometer at a regional weather station (M-2) on the middle of Chapin Mesa, at an elevation of 7,150 feet (Erdman, Douglas, and Marr, in press). This station was approximately one mile south of the trapping grid; isolation at this site would have been essentially the same as that received by the trapping grid. Below-average isolation for one day indicates cloudy conditions, which are accompanied by increased humidity, but may or may not be accompanied by precipitation. Trapping on nights preceded and followed by days of average or above average isolation with average humidities—indicative of clear days and clear moonlit nights—did not yield appreciably higher catches of mice than other nights. Hence there was no evidence that mice tended to avoid, or to seek out, traps on clear moonlit nights.

[459]

On cold, humid nights in autumn numerous mice caught in Sherman live traps succumbed from exposure, even though nesting material (kapok or cotton) and food were in the traps. Occasionally mice succumbed to heat when traps were inadvertently exposed to too much sunlight. Apparently little heat is required to kill individuals of either species. Traps in which animals died due to excessive heat usually were not hot to the touch; in most instances the traps were checked before 9:00 A. M., several hours before the sun caused maximum heating. Such individuals may have licked the fur of their chests in an attempt to lower their body temperatures. Although mice characteristically salivate before succumbing from heat, these individuals had moist fur over the entire chest and upper parts of the front legs, indicating licking. Mice killed by exposure to heat or cold usually were juveniles or young; subadult and adult individuals of both species were more tolerant. Older animals would be expected to have better homeostatic controls than younger individuals.

HABITAT PREFERENCE

In Mesa Verde *P. truei* and *P. maniculatus* occur together only at the fringes of the pinyon-juniper woodland, where ecotonal areas provide less than optimum habitats for both species. Almost all individuals of *P. truei* occur only in pinyon-juniper woodland, whereas *P. maniculatus* occurs only in more open habitats, such as grassy meadows and stands of sagebrush.

Pinyon mice were abundant in a variety of associations within the pinyon-juniper woodland. The highest population densities were in pinyon-juniper woodland having an understory of mixed shrubs. In such an association, *Poa fendleriana* usually is the dominant grass in the ground cover. *P. truei* was especially abundant along brushy slopes where mixed shrubs (*Amelanchier*, *Cercocarpus* and *Fendlera*) were codominant with pinyon pines and Utah junipers. The pinyon-juniper-mixed shrub area west of Far View Ruins was almost optimum habitat for *P. truei*.

P. truei was abundant on the rocky ridge of Wetherill Mesa near Mug House; the pinyon-juniper woodland here has a *Cercocarpus* understory, and appears to provide close to optimum conditions for this species.

Not all associations of the pinyon-juniper woodland support large numbers of *P. truei*. Pinyon-juniper woodland having a ground cover of *Poa fendleriana*, and no shrubs, supports few mice; the woodland on Wetherill Mesa near Long House is an example. Juniper-pinyon woodland having a *Purshia tridentata* understory also supports only a few mice. Such areas occur on the southern ends of the mesas and are characterized by widely-spaced trees and little ground cover—a reflection of the relatively low amounts of precipitation received by the southern end of the park. [460]

P. truei was not found in grasslands on Navajo Hill, or in meadows at the southern end of Moccasin Mesa. The old burned areas on the northern end of Wetherill Mesa and on Morfield Ridge now support numerous grasses and shrubs, but *P. truei* appears not to live there.

P. truei tends to avoid stands of sagebrush, or grasslands, lacking pinyon or juniper trees. *P. truei* may venture into such areas while feeding. This species is found in thickets of Gambel oak and in areas with an overstory of mixed shrubs only when a living pinyon-juniper canopy is present, or when a woodland adjoins these areas.

Rocky terrain apparently is not a requirement for *P. truei*, since much of the pinyon-juniper woodland that is free of rocks supports large numbers. Optimum habitat, however, had a rocky floor. In such places, rocks probably are of secondary importance, whereas the shrubs and other plants growing on rocky soils are important for food and cover. Rocks likely provide additional nesting sites, and allow a larger population to live in an area than might otherwise be possible.

In Mesa Verde the deer mouse, *P. maniculatus*, prefers open areas having dense stands of grasses, or brushy areas adjoining open terrain. This species lives in stands of big sagebrush; in grassy areas having an oak-chaparral or mixed-shrub-overstory; and in grasslands without shrubs, such as on the southern end of Moccasin Mesa. Pure stands of sagebrush did not support large numbers of mice unless there was additional cover nearby in the form of shrubs or oak brush.

Optimum habitats for *P. maniculatus* were on Navajo Hill, in the burned areas on Morfield Ridge, on the northern end of Wetherill Mesa, and in the grassy areas near the entrance of the park. The trapping areas in the first three mentioned had heavy growths of grass and an overstory of shrubs.

Some individuals of *P. maniculatus* ventured into pinyon-juniper woodland and entered traps. Such animals usually were found in places having a heavy understory of sagebrush, or in disturbed places within the woodland.

P. maniculatus, but not *P. truei*, was taken in the arid pinyon-juniper-bitterbrush stand on the southern end of Wetherill Mesa. *P. maniculatus* also was present, in about equal numbers with *P. truei*, in a pinyon-juniper-muttongrass stand north of Long House. Both of these localities supported only a few mice.

P. maniculatus is found more frequently in pinyon-juniper woodland when the population density is high, and when such woodlands adjoin grasslands or sagebrush areas. As mentioned earlier, *P. truei* and *P. maniculatus* occur together in ecotonal areas between the forest and grassy or brushy areas. In Mesa Verde the deer mouse inhabits exposed grassy areas that have mostly shrubs in the open canopy.

P. maniculatus is the first to colonize areas that have been burned; this species invades such areas as soon as primary successional vegetation becomes established. It can be stated that in general, *P. maniculatus* will be found in the harsher, more arid habitats. If the habitat is so inhospitable that only a few mice can survive there, *P. maniculatus* will be present. *P. truei* apparently requires the more moderate conditions found in the pinyon-juniper forest, and this species does not venture far from the edge of the forest.

[461]

NESTING AND NEST CONSTRUCTION

Ten individuals of *P. truei* and three of *P. maniculatus* were followed to their nesting places. Photographs were taken of the nesting sites before and after uncovering. Plants or other materials used in their construction and any commensal arthropods present were saved and later identified.

Nests of *P. truei* usually were associated with juniper trees. Dead branches and trunks of

juniper trees decay from the inside, and the resulting hollows are favored sites for the nests. Pinyon pine trees tend to decay from the outside and were not used as nesting sites by *P. truei*. Nests of *P. truei* were found in hollow trunks and branches of otherwise healthy juniper trees, and in hollow logs lying on the ground. The heartwood apparently rots rapidly in juniper trees, but the sapwood remains intact for many years—even after the tree is lying on the ground. For example, a part of the pinyon-juniper woodland on the southern end of Chapin Mesa was burned in 1858, and the hollow trunks of junipers were still standing in 1966. Almost all of the pinyon pine trees that were killed by that fire have since decayed; their former presence is verified only by the crumbling remnants of their trunks that lie on the ground throughout the burned area.

The following accounts illustrate the preferences of the two species of mice in selection of nesting sites:

No. 105, *P. truei*, adult. On July 22, 1964, after being released from a trap, this female ran to a serviceberry bush 10 feet south of station I4d, preened herself, ate a berry from the bush, and disappeared under a large rock at the base of the bush. Subsequent excavation revealed a large nest composed of grasses (*Poa fendleriana*, *Sitanion hystrix*, *Agropyron smithii*, *Koeleria cristata*), and a few leaves of serviceberry. There were three entrances to the nest, one on each side of the rock.

This mouse was captured again on August 12, 1964, released and followed to a hollow juniper log 15 feet south of station C7b, and 245 feet from the above nest. This log was dismantled, but no nest was found. A large number of chewed juniper seeds around the log indicated that this mouse, or others, had frequented the area.

On August 20, 1964, this female was followed to a large juniper log 20 feet northeast of station I4b. A small nest of shredded juniper bark was found inside the log, and there were numerous nuts of pinyon pine and seeds of Utah juniper that had been gnawed open. This site was about 320 feet from that at C7b, and about 240 feet from station I4d (Fig. 15).

No. 118, *P. truei*, young. On August 29, 1963, this male ran into a hollow branch of a partly dead juniper tree 15 feet south of station C5d. Part of this branch had been sawed off at some earlier time, and a hole about one-and-a-half inches in diameter was present in the center of the remaining part. The branch was not dissected, but probing revealed that the hole extended far into the branch and enlarged as it approached the trunk.

No. 177, *P. truei*, adult. This lactating female ran into the hollow trunk of a juniper 10 feet north of station G7a. Both lateral branches of the main trunk were rotten and hollow, but the tree appeared to be healthy. Chewed juniper seeds were present in the trunks and around the base of the tree.

This female later ran to a juniper log 30 feet north of station N4d. Apparently there was no permanent nest at this site (Fig. 15).

No. 178, *P. truei*, adult. This female ran into a hollow juniper tree 10 feet south of station H3c. Hundreds of old juniper seeds, with their embryos chewed out, were present at the base of the tree. The tree was not cut down.

No. 238, *P. truei*, adult. This male ran into a dead juniper log 10 feet south of station O4b. Chewed juniper seeds were present on the ground, but no nest was found in the log.

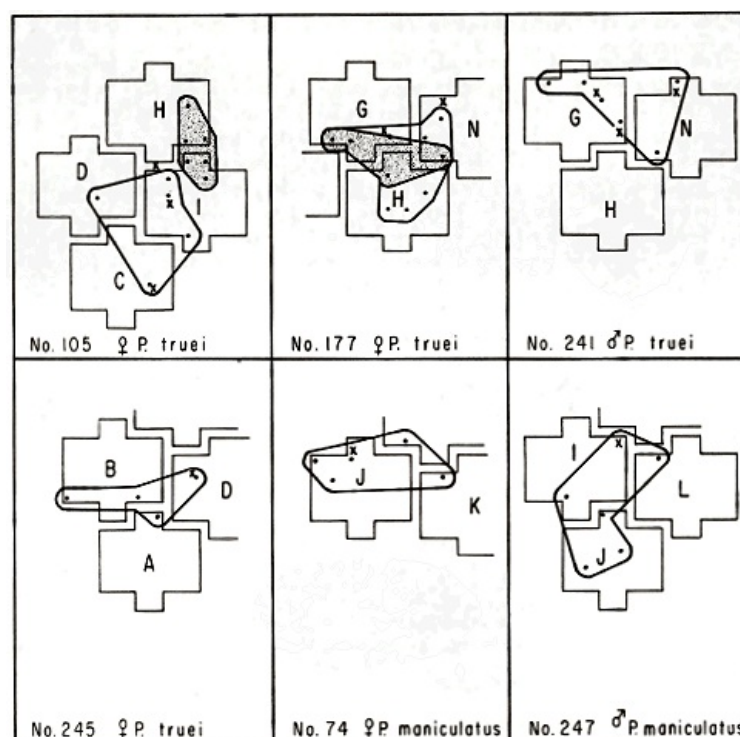


FIG. 15: Diagrams showing estimated home ranges of six individuals of two species of *Peromyscus*, and location of these ranges in the trapping grid. Nesting or hiding places are described in the text, and are indicated on each diagram by an X. Shaded areas represent home ranges estimated from trapping records for 1963; outlined, unshaded areas represent estimated home ranges for 1964.

No. 241, *P. truei*, adult. This male ran into a small hole at the base of a juniper tree 25 feet south of station G7c. The hole was at the fork of the tree, four inches above the ground, and led to a large subterranean chamber in the basal part of the trunk.

This male later ran into a dead juniper log lying on the ground 20 feet southwest of station N3b. No nest was found in the log.

After another capture, this mouse ran to a small juniper log 40 feet southeast of station G3d. There was a nest of shredded juniper bark and many juniper seeds inside the log (Figs. 15-17).

No. 245, *P. truei*, adult. This female ran into a large, hollow juniper log 20 feet northwest of station D4d. No nest was seen, but chewed juniper seeds were noted in and around the log (Fig. 15).

No. 251, *P. truei*, juvenile. This female ran into a dead juniper log beside station P4b. Chewed cones of pinyon pine and chewed juniper seeds were on the ground. A small nest of shredded juniper bark, and a few leaves of serviceberry, were found inside the log. Chewed pinyon nuts and juniper seeds also were present in the nest.



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FIG. 16: (above) Photograph of juniper log at station G3d, which contained the nest of *P. truei* # 241.

FIG. 17: (below) Photograph of dissected juniper log at station G3d, showing the nest of *P. truei* # 241, at end of mattock handle. The nest of shredded juniper bark contained chewed seeds of juniper trees.

No. 267, *P. truei*, juvenile. This male ran into a fallen juniper log 40 feet southwest of station P7a and then disappeared into a hole leading under an adjacent rock. Dissection of the log revealed many chewed juniper seeds inside and beneath the log, but no nest. I did not overturn the large rock or excavate under it.

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No. 268, *P. truei*, adult. This pregnant and lactating female ran into a hollow branch of a partly-dead juniper tree 10 feet south of station O7d. The limb and base of the tree were hollow, and there were large numbers of chewed juniper seeds nearby. Because of time limitations, the branch was not dissected.

No. 74, *P. maniculatus*, juvenile. This female ran into a small circular hole in the ground 13 feet north of station J3a. Excavation revealed that this hole led into the abandoned tunnel of a pocket gopher (*Thomomys bottae*). The tunnel was followed for about four feet, but no nest was found and the tunnel led under a thicket of oak brush which made further excavation impractical (Fig. 15).

No. 247, *P. maniculatus*, adult. This male was followed to a large nest situated at the base of a stump and under a juniper log lying beside the stump, five feet from station I2c. This large nest was built on the ground and was constructed of grasses (*Poa fendleriana*, *Stipa comata*, and *Koeleria cristata*), and contained a few leaves of Gambel oak. It was the largest nest found. Chewed pinyon nuts were in the nest. (Fig. 15).

No. 276, *P. maniculatus*, juvenile. This male ran into a small hole at the base of a dead juniper tree 40 feet north of station O2c. It would have been necessary to cut the tree down to uncover the nest, and this was not deemed to be worthwhile.

The preceding accounts indicate that, in Mesa Verde, nests of *P. truei* usually are associated with hollow juniper logs or branches. In one instance a nest of *P. truei* was found on the ground, under a rock. Shredded juniper bark, and, in one case, grasses were the materials most commonly used for nest building.

Individuals of *P. maniculatus* did not build nests in trees. One nest was found under a stump and adjacent log. Another site was in the abandoned tunnel of a pocket gopher, and a third was under a large rock. The only nest that was unquestionably built by a *P. maniculatus* was constructed of grasses and a few leaves.

It seems unlikely that competition for nesting sites between the two species of *Peromyscus* affects the local distribution of each species. The analysis of nesting sites suggests that *P. truei* is restricted, in Mesa Verde, by the availability of fallen logs, hollow branches, or hollow trunks of juniper trees. My observations lead me to think that within the pinyon-juniper woodland there is a surplus of nesting sites for individuals of *P. truei*. Many juniper trees have dead branches, and hollow juniper logs are abundant throughout the forest. It is inconceivable to me that the population of *P. truei* could reach densities sufficient to saturate every nesting site available to them in the trapping grid.

Sagebrush areas, or brushy zones adjacent to the pinyon-juniper woodland usually do not contain juniper logs; when hollow juniper trees or logs are not available, *P. truei* is not found as resident of such areas. As mentioned earlier, individuals of *P. truei* may venture into such areas to feed if they are adjacent to pinyon-juniper woodland.

An individual of *P. truei* may have more than one nest within its home range (for example Nos. 105 and 241 cited above). Each mouse probably has refuges, each containing a nest, strategically located in its home range. Thus, if a mouse is chased by a predator, or by another mouse, it need not return to its main nest, but can seek refuge in one of its secondary nests. These secondary nests were small and were invariably constructed from shredded juniper bark. Some of these nests were little more than a scant handful of shredded bark that formed a platform to sit upon. Other nests were larger and ball-shaped, with one opening on the side. All of the secondary nests that were found were inside hollow juniper logs. The bark used in construction of the nests had, in each case, been transported from nearby living trees. The logs had previously lost their bark through decay.

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The evidence indicates that these secondary refuges are prepared with considerable care. Not only is the bark transported for some distance, but it is shredded into a soft mass of fibers. When a mouse first establishes itself in a new area, perhaps it begins several such nests before settling upon the most favorable site. The less desirable sites, if still within the animal's range, are then available (barring competition by a new inhabitant) for outlying refuges.

My data do not indicate whether individuals of *P. maniculatus* use a similar arrangement of nests within their home ranges. The population of *P. maniculatus* was sparse in the trapping grid, and the habitat these mice occupied was such as to make following them extremely difficult.

In captivity, both species constructed nests that were indistinguishable to me, when the mice were given cotton, kapok, or pieces of burlap as building material. The cotton or kapok was used directly, but the burlap was shredded into a fine mass of fluffy fibers. The burlap seemed to me to be the best building material, for it maintained its shape best.

Both species constructed nests that resembled inverted bowls. Solitary mice naturally built smaller nests than those built by females with young.

The entrance to the closed nests varied; often the female would bolt through the side of the nest where there was no opening. Sometimes the mice would exit and enter through the top of the nest. In some cases it appeared that the entire nest was closed; probably the occupant had

closed the entrance. Such a closed nest would have the advantage of greatly moderating the microenvironment within the nest, and would allow the animal within to remain comfortable with a minimum expenditure of energy. The larger nests found in the trapping grid resembled those built by captives. Nests built of grasses were always larger than those built of juniper bark. Juniper bark is as easily worked into nests as are grasses, in my judgment. Therefore, difficulty of construction of nests from this material probably does not account for the smaller size of the nests composed of bark. I think the difference in insulating characteristics between the two materials probably accounts for the difference in size of the nests.

REPRODUCTION

In Mesa Verde, *Peromyscus* reproduces from April through September. Reproduction is greatly reduced in the autumn, and most females complete reproduction before October.

Ten of the 20 females of *P. maniculatus*, taken in May, contained embryos; five others were lactating. Lactating and pregnant females were collected on May 5, 1962, indicating that reproduction in some females began in early April. In September, 15 of 34 females were pregnant or lactating, whereas in October only two out of 15 females of *P. maniculatus* were reproducing. Only one female of *P. maniculatus* was found to contain embryos in October. This large adult was taken on October 3, 1963, and had six embryos, each five millimeters long. She probably would have produced a litter later in October, and would have been nursing into November. A report of October breeding in north-central Colorado described nine of 23 females of *P. maniculatus* as being in a reproductive state; seven were lactating and one was pregnant between October 26 and 31, 1952 (Beidleman, 1954:118).

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In the Museum of Natural History, the University of Kansas, there are 35 females of *P. maniculatus* more than 144 millimeters in total length taken from Mesa Verde in November, 1957 (Anderson, 1961:53). None of these contained embryos, and no pregnant females have been taken from the park in November.

P. truei and *P. maniculatus* reproduce at about the same time. A female of *P. truei* prepared as a specimen on May 10, 1964, contained four embryos, each 20 millimeters long, indicating a breeding time in mid-April. Svihla (1932:19) reported the gestation period for non-lactating *P. truei* to be 25 to 27 days and for lactating individuals, 40 days. Lactation tends to increase the gestation period of other *Peromyscus* by about five days (Asdell, 1964:266). The gestation period of nine non-lactating females of *P. m. rufinus* was reported by Svihla to be 23 to 24 days. Lactation increased the length of the period of gestation in this subspecies to between 23 and 32 days (mean for seven females 26.57 ± 0.73 , Svihla, 1932:19).

Females of *P. truei* were observed in various stages of reproduction from June through September. Ten of the 20 females of *P. truei* taken in September were reproducing; four contained embryos and the other six were lactating. In October, only one of 17 females caught in snap traps was lactating. Lactating females were caught in live-traps as late as October 23, although most females had ceased reproduction by then. No pregnant or lactating females were observed in November.

In *P. maniculatus*, puberty has been placed at 32 to 35 days for females weighing 13 grams, and in males at from 40 to 45 days, at weights of 15 to 16 grams (Jameson, 1953:45). In *P. truei*, the weight of the testes is reported to rise in March and diminish through September, with accessory organs following the same cycle (Asdell, 1964:267). Young of *P. truei* nurse for about one month, although some litters may not be weaned until 40 days of age. Young of *P. maniculatus* are weaned between 22 and 37 days of age (Svihla, 1932:30).

Twenty-six pregnant females of *P. maniculatus*, taken in the breeding seasons of 1961-1964, contained from one to eight embryos each; the mean was 4.65 ± 1.67 . Other investigators have found similar mean values in this species (Asdell, 1964:266).

Thirteen females of *P. truei* taken in the breeding seasons of 1961-1964, contained from three to six embryos each; the mean was $4.0 \pm .912$. Svihla (1932:25) reported litter sizes, at birth, of two to five and a mean of 2.84, in 19 litters. Other investigators have reported litter sizes of one to five with a mean of 3.4, and one to six with a mean of 3.6 (Asdell, 1964:268). Apparently *P. truei* does not have more than six young per litter.

In captivity, females of both species began reproduction in early February. These captives had been kept for several months at a temperature of 21 degrees Centigrade, and on a daily photoperiod of 15 hours. Some captive males had enlarged, scrotal testes in January; the extended photoperiod and warm temperature probably influenced the breeding condition. In both species testes of wild males caught in autumn after late September and on through the winter were abdominal, except for one male of *P. maniculatus* which had enlarged, scrotal testes on October 15.

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Dates at which different animals arrived at breeding condition varied, in part owing to subadults (young of the year) appearing in the catch from early summer to late autumn. Some adult females appeared to be pregnant or lactating throughout much of the summer and early autumn, whereas other females, that were caught a number of times, apparently reproduced only

once in the summer.

Some females may fail to breed even though they are mature enough to do so. One female of *P. truei* captured eight times (August 30 to September 20) was a juvenile when first caught, and was classed as young (in postjuvinal molt) on September 10. She did not reproduce in her first breeding season, unless she did so after September 20, which is unlikely. Another female of *P. truei* was an adult when first caught, and was caught 12 times (August 21 to October 25). At no time were her mammae enlarged and she was not lactating or pregnant. It is improbable that she reproduced earlier in the season, for teats of mice that have reproduced earlier usually are enlarged to such a degree that previous parturition is clearly indicated. It was surprising to catch a female, of any age, 12 times in two months without sign of reproductive activity.

Only one female of *P. maniculatus* did not show reproductive activity. She was a juvenile on July 19 when first caught; a subadult on August 28 when caught the third time, and an adult on October 23 when caught the fifth time.

Burt reported a rest period of a month or more in the summer, in Michigan, during which many females of *P. leucopus* did not reproduce. They began to breed again in late summer at about the time when young of the year began reproducing (Burt, 1940:17, 19). Abundant mast was correlated with reproductivity in autumn, according to Jameson (1953:54), who thought that "food is a basic determinant of the autumn reproduction" of *P. leucopus*.

Little has been written about the length of time males remain in breeding condition. Difficulties in determining breeding condition are many. Fertility customarily is determined by sectioning testes and noting the presence or absence, and relative abundance, of sperm. This procedure necessarily sacrifices the individual and indicates the breeding condition at only one moment and for only the individuals sacrificed. My observations of males caught a number of times in live traps shed some light on the breeding condition of males, but the investigator is likely to err in extrapolating physiological data from morphology when he notes whether the testes are abdominal or scrotal and whether they are enlarged or small. It was assumed that testes that have not descended, and that lie within the abdominal cavity, are not capable of producing viable sperm. This is the condition in most juveniles, and in all males during winter. As the breeding condition is attained, testes descend into the scrotum. Soon the testes and their accessory organs enlarge and are readily apparent.

Howard (1950:320) reported that numerous males of *P. leucopus* sired litters when their testes appeared to be abdominal, and therefore questioned whether the criterion of descended testes is valid as an indicator of breeding condition. My captive males of *P. maniculatus* and *P. truei* did not sire litters when their testes were abdominal, even though such males were left with adult females for as long as four to five months (August through December). Captive pairs of both species yielded no evidence of reproductive activity until January when, as mentioned earlier, some of the males had scrotal testes. Young were born first in early February, although their parents had been confined together since the preceding August. Jameson reported the testes of fecund males of *P. maniculatus* as almost always 8.0 millimeters or larger (Jameson, 1953:50). Testes that are at least partly scrotal must be considered as being capable of producing motile sperm, even though this may not be the case for all individuals.

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Toward the beginning and end of the breeding season the testes and accessory organs of wild mice were small and probably produced few if any sperm. At these times some males apparently were so frightened by being handled that the testes were retracted into the inguinal canals. It would have been easy to consider such males as having abdominal testes when in fact they did not. In such cases the scrotum usually was noticeably enlarged; it was found also that in many cases the testes returned to the scrotal position if the mouse was held gently for a few minutes. Careful handling of animals was found to prevent, or at least retard, retraction of the testes. Retraction of the testes from the scrotum was not a problem at the height of the breeding season when the testes were engorged.

I had originally assumed that all adult males would be fertile throughout the breeding season, and that any males with abdominal testes would be subadults or young of the year. This assumption was an oversimplification; all adult males did not reach breeding condition at the same time of year. My data do not support a firm conclusion, for it is difficult to follow non-captive individuals throughout a breeding season, owing to sporadic appearance of animals in traps. Nevertheless, observations of mice that were trapped a number of times indicated the following:

- 1) Some adult males that had abdominal testes in the middle of July reached breeding condition as late as late August and even late September.

- 2) Some juvenal males had scrotal testes at the time their postjuvinal molt was just beginning to be apparent on their sides. Most juvenal males did not have scrotal testes, and many juveniles that appeared repeatedly in traps from mid-July through late October did not attain breeding condition. A mouse that was a juvenile in mid-July must have been born in mid-June.

- 3) Apparently animals born early in the breeding season may reproduce later in that season, whereas those born later in the breeding season tend not to breed until the following year.

Possibly cooler evening temperatures in July and August, due to the relatively larger amounts of precipitation in those months, inhibit reproductive development of late-born young. Most plants have ceased vegetative growth and have produced seeds by this time; but the interrelationships between growing seasons, climatic conditions, and reproductive physiology are unknown.

Only one adult of each species had scrotal testes after late September; the *P. truei* had scrotal testes on October 24, 1963, and the *P. maniculatus* had scrotal testes on October 15 of that year.

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GROWTH

Growth of captive *P. maniculatus* and *P. truei* is discussed in several reports. One of the most complete is that of McCabe and Blanchard (1950) on *P. m. gambelii* and *P. t. gilberti* in California. A detailed discussion of the dentition in *P. truei* and wear of the teeth in different age groups is given by Hoffmeister (1951). Molt in these species has been considered by a number of authors (Collins, 1918; McCabe and Blanchard, 1950; Hoffmeister, 1951; Anderson, 1961). The report by McCabe and Blanchard is valuable because molt is compared between the two species from the first to the twenty-first week of postnatal development.

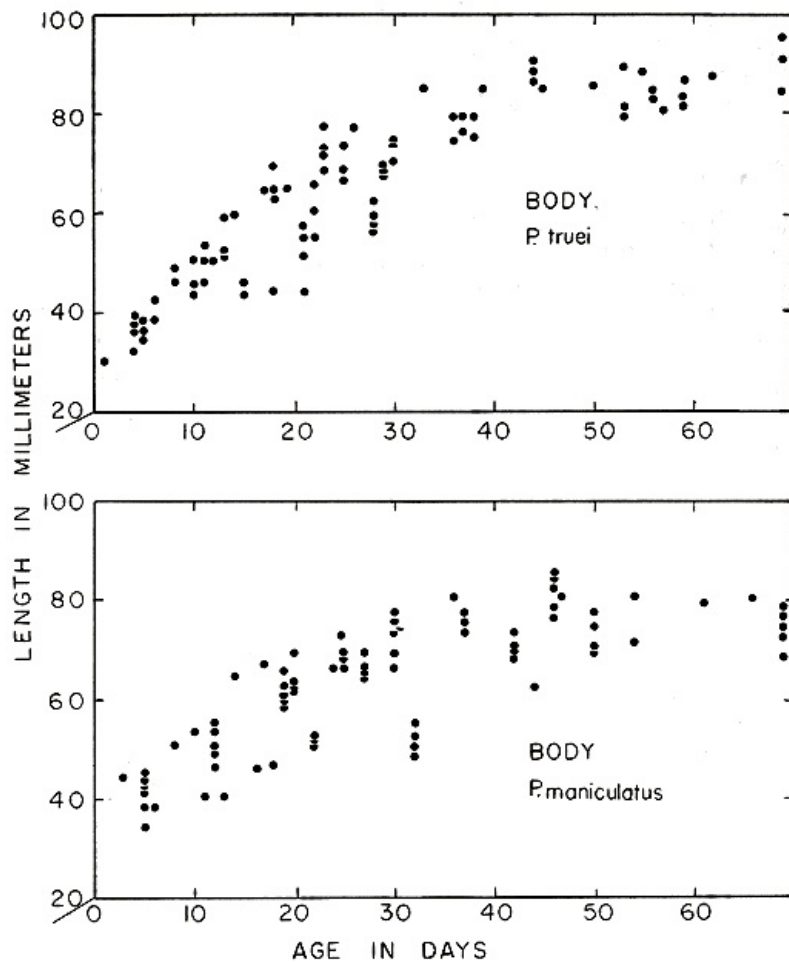


FIG. 18: Scatter diagram of postnatal growth of captive mice, showing increase in length of bodies from birth to 70 days of age. The records for *P. truei* represent 11 individuals of five litters; those for *P. maniculatus* represent 17 individuals of four litters.

The thoroughness of the above-mentioned studies is readily apparent to those who have worked with mice of the genus *Peromyscus*. Nevertheless, the ecology of local populations of *P. maniculatus* and *P. truei* as reported for the San Francisco Bay area (McCabe and Blanchard, 1950) has little relationship to the ecology of mice of other subspecies of these species, in southwestern Colorado. Indeed, the preferred habitats, and to some extent the behavior, differ strikingly in Colorado and California.

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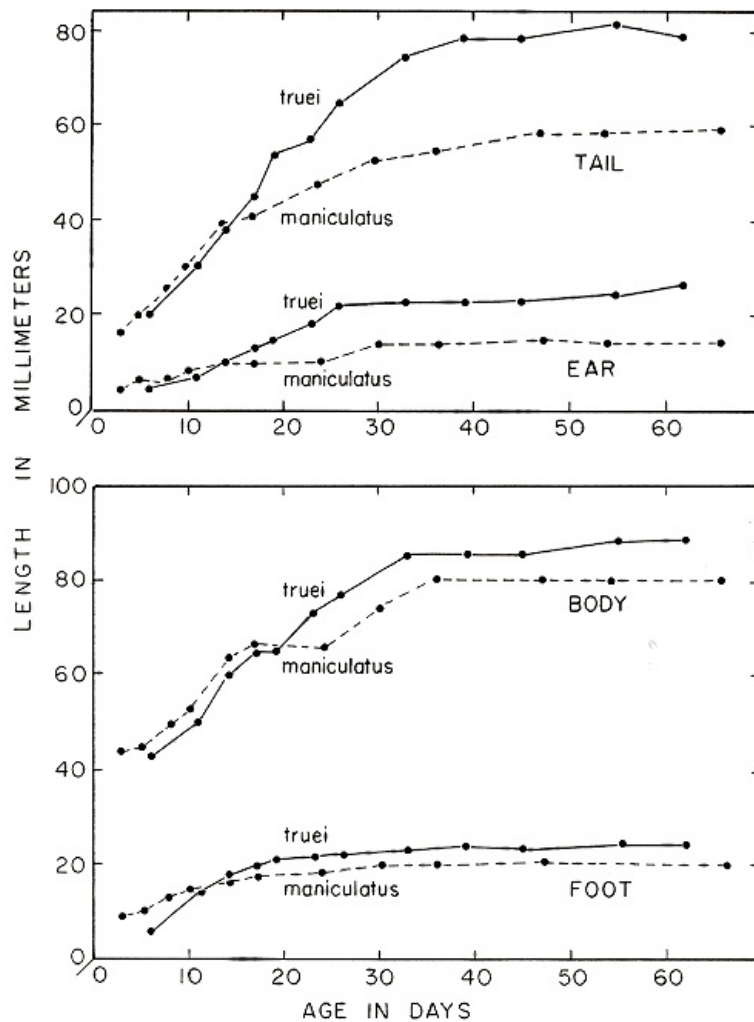


FIG. 19: Graphs showing postnatal growth of solitary captive individuals of *P. truei* and *P. maniculatus*, representing the only young in each of two litters.

Figures 18 and 19 show that some litters grow appreciably faster than others, but the end results are about the same. Since the young were measured at irregular intervals, statistical procedures for calculating confidence limits of the curves were not applicable. [471]

Solitary young reared by one female of each species, attained maximum size more rapidly than animals having litter mates (Fig. 19). Nevertheless, solitary individuals and individuals from litters all reach essentially the same size 50 days after birth.

The gestation time of *P. truei* is several days longer than that of *P. maniculatus*, and the young of *truei* are fewer and heavier than those of *maniculatus*. As would be expected, *truei* remains in the nest longer and nurses longer than *maniculatus*.

Young of each species grow rapidly for the first month, and attain, in that time, the largest percentage of their adult size; they grow rapidly up to sometime between the thirtieth and fiftieth days. Thereafter the rate of growth diminishes and the animals begin to gain weight rather than continuing to extend the lengths of the body and appendages.

Figure 19 reveals that the appendages of young *maniculatus* attain most of their length about a week earlier than those of *truei*. Young *truei* acquire mobility and coordination somewhat later than young *maniculatus*, but both species are seemingly equal in these respects by about the end of the second week.

Length of gestation period, number and size of embryos, amount of time spent in the nest, and time required for bodily growth are all of major importance in determining the relative success of *truei* and *maniculatus*. These parameters will be considered further in the discussion.

PARENTAL BEHAVIOR

In the laboratory, pregnant females were supplied with either kapok, cotton, or a piece of burlap with which to make a nest. The kapok or cotton was used directly by the mice in constructing a hollow, compact, moundlike nest. When burlap was used for nest building, the female first completely frayed the cloth by chewing it into a fluffy mass of fibers.

When the top of a nest was opened to inspect young, the female would attempt to pull the nesting material back into shape by means of forefeet and teeth. The mother's defensive posture

was to cover the young with her body, often lying over them and facing upward, toward the investigator. In this semi-recumbent position, the female would attack the investigator's fingers with her forefeet and teeth. Often the female would stand bipedally and use the forefeet and teeth to mount the attack. If at this time a young chanced to wander away from the mother, she would quickly pick it up and place it in the nest at her feet.

When disturbed, females of both species, but especially *P. maniculatus*, often dove headlong under their nest or into the wood shavings on the floor of the cage. This type of retreat was most often used when young were nursing. Time is required even by the mother to disengage nursing young, and this mode of escape is the most expedient. The mother disengaged nursing young by licking around their faces and pushing with her paws.

Nursing females of both species tolerated the male parent in the nest. A male and female often sat side by side in the nest and by means of their bodies participated in covering the young. Males were not observed to attempt any defense of the nest, or of the young. Females were tolerant of older young in the nest when another litter was born and was being nursed. In one nest, a female of *P. truei* gave birth to a litter of three when her older litter was 29 days old. The three older young continued to nurse until they were 37 days old, at which time they were removed from the cage. The female appeared tolerant of this nursing by members of the older litter, but appeared to give preference to the wants of the younger offspring. [472]

One female of *P. truei* lost or killed all but one young of her litter; at about the same time, a *P. maniculatus* and all but one of her young inexplicably died. Since the remaining young *maniculatus*, a male, was just weaned and was considered expendable, I placed him in the cage with the female *truei* and her 33-day-old, male offspring. The reaction to the newcomer was unexpected. The female immediately covered the *P. maniculatus* and her own young and prepared to defend them against me. Later, when the *P. maniculatus* was disturbed, he had only to emit a squeak and the female *truei* would run to cover and protect him. When the young male of *P. truei* was 69 days old the female kept him out of the nest, but still kept the male *maniculatus* in the nest with her. Although the female was somewhat antagonistic to her own young, she did not injure him, but only kept him out of the nest. The male *truei* was left in the cage with his mother and the *P. maniculatus* from September 23 to December 10. None of the mice had any apparent cuts on the ears or tail to indicate fighting. As much as seven months after the *P. maniculatus* was introduced into the cage, the female *truei* continued to cover him with her body whenever there was a disturbance. The male *maniculatus* not only tolerated this attention, but ran under the female *truei* when frightened. "Adoption" of young of another species has been reported for a number of animals, but, without further evidence, it is not possible to postulate that such adoptions occur between species of *Peromyscus* in nature.

Young males are tolerated by their mothers after weaning. One young male *maniculatus* was left in the cage with his mother from the time of his birth in autumn until late February of the following year. A litter was born on February 24. A young male *P. truei* was also left in the cage with his mother until he had acquired most of his postjuvinal pelage; the female and male usually sat together in the cage.

Females of both species sometimes eat their young when the young die shortly after birth. One female of each species killed three of her four young, and ate their brains and viscera. In one of these cases, the female, of *P. maniculatus*, also died; the female of *P. truei* was the same one that adopted the surviving *P. maniculatus*. The female *truei* continued to nurse her one remaining young for at least several days after killing three of his litter mates. A reason for this cannibalism might have been that I had fed these mice for several weeks on a mixture of grains low in protein content. Inadequacy of this diet for nursing females may have caused them to become cannibalistic. The feed of all captives was changed to Purina Laboratory Chow after the young were killed.

Transportation of Young

Females of both species transported their young either by dragging them collectively while the young were attached to mammae, or by carrying them one at a time in the mouth. Since mice of the subgenus *Peromyscus* have three pairs of nipples, they probably transport only six young collectively. Svihla (1932:13) has stated that both pectoral and inguinal teats are used in transporting young, in contrast to Seton's reputed assertion that only inguinal nipples were used. But Svihla neglected to cite Seton's complete statement. Seton (1920:137) recorded a litter of three as using only the inguinal mammae, but on the following page recorded the use of both inguinal and pectoral mammae by another litter of four. My findings agree with those of Svihla. Nursing females of both species were removed periodically from cages by lifting them by the tail. The young would hang onto the mammae and the female would clutch the young to her with all four feet. Young two weeks old or older crawled behind the mother while nursing. [473]

The method of transporting young in the mouth has been mentioned by Seton (1920:136) and described by Lang (1925) and Hall (1928:256). These authors report that the mother picks the young up in her paws, and places it ventral-side up in her mouth, with her incisors around it. The young are not picked up by the skin on the nape of the neck, as are the juveniles of dogs and cats. I have found that females of both species of *Peromyscus* carry their young ventral-side up in their mouth while the young are small, and sometimes when the young are older. Generally, when females of *P. truei* moved young weighing more than 10 grams, the female grasped the young

from the dorsal side, across the thorax just posterior to the shoulders, and held them with the incisors more or less around the animal. Perhaps this method was used with older young because of the observed tendency of the larger young to resist being turned over and grasped from the ventral side, and because their increased weight would have made it difficult, if not impossible, for the mother to pick them up with her paws. The young rarely resisted the efforts of the mother to move them by this method; when grasped across the thorax by the mother, the young would remain limp until released. Some females of *P. truei* would drag almost fully grown young back into the nest in this manner. I have not observed older young of a comparable age to be moved by females of *P. maniculatus*. The females of *P. maniculatus* appear to be somewhat less concerned than those of *P. truei* for the welfare of their young once they are mobile and close to being weaned.

The following listing describes changes in postnatal development of young, of each species, from birth to nine weeks of age.

<i>P. truei</i>	<i>P. maniculatus</i>
<p>FIRST WEEK: At birth, young are helpless, red overall, small with wrinkled skin. Pinna of ear folded over and closed; eyes closed; digits not separated from rest of foot. Redness diminished by fourth day.</p> <p>Hair apparent by fifth day; dorsal one-half or two-thirds of body more darkly pigmented than venter by fourth day. Young squeak loudly and suck; sometimes crawl, but drag hind legs.</p>	<p>At birth, young are helpless, red overall, smaller than <i>P. truei</i>, skin wrinkled. Ear, eyes, and digits as in <i>P. truei</i>.</p> <p>Redness decreases and disappears by fourth day.</p> <p>Hair apparent by fourth day; body bicolored by end of week.</p> <p>Young squeak loudly; sucking more pronounced than in <i>P. truei</i>; may crawl, but drag hind legs.</p>
<p>SECOND WEEK: Appreciable increase in size; head about 60 percent larger than at birth, by 14th day, and still large in proportion to body. Toes on hind foot separated more from foot. Body well haired by end of week; dorsum dark gray, venter whitish; tail bicolored in most, but not haired. Pinna of ear unfolded and open by end of week. Through day 10, use hind legs to push, but by end of week use legs to crawl; difficult to hold, squirm but do not bite. Walk behind mother while nursing; agile.</p>	<p>As in <i>P. truei</i>.</p> <p>As in <i>P. truei</i>, but somewhat more advanced.</p> <p>Body well haired by end of week; dorsum dark gray with brownish tint; venter whitish; tail bicolored in most, but not haired.</p> <p>As in <i>P. truei</i>, but developments somewhat more advanced.</p> <p>Crawl well by end of week; difficult to hold, squirm but do not bite; agile.</p>
<p>THIRD WEEK: Eyes open on 16th to 21st day. Gray pelage of dorsum brownish. Apparently there is a molt line progressing posteriorly from nose; the molt line has moved to shoulder region by end of week; pelage anterior to line browner, grayer posterior to it. Tail haired and weakly bicolored in some individuals by end of week. Young walk and jump well; squirm but rarely bite.</p>	<p>Eyes open on 16th to 20th day, partly open earlier.</p> <p>Pelage of dorsum brownish; molt line across shoulders progressing posteriorly; browner anterior to line, grayer posterior to it.</p> <p>Tail haired and bicolored in all individuals.</p> <p>Young walk and jump well; fight and bite when handled.</p>
<p>FOURTH WEEK: Begin to eat solid foods at 23-29 days, but also nurse. Molt line about 3/4 inch posterior to head. Juvenal pelage completed by end of week. Some young have brownish hair on front legs. Young roll over on backs and use feet to ward off litter mates that are dropped into nest, or into container, with them.</p>	<p>Some young eat grain by 24th day; others continue to nurse.</p> <p>Juvenal pelage complete; no sign of postjuvenal molt.</p> <p>As in <i>P. truei</i>; also, all jump well, and fight fiercely when handled.</p>

FIFTH WEEK: Young weaned on 30th to 40th day; some nurse beyond 30th day if female is lactating. Juvenal pelage complete and no postjuvenal molt apparent on dorsum.	All young weaned before or by end of week; none observed to nurse beyond 30th day, even if female is lactating. Juvenal pelage complete; postjuvenal pelage not apparent on most, but probably present on all, and concealed under juvenal pelage.
SIXTH WEEK: Postjuvenal pelage apparent in most individuals under juvenal pelage, especially along lateral line.	Postjuvenal molt apparent in most young; almost complete in some, except above tail and on flanks.
SEVENTH WEEK: Postjuvenal pelage apparent in most young; in some the molt line has progressed well up on the sides, but not to mid-dorsum.	Postjuvenal pelage apparent in all young; less distinct molt line than in <i>P. truei</i> .
EIGHTH WEEK: All individuals growing; total lengths of 156-170 millimeters; weight 17-22 grams.	Growth completed in some individuals; those in larger litters have total lengths of 128-144 millimeters; weight 14-17 grams.
NINTH WEEK: Testes partly scrotal in one male on 59th day. New brown pelage encroaching on saddle and on hind legs; postjuvenal molt completed in some individuals by eleventh week.	"Scrotum in season usually large, vaginae open, evidence of coitus common." (McCabe and Blanchard, 1950:39). Postjuvenal molt completed in some individuals by end of week. New pelage tends to be concealed under juvenal pelage longer than in <i>P. truei</i> .

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CHANGES OWING TO INCREASE IN AGE

Increase in length of limb bones, changes in proportion of bones in the skull, eruption and degree of wear of teeth, and changes in pelage can be used to ascertain relative age. Different investigators might choose different limits for the three categories young, subadult, and adult. Museum specimens were assigned to one of five age groups listed below mostly on the basis of tooth wear, essentially as described by Hoffmeister (1951:1).

Juvenile: M3 just breaking through bony covering of jaw or showing no wear whatsoever.

Young: M3 worn smooth except for labial cusps, and M1 and M2 showing little or no wear.

Subadult: M3 worn smooth; labial cusp may persist, but is well worn; M1 and M2 having lingual cusps worn, but not smooth; labial cusps showing little wear.

Adult: Lingual cusps worn smooth and labial cusps showing considerable wear; labial cusp of M3 may persist.

Old: Cusps worn smooth; not more than one re-entrant angle per tooth discernible, frequently none.

For live animals examined in the field, criteria based on pelage and breeding condition were used, as follows:

Juvenile: Only gray, juvenal pelage present.

Young: Subadult pelage apparent on lateral line or on sides; body usually smaller than in adults.

Subadults: Subadult pelage having mostly replaced juvenal pelage; mice often as large as adults; testes of males often abdominal in breeding season; gray juvenal pelage may persist on head of some individuals.

Adult: Adult pelage present; body usually largest of all animals in population; females may have enlarged mammae from nursing previous litters; testes of males usually scrotal in breeding season; gray pelage may be present on head of some individuals.

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Old individuals in the field could not be distinguished from adults; hence any animals that appeared older, or more developed, than subadults were classified as adults.

In *P. truei*, subadult pelage appears first on the lateral line or on the flanks; new pelage is ochraceous and contrasts markedly with the gray juvenal coat. In *P. maniculatus*, the subadult pelage contrasts less with the juvenal coat; the new pelage progresses from anterior to posterior

over the body in the same manner as in *truei*, but replaces the juvenal coat in a less distinct manner than in *truei*. As a result, contrast often is lacking between juvenal and subadult pelages in *maniculatus* making it difficult to assign an individual to one of these two age categories when examined in the field. In museum specimens, the subadult pelage is much more noticeable because it can be compared with the pelages of other specimens. The subadult pelage in *P. maniculatus* is duller than the adult pelage: In *P. truei* the subadult and adult pelages appear to have an equal sheen.

In early winter, the postjuvenal pelage acquired by young individuals of *P. truei* was thick and luxuriant and indistinguishable from the winter pelage of adults. My observations lead me to conclude that individuals born late in the breeding season molt from juvenal summer pelage directly into winter adult pelage. Technically, this new coat is the postjuvenal one, yet it cannot be distinguished as such after the molt is completed.

ANOMALIES AND INJURIES

Anatomical anomalies were rare in the individuals of *Peromyscus* that I examined. When anomalies were found they were striking, principally because of their low rate of occurrence.

One female of *P. truei*, born in captivity, had a congenital defect of the pinna of the right ear, noted on the fifteenth day after birth. Closer examination then and later revealed that the pinna was normal in all respects except that the tip was missing. The tip showed no evidence of injury. When the mouse was subadult, this defective pinna was approximately half as long as the normal pinna. The topmost part of the defective pinna was somewhat more constricted in circumference than the normal one.

On September 11, 1963, a subadult male of *P. truei* was captured that had five functional toes on its right front foot, the only one of more than 175 individuals caught and handled in the field that exhibited polydactyly. The front foot was examined closely in the field, but it could not be determined how or where the extra bones of the sixth toe articulated. *Peromyscus* normally has four full-sized toes on each front foot, and a small inner toe hardly more than an enlarged tubercle, having no nail.

A few mice of both species had broken toes or claws torn off. Such injuries were more common on toes of the hind foot. In several instances the toes were shortened, as if by marking, although the animals concerned had been marked earlier by clipping toes other than the injured toes. The reason for these injuries is not apparent, although they could have been caused by fighting, or from having been caught in doors of Sherman live traps. [477]

Toes of several mice were swollen and inflamed due to small glochids of cacti that were stuck in them. Apparently the mice had stepped on the glochids by chance, for I found no evidence that *Peromyscus* of either species eats cacti.

One *P. truei* had a broken tail; three other individuals had tails about one-half normal length. One *P. maniculatus* had a shortened tail. Some of these injuries probably were caused by the Sherman live traps; several individuals of *P. truei* were released after having been caught by the tail by the spring-loaded door of these traps.

On October 17, 1963, an adult *P. truei* had a bleeding penis; when this mouse was recaptured on October 25, the injury was healed.

Losses Attributed to Exposure in Traps

Observations of wild mice caught in live traps suggest that metabolic maturity is reached later than physical and reproductive maturity. In such trapping, it became apparent that juvenal and young mice suffered from exposure to cold and to heat much more than did subadult or adult mice. Although traps were carefully shaded and ample nesting material and food provided, some mice died in the traps. An overwhelming majority of these mice were juveniles and young.

Traps were checked in the morning, both in the summer and autumn, yet mice died in traps that were barely warm to the touch, in summer, and cool to the touch in autumn. Older mice frequently were found in traps that were warm, or even hot, to the touch; yet the older mice rarely died in such traps. Apparently the tolerance of adults is much greater to heating and chilling. Greater bulk and perhaps longer pelage in adults might provide sufficiently better insulation to account for this difference.

Occasionally juvenal mice were found in traps in a sluggish and weakened condition, especially in autumn when nights were cool. In such cases the mice were either cupped in the hands and warmed until lively enough to fend for themselves, or, if especially weakened, were taken to the laboratory. None of such animals that were returned to the laboratory lived for more than two weeks. Most of those released in the field did not reappear in the traps.

I conclude that juvenal and young mice placed under stress by overheating or cooling die immediately or live only a few days. Subadult and adult animals tolerate more extreme conditions of overheating or cooling, presumably because they are able to regulate their internal

temperature better, by either losing or retaining heat more effectively.

Mice found dead in overheated traps had salivated heavily, and may also have licked the fur on their chests to increase heat dissipation. One such adult, of *P. truei*, had a wet chest when he was taken from a warm trap; when released, this mouse ran to a nearby plant of *Comandra umbellata*, and ate a few of the succulent leaves before running off. This individual was trapped several times later in the summer, and apparently suffered no ill effects from the exposure.

Dental Anomalies

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Abnormalities in the formation and occlusion, or decay of teeth, are relatively rare in wild mammals. Of all bodily structures, the teeth apparently are under the most rigid genetic controls; they form early in the embryo and follow rigidly specified patterns in their ontogeny. Apparently any deviation from the normal pattern of tooth formation is quickly selected against. All specimens of *P. m. rufinus* and *P. t. truei* in the collection of the Museum of Natural History at the University of Kansas, and in my collection, were examined for dental anomalies. A total of 317 specimens of *P. m. rufinus* and 54 specimens of *P. t. truei* were examined. The following specimens were found to have abnormalities:

K. U. 69361, *P. maniculatus*, adult: Small bundles of plant fibers are lodged between all upper teeth and have penetrated the maxilla anterior to the left M1. The maxillary bone is eroded away from the roots of all teeth. The anteriormost roots of both lower first molars are almost completely exposed, because the dentary has been abraded away.

K. U. 76041, *P. maniculatus*, young: A piece of plant fiber is wedged between the left M2 and M3. The maxillary bone has eroded away from around the roots of M3, indicating the presence of an abscess in this area.

K. U. 69362, *P. maniculatus*, adult: All teeth in the lower right tooth-row are greatly worn, especially on the lingual side. The labial half of the right M1 is all that remains; decay is apparent both in the crown and roots on the lingual side of this tooth.

K. U. 69397, *P. maniculatus*, old: The maxillae have eroded away from around the anterior roots of each first upper molar, leaving these roots unsupported.

C. L. D. 231, *P. maniculatus*, old: The teeth in this female are greatly worn; re-entrant angles are not visible in any teeth. A circular hole, 0.1 millimeter in diameter, exists in the dentine immediately over (when viewed from the underside of the skull) the posterior root of the right M1. The crowns of the teeth are greatly reduced in height, and the dentine is thin.

Anomalies in the Skull

Wormian bones and other abnormalities in the roofing bones are noted, as follows:

K. U. 76090, *P. maniculatus*, young: The interparietal is divided; the divided suture is in line with the suture between the parietals. The interparietal is 7.8 millimeters long.

K. U. 76091, *P. maniculatus*, young: A wormian bone, 0.5 millimeter by 0.2 millimeter, lies between the anterior border of the interparietal and the posterior border of the left parietal, at a point midway between the center line of the skull and the posterolateral border of the parietal bone.

C. L. D. 248, *P. maniculatus*, adult: An oval wormian bone, 1.1 millimeters long and 0.6 millimeter wide, lies between the parietals at their posterior margin; the long axis of the bone is parallel to the long axis of the skull.

C. L. D. 246, *P. maniculatus*, juvenal: The interparietal is divided equally by a suture. An oval wormian bone, 0.3 millimeter long and 0.1 millimeter wide, lies between the frontals, midway between the anterior and posterior borders of these bones.

C. L. D. 656, *P. maniculatus*, young: A small, rounded wormian bone lies between the right parietal and interparietal, lateral to the posterior junction of the suture between the parietals. This bone extends anteriorly into the parietal bone from the suture of the interparietal and parietal. This bone is 0.7 millimeter wide, and extends 0.6 millimeter into the parietal.

C. L. D. 662, *P. maniculatus*, subadult: An elongated, diamond shaped wormian bone closes the suture between the parietal bones. This bone is 2.3 millimeters long and 0.8 millimeter wide.

K. U. 34735, *P. truei*, old: The anterior one-quarter of the left parietal bone is slightly depressed; and the posterior one-third of the left frontal and anterior one-quarter of the left parietal are thin and sculptured. This malformation of the roofing bones posterior to the orbit probably is not the result of a break, for the orbital part of the frontal bone is normal. The frontal-parietal sutures are in the normal positions on both sides of the skull.

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The above-mentioned anomalies do not appear to be correlated with age or locality at which the specimens were taken. Apparently such anomalies are present throughout the population, but in a small percentage of specimens.

FOOD HABITS

Mice of the genus *Peromyscus* are known to eat a wide variety of plants and arthropods, and to be highly opportunistic in selection of food (Cogshall, 1928; Hamilton, 1941; Williams, 1955, 1959a; Jameson, 1952; Johnson, 1962). In order to determine possible food preferences, captive mice of both species were fed plants indigenous to Mesa Verde. Entire plants were used whenever possible; available seeds also were offered (Tables 5, 6). All feeding experiments were replicated with at least six different individuals in order to minimize the trends resulting from individual preferences or dislikes. The mice of each species tended to be consistent in their feeding.

The plant species listed in Tables 5 and 6 were those that were eaten or rejected by a majority of the individuals tested.

Plant material eaten by *P. maniculatus* and refused by *P. truei* included only the leaves and stem of *Viguiera multiflora*. Plant material eaten by *P. truei* and refused by *P. maniculatus* included the leaves of *Calochortus gunnisonii* and the leaves and stem of *Erigeron speciosus*.

TABLE 5—Plants, or Parts of Plants, Eaten by Captive Individuals of *P. truei* in Mesa Verde National Park, Colorado. 0 = not eaten, + = eaten, - = not offered.

Species of Plant	Leaves	Stem	Flower	Seeds
<i>Amelanchier utahensis</i>	-	-	-	+
<i>Calochortus gunnisonii</i>	+	+	-	+
<i>Chaenactis douglasii</i>	0	0	-	-
<i>Chrysothamnus depressus</i>	0	0	0	-
<i>Chrysothamnus nauseosus</i>	+	0	0	-
<i>Comandra umbellata</i>	+	+	-	-
<i>Erigeron speciosus</i>	+	+	-	-
<i>Eriogonum alatum</i>	-	-	-	+
<i>Juniperus osteosperma</i>	-	-	-	+
<i>Lupinus caudatus</i>	0	0	+	-
<i>Lithospermum ruderales</i>	0	0	-	0
<i>Mellilotus alba</i>	+	+	+	+
<i>Mellilotus officinalis</i>	+	+	+	-
<i>Orthocarpus purpureo-albus</i>	+	+	+	+
<i>Pedicularis centranthera</i>	+	+	-	-
<i>Penstemon linarioides</i>	+	+	-	+
<i>Pinus edulis</i>	-	-	-	+
<i>Polygonum sawatchense</i>	+	+	-	0
<i>Solidago petradoria</i>	0	0	0	-
<i>Viguiera multiflora</i>	0	0	0	0

Plant material eaten by captives of both species included *Calochortus gunnisonii*—stem and seeds; *Comandra umbellata*—leaves and stem; *Eriogonum alatum*—seeds; *Penstemon linarioides*—leaves and stem; *Pinus edulis*—seeds; and *Juniperus osteosperma*—seeds. [480]

Plant materials refused by both species of mice included the leaves and stem of *Chaenactis douglasii*, the leaves, stem and seeds of *Lithospermum ruderales*, and the leaves, stem and flowers of *Solidago petradoria*.

Cricetine rodents chew plant and animal foods thoroughly; contents of their stomachs appear as finely-particulate fragments. These fragments invariably contain pieces of epidermis from ingested plants. Due to the presence of cutin in the cell walls, epidermis is last to be digested.

Microscopic analysis of plant epidermis is useful in helping to determine food habits of various animals (Dusi, 1949; Williams, 1955, 1959a; Brusven and Mulkern, 1960; Johnson, 1962). The microscopic analysis of stomach contents provides a practical method of determining which plants are eaten by rodents. Contents of stomachs and intestines were removed from mice caught in snap traps, and from preserved specimens. The contents were placed on a piece of bolting silk, washed thoroughly with running water, stained with iron-hematoxylin and mounted on slides, or stored in 70 per cent ethanol (Williams, 1959a; Douglas, 1965).

TABLE 6—Plants, or Parts of Plants, Eaten by Captive Individuals of *P. maniculatus* in Mesa Verde National Park, Colorado. 0 = not eaten, + = eaten, - = not offered.

Species of Plant	Leaves	Stem	Flower	Seeds
<i>Artemisia ludoviciana</i>	0	0	-	-
<i>Calochortus gunnisonii</i>	0	+	-	+
<i>Chaenactis douglasii</i>	0	0	-	-
<i>Comandra umbellata</i>	+	+	-	-

Erigeron speciosus	0	0	-	-
Eriogonum alatum	-	-	-	+
Juniperus osteosperma	-	-	-	+
Lappula redowskii	0	0	-	+
Lithospermum ruderales	0	0	-	0
Orthocarpus purpureo-albus	0	0	+	+
Penstemon linarioides	+	+	+	-
Pinus edulis	-	-	-	+
Purshia tridentata	+	+	-	-
Sitanion hystrix	0	0	-	0
Solidago petradoria	0	0	0	-
Sphaeralcea coccinea	+	+	-	+
Stipa comata	0	0	-	+
Viguiera multiflora	+	+	-	-

In order to analyze these epidermal fragments, a collection of plants was made within the park. Slides of the epidermis of these plants were prepared and analyzed for diagnostic characters (Douglas, 1965:197-199). Features such as the stomatal arrangement in relation to subsidiary cells; the types of trichomes, scales and glands; the cellular inclusions such as starch grains, mucilage and resins are of taxonomic value (Metcalf and Chalk, 1950). The configuration of the anticlinal cell walls is useful in separating species that are similar in other respects (Douglas, 1965:199).

The following species of plants, and other food items, were identified in the stomach or intestinal contents of *Peromyscus maniculatus*: [481]

Agropyron smithii
Artemisia sp.
Eriogonum umbellatum
Lupinus ammophilus
Penstemon linarioides
Phlox hoodii
Stipa comata
 Arachnid legs

Stomach and intestinal contents of *P. truei* contained the following food items:

Artemisia nova
Artemisia sp.
Penstemon cf. *barbatus*
Penstemon cf.
linarioides
Poa fendleriana
 Arachnid legs
Eriogonum sp.
Gutierrezia sarothrae
Yucca sp.
 Chitin
 Feathers

Many of the plants eaten by the mice had large numbers of crystals in the epidermis. Druses were the most abundant, but raphid crystals also were seen. Every slide contained at least one species of plant which contained druses. Such crystals are composed mostly of calcium oxalate (Esau, 1960:41). In Mesa Verde, families of plants having crystals include: Boraginaceae, Chenopodiaceae, Compositae, Cruciferae, Leguminosae, Liliaceae, Malvaceae, Ornargraceae, Rosaceae, and Saxifragaceae. Calcium oxalate is a highly insoluble compound and is innocuous if it passes through the gastro-intestinal tract without being absorbed. In rats of the genus *Neotoma*, some calcium oxalate passes through the intestines unchanged, but large amounts of calcium are absorbed through the intestine. The urine of pack rats is creamy in color and contains calcium carbonate. It is not understood how these rats metabolize the highly toxic oxalic acid, when converting calcium oxalate to calcium carbonate (Schmidt-Nielsen, 1964:147-148). Apparently calcium oxalate passes through the intestine unchanged in both species of *Peromyscus*, for their urine is clear and yellowish.

Although both species of mice appear to prefer plants having soft leaves, some plants having coarse leaves also are eaten. Many of the slides contained isolated sclerids. The stomach contents of one individual of *P. truei* contained a small fragment of the epidermis of *Yucca*. This fragment may have come from a young shoot. It is unlikely that *Peromyscus* would eat the larger, coarser leaves of *Yucca*.

Pinyon and juniper nuts were found in nests of all mice. Captive mice were especially fond of pinyon nuts, and these probably provide a substantial part of the diet of *Peromyscus* in the autumn and early winter. The winter staple of *P. truei* appears to be juniper seeds. Nesting sites of this mouse often could be located by the mounds of discarded seeds lying nearby.

Both species eat pinyon and juniper seeds; since *P. truei* lives in the forest, it has better access to these foods than does *P. maniculatus*. Mice remove the embryos of juniper seeds by chewing a small hole in the larger end of the seed. The seed coats of juniper are extremely hard, and a considerable amount of effort must be expended to remove the embryo. Captives discarded the resinous and pithy, outer layers of juniper berries. Individuals of *P. truei* are adept climbers. Since many juniper berries remain on branches throughout the winter, the ability of these mice to forage in the trees would be especially advantageous when snow covers the ground.

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WATER CONSUMPTION

Peromyscus maniculatus is ubiquitous, occurring in habitats ranging from mesic boreal forests to arid southwestern deserts. Most subspecies of *P. maniculatus* live in moderately mesic or near-mesic environments, but a few have adapted to arid conditions. It has been assumed that the success of *P. maniculatus* in inhabiting such diverse habitats is associated with its adaptability to different kinds of food and varying amount of available water (Williams, 1959b:606).

Throughout its range *P. maniculatus* coexists with one or more other species of *Peromyscus* that are more restricted in distribution. *Peromyscus truei* is one such species.

Both species live under xeric or near-xeric conditions, for the climate of Mesa Verde is semi-arid. Other than a few widely-scattered springs, there are no sources of free water on the top of the Mesa Verde land mass; thus animals inhabiting the park must rely upon moisture in the plants and other foods they eat, or upon dew.

Several investigators have studied water consumption in mice of the genus *Peromyscus* (Table 7). Dice (1922) did so for the prairie deer mouse, *P. m. bairdii*, and the forest deer mouse, *P. leucopus noveboracensis*, under varying environmental conditions. He found that both species drank about the same amounts of water per gram of body weight, and that food and water requirements did not differ sufficiently to be the basis for the habitat differences between these species. Neither of his samples was from an arid environment. Chew (1951) studied water consumption in *P. leucopus*, and recently reviewed the literature on water metabolism of mammals (Chew, 1965). In his studies of five subspecies of two species of *Peromyscus*, Ross (1930) found significant differences in water consumption between species but not between subspecies within a species. One of the subspecies of *P. maniculatus* tested was from a desert region, whereas the other two were from mesic areas along the coast of California.

Lindberg (1952) was the first to measure water consumption of both *P. m. rufinus* and *P. t. truei*, the species and subspecies with which my experiments are concerned. Lindberg also tested the ability of five races of *Peromyscus* to survive reduced water rations. Unfortunately, the subspecies chosen for these experiments did not include *P. t. truei* or *P. m. rufinus*. Lindberg (1952:25) found that the "amounts of water consumed by various species of *Peromyscus* from different habitats within the same climatic region were not conclusively different." However, he did find significant differences between some subspecies from different geographical areas. For example, he found no significant difference in water consumption between *P. m. bairdii* from Michigan and either *P. m. blandus* or *P. m. rufinus* from New Mexico, but he found a highly significant difference between *P. l. noveboracensis* from Michigan and *P. l. tornillo* from New Mexico. Lindberg also found that the subspecies of *Peromyscus* that consumed the least water, and that were best able to survive a reduced water ration, were those from the more xeric climatic areas.

Some mammals may be able to change their diets in times of water stress, and thereby compensate for a shortage of water. At such times, *Dipodomys* selects foods with high percentages of carbohydrates and conserves water by reducing the amounts of nitrogenous wastes to be excreted (Schmidt-Nielsen *et al.*, 1948).

Williams (1959b) found that *P. m. osgoodi* from Colorado drank more water on a diet rich in protein than on one rich in carbohydrates. But, her mice on a high carbohydrate diet used less than a normal amount of water for a period of only five weeks; at the end of the five weeks they were drinking about as much as they had been when on the control diet of laboratory chow. Likewise, mice adjusted to the high protein diet by consuming more water; but by the end of the fifth week their daily water consumption approximated the amount drunk when fed on laboratory chow. Because of these results, Williams questioned the validity of the assumption that *P. maniculatus* is able to inhabit a diversity of habitats because of its adaptability with respect to food and water requirements.

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I conducted a series of experiments on water and food consumption by individuals of *P. truei* and *P. maniculatus*. It was thought that if there were differences in water or food consumption, or both, knowledge of them might help to explain the obvious differences in habitat preferences of these two species in Mesa Verde National Park.

In August of 1965, 30 individuals of *P. truei* and *P. maniculatus* were trapped in Mesa Verde National Park at elevations of 7000-8400 feet, and transported to Lawrence, Kansas, where the experiments were carried out.

Mice were housed in individual metal cages (10 x 7.5 x 5 inches), having removable tops of

wire mesh, and an externally-mounted water bottle that had a drop-type spout extending into the cage. Cages were on one of five shelves of a movable tier of shelving, and were rotated randomly, from one shelf to another, each week. A layer of dry wood shavings covered the bottom of each cage. A control cage was similarly equipped.

The mice were kept in a room in which temperature and photoperiod were controlled. The ambient air temperature of this room was 20 to 23 degrees Centigrade throughout the experiments, and averaged 21 degrees. Humidity was not controlled, but remained low throughout the experiments. The room was illuminated for eight hours each day, from about 9 A. M. to 5 P. M.

The animals were fed at least once a week, at which time all remaining food was weighed and discarded, and the remaining water was measured. Tap water was used in all of the experiments. The cages were cleaned each week. Each time the cages containing mice were handled, the control cage was handled in the same way. The amount of evaporation was determined each week by measuring the water remaining in the bottle of the control cage.

Water and food consumption of individuals of *P. maniculatus* and *P. truei* were measured when the mice were fed diets of differing protein content. To my knowledge, the only other study in which water consumption was measured for mice of the genus *Peromyscus* on diets of different protein contents was by Williams (1959b). Because of the limited number of animals available, it was decided that the best results could be obtained by placing all individuals on the same diet for a predetermined number of weeks, then on a second diet for a certain period, and so on.

Each mouse was weighed at the beginning, at the mid-point, and at the end of each experiment. The mice were weighed on the same days, at times when they were inactive. Because weights of individual mice differ, water and food consumption was calculated on the basis of the amount consumed per gram of body weight per day. All foods were air-dry and contained a negligible amount of water.

First, food and water consumption was measured for nine individuals of each species on a diet of Purina Laboratory Chow. This chow contains not less than 23 per cent protein and 4.5 per cent fat, and about 57 per cent carbohydrate. Since the mice had been maintained on this diet for several months prior to the experiments, food and water consumption was measured for a period of only two weeks. Individuals of *P. truei* consumed more total water and more water per gram of body weight than individuals of *P. maniculatus* (Table 7).

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Next, 10 mice of each species were placed on a diet of Purina Hog Chow for a period of four weeks. This chow contains not less than 36 per cent protein and one per cent fat, and about 42 per cent carbohydrate. Both species increased their daily water consumption immediately after being placed on this diet (tables 7 and 11). On the high protein diet, *P. truei* again consumed much more water than did *P. maniculatus* (tables 7 and 9).

TABLE 7—Food and Water Consumption of *Peromyscus maniculatus* and *P. truei* When Fed Diets of Different Protein Content. Food and Water Consumption Are Determined for the Grams, or Milliliters, Consumed per Gram of Body Weight per Day; Daily Totals Are also Given.

<i>Peromyscus maniculatus rufinus</i>						
Diet per cent protein	No. mice	Food /gram /day ± S. D.	Total grams /day	Water /gram /day ± S. D.	Total water /day	
Lab Chow 23	9	.201 .074	4.455	.262 .183	5.751	
Hog Chow 36	10	.238 .060	5.232	.496 .186	10.749	
Corn 11	11	.149 .044	3.144	.174 .012	3.696	
<i>Peromyscus truei truei</i>						
Diet per cent protein	No. mice	Food /gram /day ± S. D.	Total grams /day	Water /gram /day ± S. D.	Total water /day	
Lab Chow 23	10	.216 .070	6.353	.373 .119	10.880	
Hog Chow 36	10	.230 .079	6.966	.653 .189	19.571	
Corn 11	10	.158 .010	4.318	.332 .016	9.034	

The tendency of both species to eat more of the hog chow than they ate when fed standard laboratory chow may reflect a higher palatability of the hog chow. Both species consumed similar amounts of food per gram of body weight, on each of the diets (Table 7). The larger *P. truei* requires more grams of food per day than the smaller *P. maniculatus*, but this slight difference in food consumption probably has no effect on the distribution of these species within Mesa Verde.

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The results obtained with the low protein diet were strikingly different from those of the first two experiments. In this experiment the same groups of mice were placed on a diet of whole, shelled corn for a period of six weeks. The corn contained less than 11 per cent protein, about three per cent fat, and about 80 per cent carbohydrate.

By the end of the first week, on the low protein diet, all mice had reduced their water intake by about half the amount used per day on the high protein diet (Table 7). There was not a statistically significant difference, for either species, between the average amounts of water

drunk in the first and in the sixth weeks of the experiment.

The data in [Table 7](#) show that on all three diets, individuals of *P. maniculatus* drank less water per gram of body weight than individuals of *P. truei*. Variation in water consumption was high; some individuals of *P. maniculatus* that drank more than the average amount for the species, consumed as much water as some individuals of *P. truei* that drank less than the average amount. In general, individuals of *P. maniculatus* drank about half as much water each day as individuals of *P. truei*. Individuals of both species were consistent in their day-to-day consumption.

TABLE 8—Amounts of Mean Daily Water Consumption as Reported in the Literature for Species of *Peromyscus*. Figures in Parentheses are Means; Those Not in Parentheses Are Extremes.

	Mean daily ml./gm. wt./day	Water consumption total ml. per day	Temperature	Humidity	Per cent dietary protein	Investigator
<i>P. m. rufinus</i>	(.262) .124-.699	(5.70) 2.71-15.07	20-23	low	23	[A]
<i>P. m. rufinus</i>	(.101)	(2.39)	20-25	24-47		[B]
<i>P. m. osgoodi</i>	.16-.25	3.2-4.3	18-22	10-20	23	[C]
<i>P. m. bairdii</i>	(.126) .082-.177	(1.74) 1.12-2.72	21	25-68		[D]
<i>P. m. bairdii</i>	.124-.182	(2.37-3.17)	20-25	24-47		[B]
<i>P. t. truei</i>	(.372) .224-.561	(10.80) 7.0-16.92	20-23	low	23	[A]
<i>P. t. truei</i>	(.085)	(2.77)	20-25	24-47		[B]
<i>P. l. nov.</i>	.057-.117	1.36-2.29	21	25-68		[D]
<i>P. l. nov.</i>		(5.36)	18	62.5		[E]

[A] Douglas [B] Lindeborg, 1952 [C] Williams, 1959 [D] Dice, 1922
[E] Chew, 1951

[Table 8](#) shows average water consumption for several species of *Peromyscus* as reported in the literature, and as determined in my study. It is difficult to compare my results with most of the data in the literature, because of a lack of information as to protein, fat, carbohydrate, and mineral contents of foods used in other studies. Lindeborg (1952) and Dice (1922) fed mice on a mixture of rolled oats, meat scraps, dry skimmed milk, wheat germ, etc. described by Dice (1934). Their data on water consumption in *P. maniculatus* indicate that this mixture probably is lower in protein content than Purina Laboratory Chow, that was used in my experiments and those of Williams' (tables [8](#) and [9](#)).

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The amount of dietary protein consumed under natural conditions is not known for most wild animals. One index of the minimum amount of protein necessary is the amount required for an animal to maintain its weight. At best, this can be only an approximation of the required amount, for other factors, such as stress, disease, change in tissues during oestrus or gonadal descent, and changes in constituents of the diet other than protein, would all be expected to affect the body weight (Chew, 1965:145-147).

The data in [Table 7](#) show that both species vary their food intake with changes in diet. [Table 10](#) shows weight changes that took place in individual mice when fed each of the three diets. A change in weight of one gram cannot be considered as important, for the weight of an individual mouse fluctuates depending upon when he last drank, ate, defecated or urinated.

The only significant changes in weight occurred when mice were fed low protein food ([Table 10](#)). Individuals of *P. truei* lost 15.72 per cent and individuals of *P. maniculatus* lost 10.03 per cent of their total body weights on this diet. This indicates that food having a protein content of more than 10 per cent but less than 23 per cent is required for maintenance of weight in these animals.

Although knowledge of the amount of water consumed, *ad libitum*, by adult mice is valuable information, maintenance of the population depends upon reproduction and dispersal of young individuals. My trapping data indicate that only two to three per cent of the adults live long enough to breed in consecutive breeding seasons. In spring, the breeding population is composed largely of mice that were juveniles or subadults during the latter parts of the breeding season. Therefore, the critical time for the population may well be the time when the season's young are being produced. Any unfavorable circumstances, such as a shortage of food or water, that would affect pregnant or lactating females would be of primary importance to the integrity of the population.

TABLE 9—A Comparison of Mean Daily Water Consumption of Mice on High Protein Diets. Numbers in Parentheses Are Average Values; All Others Are

Species	Mean daily H ₂ O consumption		Temperature	Relative humidity	Investigator
	cc./gm. wt.	Total cc.			
<i>P. m. osgoodi</i>	(0.27-0.54)	(4.6-9.3)	18-22 C	10-20	Williams, 1959
<i>P. m. rufinus</i>	(0.496) 0.186-0.764	(10.74) 4.54-16.57	20-23 C	low	Douglas
<i>P. t. truei</i>	(0.653) 0.429-1.031	(19.57) 13.28-30.28	20-23 C	low	Douglas

One would assume that pregnant and lactating females require more water than non-pregnant females. One might also assume that juveniles require different amounts of water and food than adults. Juveniles have less dense pelage than adults, and probably are affected more by their immediate environment because of their relatively poor insulation. Juveniles might also be in an unfavorable situation insofar as water conservation is concerned, because they are actively growing, and in most cases, acquiring new pelage; it is well known that these are times of stress for the individual.

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TABLE 10—Weights of Mice at Start and Finish of Experiments, Showing Changes in Weight and Mean Weights, and Means of Changes in Weight (mean delta).

<i>Peromyscus truei truei</i>									
No.	Lab Chow			Hog Chow			Corn		
	Start	End	Δ	Start	End	Δ	Start	End	Δ
1	31.0	31.3	0.3	31.3	32.3	1.0	32.3	29.0	3.3
5	31.1	30.5	0.6	30.5	32.8	2.3	32.8	28.7	4.1
6	27.6	27.1	0.5	27.1	29.5	2.4	29.5	27.3	2.2
7	28.0	26.3	1.7	26.3	27.5	1.2	27.5	22.2	5.3
13	25.8	30.6	4.8	30.6	27.0	3.6	27.0	22.2	4.8
14	26.9	30.7	3.8	30.7	31.4	0.7	31.4	27.3	4.1
15	25.4	29.4	4.0	29.4	29.8	0.4	29.8	24.0	5.8
16	33.0	32.9	0.1	32.9	30.5	2.4	30.5	26.0	4.5
19	37.6	38.1	0.5	38.1	31.8	6.3	31.8	22.0	9.8
20	23.5	25.8	2.3	25.8	26.2	0.4	26.2	22.9	3.1
Ȳ	28.9	30.2	1.8	30.2	29.8	2.0	29.8	25.2	4.7

<i>Peromyscus maniculatus rufinus</i>									
No.	Lab Chow			Hog Chow			Corn		
	Start	End	Δ	Start	End	Δ	Start	End	Δ
2	23.0	20.7	2.3	20.7	21.1	0.4	21.1	18.6	2.5
3	22.7	23.1	0.4	23.1	23.8	0.7	23.8	20.7	3.1
4	22.0	21.1	0.9	21.1	21.8	0.7	21.8	21.3	0.5
8	26.3	28.1	1.8	28.1	15.8	2.3	25.8	23.8	2.0
9	21.5	24.0	2.5	24.0	25.1	1.1	25.1	21.8	3.3
10	22.5	20.0	2.5
11	21.0	22.1	1.1	22.1	20.8	1.3	20.8	19.0	1.8
12	22.3	23.2	0.9	23.2	21.3	1.9	21.3	20.4	0.9
17	18.9	20.0	1.1	20.0	19.2	0.8	19.2	19.4	0.2
18	17.0	17.5	0.5	17.5	19.5	2.0	19.5	17.3	2.2
21	18.9	18.1	0.8	18.1	20.2	2.1	20.2	17.3	2.9
Ȳ	21.4	21.8	1.2	21.8	21.8	1.3	21.9	19.9	2.2

Lindeborg (1950:76) found that 15 days before parturition, pregnant and non-pregnant females of *P. m. bairdii* drank about the same amounts of water, that females consumed more water after the young were born and until they were weaned, and that water consumption increased with an increase in weight in young, growing individuals. He found that in the later stages of pregnancy, females of *P. m. bairdii* required 36 per cent more water than non-breeding females; at 14 days after parturition, nursing females required 111 per cent more water than non-breeding females, and at weaning time, 158 per cent more water. Dice (1922:35) reported a 217 per cent increase in drinking of *P. m. bairdii* before parturition, and 171 per cent increase while nursing.

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Several females of both species were bred prior to the start of the experiments described herein. As a consequence, it was possible to determine water and food consumption for lactating females of each species, and later, for their litters. Pregnant and lactating females, and newly-weaned litters, were fed laboratory chow throughout this experiment. The litters were separated from their mothers as soon as the young were observed to be eating, or no later than 33 days

after birth.

Table 11 shows the amounts of water and food consumed by two females of each species while they were either in the later stages of pregnancy, or were nursing. Although the data in Table 11 do not cover the full developmental time of the litters involved, it is obvious that both lactating females of *P. truei* and one female of *P. maniculatus* consumed more water than the average for their species (Table 7). Water and food consumption was measured for both females of *P. truei* while they were nursing. The female that gave birth to litter A was left in the cage with the male for several days after the litter was born, resulting in another litter being born about 27 days after the first. Therefore, the record of this female represents an extreme case of stress (probably a common occurrence in nature) in which a female is nursing one litter while she is pregnant with a second.

The record of the female of *P. truei* that gave birth to litter B is the most complete, including data from the fifth day after parturition until the young were weaned on the thirty-third day after parturition. The record of the female of *P. maniculatus* that gave birth to litter C covers the last 10 days of nursing before the young were weaned. After being separated from her litter, this female drank more than the average amounts of water, on both high and low protein diets. Although the food and water were lost several times for the female of *P. maniculatus* with litter D, the period of time covered by the 14 days when water and food consumption were measured includes times just prior to parturition and to weaning of the young.

TABLE 11—Water and Food Consumed by Nursing Females of *P. truei* and *P. maniculatus*. Consumption Is Calculated on the Basis of Amount (Milliliters or Grams) Consumed per Gram of Body Weight per Day, as well as Total Amounts Used per Day.

Female	Water used	No. days	Average weight	ml. H ₂ O/gm./day	Total water/day	No. in litter
<i>P. truei</i> (A)	447	17	33.00	.796	26.29	3
<i>P. truei</i> (B)	676	28	32.70	.738	24.14	3
<i>P. maniculatus</i> (C)	191	10	19.45	.983	19.10	5
<i>P. maniculatus</i> (D)	133	14	24.35	.224	5.46	6
Female	Food used	No. days	Average weight	gms. food/gm./day	Total food/day	No. in litter
<i>P. truei</i> (A)	214.7	26	33.00	.250	8.26	3
<i>P. truei</i> (B)	120.5	24	32.70	.153	5.02	3
<i>P. maniculatus</i> (C)	47.8	10	19.45	.246	4.78	5
<i>P. maniculatus</i> (D)	180.1	21	27.42	.312	8.58	6

It is interesting that the female of *P. maniculatus* with litter C used much more than the average amount of water for the species, and even more per gram of body weight than lactating females of *P. truei*. Conversely, water consumption of the female with litter D was within one standard deviation of the mean for all adults of *P. maniculatus*. I infer that at least some lactating females of *P. maniculatus* are better adapted to aridity than are some lactating females of *P. truei*.

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Table 11 also shows food consumption of the four females discussed above. All females, with the exception of the female with litter D, consumed amounts of food that lie within one standard deviation of the means for their species. The female with litter D had the most young, consumed the most food but drank the least water of the four females. Later, when separated from her litter and placed on the low protein diet, this female drank only .046 milliliters of water per gram of body weight per day. This figure is less than one-third of the average amount (.174) for this species (Table 7).

The records of water and food consumption for litters A, C, and D are given in Table 12; the mice in litter B persisted in placing wood shavings in the opening of the spout on their water bottle, causing loss of the water. The data show that mice in all three litters had an average water and food consumption within one standard deviation of the mean for adults of their respective species (Tables 7 and 12). It is interesting that juveniles of both species require no more food and water per gram of body weight than adults. This indicates that if a young animal survives the rigors of postnatal life until it is weaned, it is then at no disadvantage as far as food and water consumption are concerned. This would be greatly advantageous to the species, as a population, for the young could disperse immediately upon weaning, and go into any areas that would be habitable for adults of the species.

TABLE 12—Food and Water Consumed by Young Mice in Litters, After Weaning. Consumption Is Calculated on the Basis of the Amount (Milliliters or Grams) Consumed per Gram of Litter Weight per Day; Total Amounts Are Shown and Can Be Divided by Litter Size for Average Individual Consumption. Litter Sizes Are as Follows: A=3; C=5; D=6.

Litter	Total water used	Total corrected	No. days	Average total weight	ml. H ₂ O/gm./day	Total water/day
<i>P. truei</i> (A)	1207	1120	57	58.30	.337	19.64
<i>P. maniculatus</i> (C)	1427	1340	57	76.14	.308	23.50
<i>P. maniculatus</i> (D)	700	670	31	58.80	.367	21.61
Litter	Total food used	No. days	Average total weight	Gms./gm. wt./day	Total food/day	
<i>P. truei</i> (A)	651.2	50	58.30	.223	13.02	
<i>P. maniculatus</i> (C)	743.8	57	76.14	.171	13.04	
<i>P. maniculatus</i> (D)	471.1	31	58.80	.258	15.19	

The young of pregnant and lactating females are the animals in the population most likely to be affected by a deficient supply of water. Drought could reduce the water content of the vegetation to such a level that pregnant or lactating females might find it difficult, if not impossible, to raise litters successfully. If such a drought persisted throughout an entire breeding season, the next year's population would be reduced in numbers, for even under normal climatic conditions it is almost exclusively the juveniles that survive from one breeding season to the next. If such a hypothetical drought occurred, lactating females of *P. truei* would be in a more critical position than lactating females of *P. maniculatus*.

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In order to determine how much water was available to mice in the peak of the breeding season, samples of the three most common plants in the study area were collected each week for analysis of their moisture content. Plants were placed in separate plastic bags that were sealed in the field. About a dozen plants of each species were used in each determination. Only the new tender shoots of the plants were collected, for it was assumed that mice would eat these in preference to the tougher basal portions of the plants. The plants were taken immediately to the laboratory and were weighed in the bag. Then the bag was opened and it and the contents placed in an incubator at 85 degrees Fahrenheit for a period of at least 72 hours. About 48 hours were required to dry the plants to a constant weight. The dried plants were weighed and their percentages of moisture were determined. Plants lose some water upon being placed in a closed bag; small drops of water appear immediately on the inner surface of the bag. Therefore, the bag must be weighed at the same time as the plants and the weight of the dried bag must be subtracted later.

The three kinds of plants chosen were among the most widely distributed species in the study area, and all three grow close to the ground, within reach of mice. Stems and leaves of two of the plants, *Comandra umbellata* and *Penstemon linarioides*, were readily eaten by captive animals. Mice also were observed to eat leaves of *Comandra* after being released from metal live traps. The third species, *Solidago petradoria*, differs from the other two in having a short woody stem that branches at ground level. The more succulent shoots arise from this woody stem. The leaves of *Solidago* are coarse and were not eaten by captive mice. Nevertheless, this species was chosen because it is widely distributed and has the growth form of several other species of plants in the area.

The graph in [Figure 20](#) shows that *Comandra* contains the highest percentage of water through most of the summer. Water content of both *Penstemon* and *Comandra* was greatly reduced in the dry period that occurred in early July. *Solidago* maintained a relatively constant percentage of moisture; perhaps its woody stem serves for water storage. The rains of July and August increased the percentage of moisture in the plants, but not to the extent expected. Neither *Solidago* nor *Comandra* reached the levels of hydration of early June. All plants were collected at or about 11 A. M. At night, when mice are active, these plants would be expected to contain a higher percentage of water than in the daytime.

The data in [Figure 20](#) indicate that mice probably are not endangered by water shortages in most years. The average percentage of moisture in the plants studied was as follows: *Comandra umbellata* 62.33 per cent; *Solidago petradoria* 53.0 per cent; *Penstemon linarioides* 49.28 per cent. If a mouse were to eat ten grams of plant material containing 50 per cent moisture, it would provide him with five grams of food and five grams of water, both of which exceed the minimum daily needs for non-pregnant adults of either species.

The data indicate that there are sufficient differences in water consumption between *P. maniculatus* and *P. truei* to account for their habitat preferences in Mesa Verde National Park. In

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years having average precipitation, water present in the vegetation has the potential for providing enough moisture for the needs of both species. Extended drought would affect individuals of *P. truei* more adversely than individuals of *P. maniculatus*.

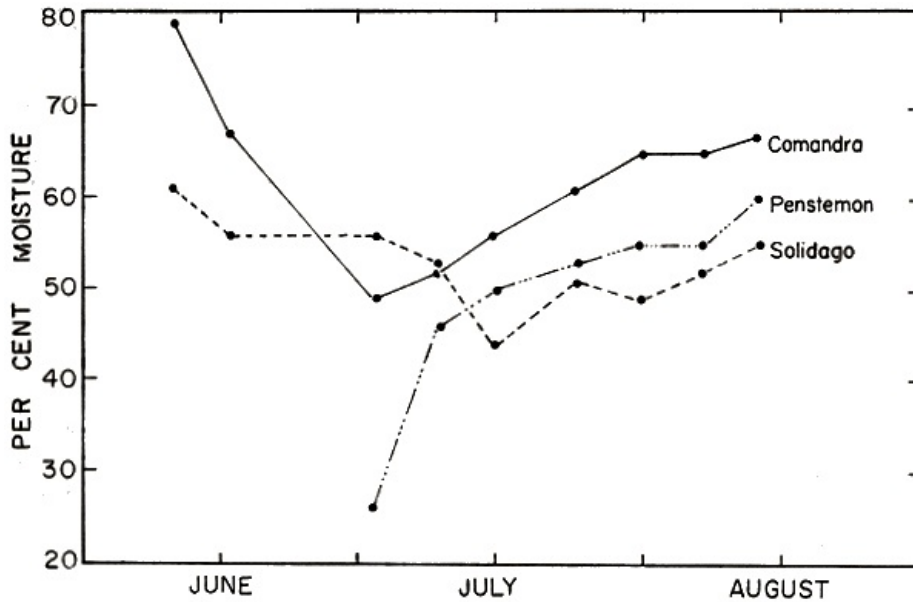


FIG. 20: Graph showing percentages of moisture contained during the summer of 1964, by three abundant and widely-distributed species of plants in Mesa Verde National Park, Colorado.

PARASITISM

Ectoparasites were collected by placing specimens of *Peromyscus* in separate plastic bags soon after death, adding cotton saturated with carbon tetrachloride, closing the bag for about five minutes, then brushing the fur of the specimen above a sheet of white paper. The ectoparasites were sorted and sent to specialists for identification. Endoparasites were saved when stomach and intestinal contents were examined. Larvae of botflies were collected from mice in the autumn of 1962, placed in sand in containers, and kept over winter until they hatched. Eyelids of alcoholic specimens were inspected for mites by an authority on these organisms.

In 1961, the incidence of parasitism by botflies was the highest for the period 1960-1966. *P. maniculatus* was more heavily infected with warbles than was *P. truei*. In 84 individuals of *P. maniculatus* taken in September 1961, from Morfield Ridge, 32.1 per cent had warbles. The average number of warbles per animal was 1.24, and it was not uncommon to find two or three warbles per mouse. Sixty-nine per cent of the warbles were in the third instar stage, and the rest were in the second instar stage. Warble infestation was higher in the first half of September (40 per cent of mice infected) than in the second half of the month (30 per cent infected), but a larger percentage of the warbles were found (69 per cent) in the second half of the month.

In October 1961, 12.9 per cent of 62 *P. truei* were infected with warbles. The average number of warbles per infected mouse was 1.37. Seventy-three per cent of the warbles were in the third instar stage; the rest were in the second instar stage. Warble infestation was higher in the first half of October (16 per cent of the mice infected) than in the second half of the month (5.5 per cent infected). These mice were collected from several localities on Chapin Mesa, in pinyon-juniper woodland. [492]

In Mesa Verde the greatest incidence of infestations is in late September and early October. This agrees with the finding of other investigators (Sealander, 1961:58).

Sealander (1961) investigated hematological values in deer mice infected with botflies, and found that infected mice had significantly lower concentrations of hemoglobin than non-infected mice. Myiasis, associated with infection by *Cuterebra*, is likely to lead to a lowering of the physiological resistance of a segment of the population, and perhaps to a subsequent decline in the population (Sealander, 1961:60).

Mice infected by warbles were less agile than non-infected mice. Other investigators also have reported awkwardness in locomotion in infected mice (Scott and Snead, 1942:95; Sealander, 1961:58). Test and Test (1943:507) noted that parasitized mice did not appear to be emaciated, and this was also true of parasitized mice at Mesa Verde. Healed wounds, where warbles had emerged, were apparent on a number of mice. The warbles, and wounds, usually were found on the flanks and backs of the mice. The large, third instar larvae weighed about one gram apiece; there is little doubt that such large larvae induce trauma in their hosts.

The highest rate of infestation by botflies occurred in 1961, the year in which the population

density of *P. maniculatus* was near its peak. The population of this species was reduced considerably in 1962, and remained low through 1964. In 1965, the density of *P. maniculatus* appeared to be increasing. Other investigators have reported that increased incidence of *Cuterebra* infestation in deer mice coincides with lower population densities and with a downward trend in the population (Scott and Snead, 1942:95; Wilson, 1945). My data indicate that this may not be the situation in Mesa Verde.

The intestines or stomachs of almost all individuals of *P. maniculatus* contained parasites. Endoparasites were less abundant in individuals of *P. truei*. This heavier infestation of *P. maniculatus* by tapeworms, roundworms, and spiny-headed worms probably reflects the larger proportion of insects eaten by *P. maniculatus* than by *P. truei*.

The most common endoparasite encountered was the nematode, *Mastophorus numidica* Seurat, 1914; it was found in the stomachs of many individuals of both species of *Peromyscus*. This nematode has been reported from *Felis ocreata* in Algeria, *Bitis arietans* in the Congo, and from the following mammals in the United States: *Canis latrans*, *Peromyscus crinitus*, *P. gossypinus*, *P. maniculatus*, *P. truei*, *Onychomys leucogaster*, *Dipodomys ordii*, *Reithrodontomys megalotis*, and *Eutamias minimus*.

Individuals of *P. maniculatus* obtained on the northern end of Wetherill Mesa in May and June of 1962 had numerous ectoparasites. At this time, the population of *P. maniculatus* was high, but on a downward trend.

My data and observations lead me to conclude that individuals of *P. maniculatus* are more heavily parasitized by both botflies and endoparasites than are individuals of *P. truei*. The reasons for this unequal amount of parasitism in two species of mice occurring in the same general area remain obscure. [493]

The kinds of endoparasites and ectoparasites collected from *P. maniculatus* and from *P. truei* are listed below (m = present in *P. maniculatus*, t = present in *P. truei*).

ACARINA: Ixodidae: *Dermacentor andersoni* mt, *Ixodes angustus* mt, *Ixodes spinipalpis* m. Laelaptidae: *Androlaelaps glasgowi* m. Myobiidae: *Blarinobia* sp. m. Trombiculidae: *Euschoengastia lanei* mt, *Euschoengastia criceticola* m, *Euschoengastia diciptiens* t, *Euschoengastia peromysci* m, *Leewenhoekia americana* m, *Trombicula loomisi* m.

DIPTERA: Cuterebridae: *Cuterebra cyanella* mt.

SIPHONAPTERA: *Callistopsyllus deuterus* m, *Catallagia decipiens* m, *Epetedia stanfordi* mt, *Malaraeus sinomus* mt, *Malaraeus telchinum* mt, *Megarhroglossus procius* mt, *Monopsyllus wagneri wagneri* mt, *Orchopeas leucopus* mt, *Peromyscopsylla hesperomys adelpha* mt, *Phalacroscopsylla allos* t, *Rhadinopsylla sectilis goodi* t, *Stenistomera macrodactyla* m, *Stenoponia (ponera or americana)* mt.

CESTODA: *Choanotaenia* sp. m, *Hymenolepis* sp. t.

NEMATODA: *Mastophorus numidica* mt, *Syphacia obvelata* mt, *Trichuris stansburyi* t.

ACANTHOCEPHALA: *Moniliformis clarki* mt.

PREDATION

In order to determine the relative numbers of each species of *Peromyscus* that were taken on a seasonal basis by predators, scats of coyotes and foxes were collected from trails and roads at least twice each month, from September 1963 through August 1964. Scats were identified, labeled and dried; all bones and samples of hair were later removed from each scat. Scats that were intermediate in size between the droppings of foxes and coyotes, and that could not be identified readily in the field, were not collected. Bones from the scats were identified to species, and hair was identified to genus or species by comparing color patterns or cuticular patterns with samples from known mammals. More than 200 impression slides and whole mounts of guard hair and underfur were prepared.

Seven individuals of *P. truei* and three individuals of *P. maniculatus* were represented in 114 coyote scats (Table 13). Both species of *Peromyscus* comprised only 3.9 per cent of the 253 items of food represented in the 114 scats. Rabbits, *Sylvilagus* sp. and mule deer, *Odocoileus hemionus* were the major food items of coyotes. Mice of the genus *Peromyscus* apparently were preyed upon mostly in autumn (September through November), when mouse populations were near their yearly peaks.

Foxes also prey upon *Peromyscus* in the park. One *P. truei* was represented in the 16 scats of foxes that were analyzed. This individual was taken in the winter quarter (December through February).

The bobcat may be an important predator upon *Peromyscus* in this region, but few scats of this animal were found. Since these could not be assigned to a specific month, they were not saved for analysis. Anderson (1961:58) believed that bobcats and gray foxes were the most [494]

abundant predators in the park. My observations over a period of two years led me to conclude that coyotes were more abundant than foxes and that foxes were, in turn, more abundant than bobcats.

TABLE 13—Food Present in 114 Coyote Scats Collected at Mesa Verde National Park each Month from September 1963 through August 1964.

Food Item	Number of occurrences	Percentage of total items
<i>Sylvilagus</i> sp.	32	12.65
<i>Spermophilus variegatus</i>	5	1.97
<i>Eutamias</i> sp.	12	4.74
<i>Reithrodontomys megalotis</i>	4	1.58
<i>Peromyscus boylei</i>	2	0.79
<i>Peromyscus maniculatus</i>	3	1.18
<i>Peromyscus truei</i>	7	2.76
<i>Neotoma cinerea</i>	2	0.79
<i>Neotoma mexicana</i>	9	3.56
<i>Neotoma albigula</i>	5	1.97
<i>Neotoma</i> sp.	3	1.18
<i>Microtus longicaudus</i>	1	0.39
<i>Microtus mexicanus</i>	11	4.34
<i>Microtus montanus</i>	1	0.39
<i>Microtus</i> sp.	1	0.39
<i>Odocoileus hemionus</i>	59	23.32
Grass	34	13.44
Juniper berries	23	9.09
Pinyon needles	14	5.53
Pinyon nuts	1	0.39
Arthropods	7	2.76
Juniper needles	3	1.18
Rodent or Lagomorph bones	5	1.97
<i>Sceloporus</i> sp.	1	0.39
Unidentified fruit	2	0.79
Rocks	3	1.18
Paper	4	1.58
Soil	3	1.18
Feathers	5	1.97
Total	253	

Hawks, owls and eagles live in the park. Red-tailed hawks were seen frequently in the burned area on the northern end of Wetherill Mesa. Both hawks and owls probably prey upon *Peromyscus* in Mesa Verde, for they are well-known predators upon mice and small rodents in other areas. I tried to find owl and hawk nests that were occupied, but located only nests that were abandoned or impossible to reach.

Captive gopher snakes, *Pituophis melanoleucus*, ate adults of both species of *Peromyscus*. Gopher snakes probably are the most abundant snake in the park; they feed mostly on mice and other rodents. Fur of *Peromyscus* was found in the stomach of a striped whipsnake, *Masticophis taeniatus* (Douglas, 1966:734).

[495]

DISCUSSION

Five species of *Peromyscus* inhabit Mesa Verde National Park (Anderson, 1961). Two of these species, *P. crinitus* and *P. difficilis* are rare, and none was taken in more than 14,000 trap nights. Several individuals of *P. boylei* were taken in live traps, but this species could not be regarded as common. The two remaining species, *P. truei* and *P. maniculatus*, are the most abundant species in the park. Comparison of the habitats and life-cycles of these two forms and analyses of their interrelationships have been the objectives of this study.

The distribution of *P. truei* in the park is regulated by the presence of living pinyon-juniper woodland where logs and hollow trees of *Juniperus osteosperma* provide nesting and hiding places, and where seeds of juniper trees and nuts of pinyon trees provide food. Several other investigators have reported *P. truei* to be associated with trees, but apparently these findings have not assumed the importance they warrant in understanding the ecology of this species. Bailey (1931:152) observed an individual of *P. truei* nesting in a tree on Conchas Creek, New Mexico, and thought that this species might be more arboreal than was generally supposed. The type specimen of *P. t. truei* was taken by Shufeldt from a "nest protruding from an opening in the dead and hollow trunk of a small pinon, at least 2 feet above the ground#8230. The nest, composed of the fine fibers of the inner bark of the pinon, was soon pulled out, and its owner

dislodged...." (Shufeldt, 1885:403). Individuals of *P. truei* usually build nests in trees, or in hollow logs, and are therefore more abundant in pinyon-juniper woodland where there are many such nesting sites.

Rocks and stones are not necessary in the habitat of *P. truei*, although this species was most abundant where there was stony soil. The coincidence of rock or stones and a high density of *P. truei* is thought to be explainable in terms of vegetation. Stony soils support mixed shrubs as well as pinyon and juniper trees; the additional cover and source of food probably allow a greater abundance of *P. truei* than would be possible without the shrubs. Secondly, the rock provides nesting sites for more mice.

Stands of mixed shrubs, lacking a pinyon-juniper canopy, do not support *P. truei*. Its absence was noteworthy on Navajo Hill and on the northern end of Wetherill Mesa where only *P. maniculatus* lived among the mixed shrubs and grassland. On the Mesa Verde, pinyon and juniper trees must be present in order for *P. truei* to live in an area; and, these trees must be alive. Dead pinyons and junipers still stand in the burned part of Morfield Ridge, but no *P. truei* were found there. [496]

Although a few individuals of *P. truei* were taken in stands of sagebrush adjacent to pinyon-juniper woodlands, this species does not ordinarily venture far from the forest.

P. maniculatus lives almost everywhere in Mesa Verde; the preferred habitats are open and grassy with an overstory of mixed shrubs. Individuals of *P. maniculatus* venture into ecotonal areas lying between grasslands and pinyon-juniper forest, or between sagebrush and pinyon-juniper forest. *P. maniculatus* is found also in disturbed areas and in stands of sagebrush that occur in clearings of the pinyon-juniper woodland. In such areas, *P. maniculatus* and *P. truei* are sympatric; their home ranges overlap and any inter-specific competition that might occur would be expected in these places.

The ability of *P. maniculatus* to live in many different habitats is correlated in part with its ability to build nests in a variety of sites. Whereas *P. truei* usually builds nests only in dead branches or logs, *P. maniculatus* builds nests in such varied places as spaces under rocks, at the bases of rotten trees, and in abandoned tunnels of pocket gophers. This adaptability is advantageous for the dispersal of young individuals and the movement of adults into new areas.

Nesting sites have important bearing on survival of the young. In Mesa Verde the rainy season occurs in July and August, while both species of *Peromyscus* are reproducing. It is reasonable to assume that young animals that remain dry survive better than those that become wet and chilled. The nestling young of *P. truei* are in a more favorable position to remain dry and warm than are nestling young of *P. maniculatus*.

Captives of each species differed in the amounts of water consumed per gram of body weight. Individuals of *P. truei* consumed more water per gram of body weight than individuals of *P. maniculatus*. Animals may drink more water than they require when allowed to drink *ad libitum*, but Lindeborg (1952) has shown that species which consume less water when it is not restricted also fare better on a reduced ration. *P. maniculatus* appears to be better adapted to aridity than *P. truei*. The preferred habitats of each species are in accord with these findings.

Within the trapping grid, the most moderate microenvironment, in terms of temperature and humidity, was in the pinyon-juniper forest, where *P. truei* lives. The temperature extremes were wider in the microenvironments of a thicket of oak brush and of two different stands of sagebrush, where *P. maniculatus* lives, than in the forest. *P. maniculatus* tends to live in the harsher, more arid parts of Mesa Verde. Because of its propensity to build nests under things, or in the ground, and because of its ability to use less water per gram of body weight, *P. maniculatus* is better adapted to withstand harsh environments than is *P. truei*. [497]

P. truei may be restricted to the pinyon-juniper woodland because of its need for more mesic conditions. Still, Mesa Verde is semi-arid and there are few permanent sources of water available for animals. The primary source of moisture for rodents must be their food. Analysis of the percentages of moisture contained in the three most common plants in the trapping grid showed that *P. truei* could obtain the required moisture by eating about ten grams of these plants daily; individuals of *P. maniculatus* would need to eat less in order to satisfy their water needs.

Individuals of *P. truei* died more frequently in warm live-traps than did individuals of *P. maniculatus*. This indicates that *P. truei* can tolerate less desiccation, or a narrower range of temperatures, than can *P. maniculatus*.

Both species of mice eat some of the same plants, but these plants occur widely. *P. truei* seems to rely more upon the nuts of pinyons and the seeds of junipers than does *P. maniculatus*. Mounds of discarded juniper seeds were associated with all nesting sites of *P. truei*. Bailey (1931:153) also noticed the fondness of this species for pine nuts and juniper seeds. Apparently, the availability of these foods is one of the major factors affecting the distribution of *P. truei*. However, this is not the only factor, as is shown by the presence of *P. maniculatus* but lack of *P. truei* in a juniper-pinyon association with an understory of bitterbrush. This habitat was seemingly too arid for *P. truei*.

Factors Affecting Population Densities

The production of young, and success in rearing them, is essential to continuity of any population. *P. maniculatus* is favored in this respect, because the females produce more young and wean them sooner than do females of *P. truei*. In addition, lactating females of *P. maniculatus* require significantly less water than do females of *P. truei*. Since young mice of both species require no more water per gram of body weight than do adults, the young can disperse into any area that is habitable by their species. *P. maniculatus* probably is affected less by prolonged drought than is *P. truei*. Since lactating females require the most water of any animal in the population, they are the weakest link in the system. Females of *Peromyscus* are known to reabsorb embryos when conditions are unfavorable for continued pregnancy. If prolonged drought occurred in the reproductive season, and desiccated the vegetation upon which the mice depend for moisture, the populations should diminish the following year. Lactating females of *P. truei* would be affected more seriously by a shortage of water than would lactating females of *P. maniculatus*. [498]

Of two species, the one producing the more young probably would be subjected to more parasitism and predation than the species producing fewer young. A favorable season for botflies, *Cuterebra* sp., revealed that *P. maniculatus* has a higher incidence of parasitism by these flies than has *P. truei*; possibly the adult flies concentrate in the open, grassy areas where *P. maniculatus* is more abundant, rather than in the woodlands where *P. truei* lives. Perhaps the lower parasitism of *P. truei* by warbles is related to the physiology of this species of mouse. Near Boulder, Colorado, the incidence of infection by warbles is lower in *P. difficilis*, a species closely related to *P. truei*, than in *P. maniculatus* (V. Keen, personal communication).

Although predation by carnivores would be expected to be higher on *P. maniculatus*, because this species does not climb, my data show that more individuals of *P. truei* were taken by coyotes. I lack confidence in these findings, suspecting that another sample might indicate the reverse. Birds of prey probably catch more individuals of *P. maniculatus*, because this species lives in more open habitats. My data do not warrant firm conclusions regarding predation.

The length of time females must care for their young influences the rate at which individuals can be added to the population. Females of *P. truei* nurse their young longer and keep them in the nest longer than do females of *P. maniculatus*. Although this may enhance the chances of survival of young of *P. truei*, it also reduces the number of litters that each female can have in each breeding season. Females of *P. maniculatus* can produce more young per litter, and each female probably can produce more litters per year than females of *P. truei*.

Captives of *P. truei* were tolerant of other individuals of the same species, even when kept in close confinement. However, when there was slight shortage of food or water they killed their litter mates, or females killed their young. Only a short period of time was necessary for one mouse to dispatch all others in the litter. The attacked mice were bitten through the head before being eaten; the brains and viscera were the first parts consumed. The population might be decimated rapidly if drought forced this species to cannibalism. When the supply of food or water was restored, the captive mice resumed their tolerant nature. [499]

In captivity, *P. maniculatus* is amazingly tolerant of close confinement with members of the same species; individuals did not tend to kill their litter mates, or their young, even during shortage of food and water. This tolerance, especially under stressful conditions, probably enables *P. maniculatus* to persist in relatively unfavorable areas.

Adaptations to Environment

Each of the two species of *Peromyscus* illustrates one or more adaptations to its environment. *P. truei* is adapted to climbing by possession of long toes, a long tail, and large hind feet. The tail is used as a counterbalance when climbing (Horner, 1954). When frightened, individuals of *P. truei* often ran across the ground in a semi-saltatorial fashion, bounding over clumps of grass that were as much as 18 inches high. Such individuals usually ran to the nearest tree and climbed to branches 10 to 20 feet above the ground.

Large eyes are characteristic of the *truei* group of mice, and may be an adaptation to a semi-arboreal mode of life. A similar adaptation is shared by some other arboreal mammals, and of arboreal snakes. The large eyes of *P. truei* in comparison to those of *P. maniculatus*, probably increase the field of vision, and permit the animal to look downward as well as in other directions.

The above-mentioned adaptations of *P. truei* permit these graceful mice to use their environment effectively. By climbing, this species can nest above-ground in the hollow branches of trees, and can rear its young in a comparatively safe setting. The ability to climb also permits vertical as well as horizontal use of a limited habitat. Because of the three-dimensional nature of the home range of *truei*, its range is actually larger than that of *maniculatus* although the standard trapping procedures makes the home range of the two appear to be about the same size. Finally, trees may offer safety from predators, and a source of food that probably is the winter staple of this species.

Peromyscus maniculatus has adapted differently to its environment. Small size of body and

appendages permit this species to use a variety of nesting sites and hiding places even though it is restricted, by its anatomy, to life on the ground. The tail and hind feet are shorter than in *P. truei*, and *P. maniculatus* is an inefficient climber. I have placed individuals in bushes, and found that many walk off into space from a height of several feet. Perhaps the relative smallness of their eyes accounts for their seeming lack of awareness of how high they are above the ground.

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When frightened, individuals of *P. maniculatus* ran rapidly in a zig-zag path and dove into the nearest cover. Mice, released from live traps, often stuck their heads under leaves, leaving their bodies exposed. This species tends to hide as rapidly as possible, and remain motionless. This tactic would not be of much value as an escape from carnivores, but it could be effective against birds of prey.

In Mesa Verde, *P. maniculatus* inhabits the more arid, open areas. When the population is dense, individuals of this species are found also in pinyon-juniper woodland. Apparently *P. maniculatus* prefers the grassy areas and the thickets of oak brush. Although such habitats have harsh climatic conditions, they offer innumerable hiding places, and thus have great advantage for a species confined to the ground.

The low requirements of water per gram of body weight, the ability to eat diversified foods, the use of varied habitats, the high fecundity, and the ability to use any nook for retreat or nesting make *P. maniculatus* a successful inhabitant of most parts of Mesa Verde, and indeed, of most of North America.

[501]

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Transcriber's Notes

All obvious typographic errors corrected. For consistency, the species listings for *boylii* has been standardised to *boylei*.

Typographical Corrections

Page	Correction
429	nuaseosus = nauseosus
430	Orthocarpos = Orthocarpus
447	unbellata = umbellata
450	ludovociana = ludoviciana
456	phrheliometer = pyrheliometer
480	rudale = ruderale
481	rates = rats
482	bases = basis
499	clumbs = clumps

*** END OF THE PROJECT GUTENBERG EBOOK COMPARATIVE ECOLOGY OF PINYON MICE AND DEER MICE IN MESA VERDE NATIONAL PARK, COLORADO ***

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