

T H E S I S

VARIATION IN DEER MICE FROM
DIFFERENT ELEVATIONS

Submitted by
Albert William Spencer

In partial fulfillment of the requirements
for the Degree of Master of Science
Colorado State University
Fort Collins, Colorado
December, 1961

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Chapter I
INTRODUCTION

In Northern Colorado, the abrupt rise of the Rocky Mountains from the plains, accompanied by increased rainfall and decreased temperature, produces a range of environmental conditions nearly equal to what may be found in passing from Colorado north to the Arctic. A line drawn from Coal Creek in Weld County to Comanche Peak in Larimer County crosses five life zones (Merriam, 1898). At Coal Creek, the vegetation type is grassland; at Comanche Peak, it is alpine tundra. Between, the line passes through cropland, valley forest, brushland, open pine woodland, dense spruce fir forests, and krummholz. A single species of deer mouse ranges throughout this gamut of ecological types.

Presumably, this species, Peromyscus maniculatus, Bangs 1898, has inhabited the area for thousands of years. It is a reasonable supposition that during this time the direction of evolution has not been the same for the segment of the population living on the arid plains as it has been for that segment occupying the mountain forests. Therefore, the results of those years of evolution should be manifest in some demonstrable variation between local populations of mice.

Need for the study.

Although the concept of evolution has been accepted and the role of selection in evolution is well founded, the intricacies of its action are not perfectly understood. All is not known of the importance of other forces that may alter gene frequencies and contribute to evolutionary change. More studies of evolutionary forces at work in natural populations are needed. The study of variation within one living population is a step toward fulfilling this need.

Problem.

What differences can be observed among sample populations of deer mice, Peromyscus maniculatus, taken along an east-west line across Weld and Larimer Counties, Colorado? If differences occur do they arise in direct response to the environment or as heritable traits?

Problem analysis.

Although this problem has many ramifications the study was concerned with only the following:

1. What morphological differences exist between the populations?
2. What is the nature and extent of variation in pelage color among populations?
3. How do the populations differ in respect to reproduction?

4. In what kind of habitat is each population found?

Delimitations.

The study was limited to the samples of mice procured from seven localities approximately twelve miles apart along an east-west line running from 104° 30' West to 105° 40' West in Weld and Larimer Counties, Colorado.

The study began in the summer of 1957 and was terminated in the spring of 1959. Its plan and scope are substantially similar to earlier ones by Dice and Lerass. The results are similar. The study may be considered to extend knowledge of variation in P. maniculatus into still another locality.

Acknowledgements.

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Definition of terms.

By "population" is meant all the individual deer mice within a sample plot of one square mile but represented by only the trapped specimens.

"Statistically significant" will mean that the probability is less than one in one hundred of obtaining, by chance, values of F, t, or X^2 as large or larger than the value observed.

The term "mountain" will distinguish specimens, samples, and data obtained at Sulzer Gulch, Rist Canyon, Buckhorn Ranger Station, and Cirques from those obtained at the "plains" sites of Coal Creek, Cobb Lake, and Pierce.

Chapter II
REVIEW OF LITERATURE

The races of P. maniculatus are distinguished primarily by differences in pelage coloration. The two races P. m. osgoodi and P. m. rufinus whose ranges lie within the area of the present study were described by Osgood (1909) chiefly on this basis. The race P. m. osgoodi (see J. Knox Jones, 1958 for the taxonomic status of the subspecific designation) is described as lighter and more buffy than P. m. rufinus. The principal hues of the pelage are ochraceous-buff and cream mixed with tawny or dusky. The back is said to be scarcely darker than the sides. P. m. rufinus is similar but duller and more tawny. The dusky coloration is more extensive. In both races the white in the subauricular tuft is usually conspicuous and the tail sharply bicolored. The tail pencillation of P. m. rufinus is dark blackish-brown. The color of the pencillation in P. m. osgoodi is not described. Northern Colorado is a zone of intergradation between the two races in which specimens referable to either subspecies occur together. Local variation in coat color is large within all races of P. maniculatus and especially in Western North America (Osgood, 1909).

Osgood did not separate the two subspecies on the basis of any proportion. He remarked only that P. m. rufinus resembles P. m. osgoodi closely except in pelage. Nevertheless, the specimens of rufinus which he lists have on the average a greater total length, longer tail, and longer ear than the specimens of osgoodi.

Collins (1923) investigated the growth and replacement of the pelage in P. m. gambeli and found that the molt from juvenal to post-juvenal pelage was very regular. It began under the neck and proceeded forward and backward. The last areas to molt were the top of the head and the base of the tail. The post-juvenal molt began at about four weeks and ended at about eight weeks. Subsequent molts were less regular. The molts of adult males were extremely variable in pattern although constant for the individual. Pregnancies interrupted the molting sequence for females. Among five hundred wild-caught mice, Collins found evidence of molt during every month of the year with a peak during late summer and early fall.

There are several types of hairs found in the pelage of P. m. gambeli. The dorsal part of the body is covered by two types, long, uniformly dark guard hairs and short, banded or agouti underfur. The pigment granules of the guard hairs and the tip of the agouti hairs are concentrated in the cortex. The yellow pigments of the agouti hair occur in the medulla. The size, density, and

arrangement of granules varies along the hair producing gradations of color.

The young mice have a different pelage than the adults with hairs of a bluish-gray color. As the mouse develops to maturity succeeding pelages are increasingly buffier. However, there are no appreciable changes in color after the mouse reaches six months of age.

Apparently, external conditions do not greatly affect the development of P. maniculatus. Sumner (1924) studied specimens from several subspecies raised from birth under identical conditions and in temperatures, humidities, etc. often very different from those of their wild-caught parents and found that they developed the features characteristic of their subspecies. The mice, with the exceptions of a few "sports," bred true to type over several generations. Sumner did note that captive mice tended to be smaller than wild-grown mice. The limbs seemed specially affected. (Sumner, 1932).

Huestis (1931) counted, microscopically, the numbers of three kinds of hairs on small patches of hide from the flanks of 180 specimen skins representing two seasons and three localities, Mojave Desert, Oregon sage brush, and Oregon coast. The proportions and numbers of dark overhairs, of light-banded overhairs, and of fur hairs were found to vary with the season. Light-banded hairs and fur hairs were most abundant in winter pelages. The lighter

hue of summer pelages was attributed to the bleaching of the black pigment. The specimens from the Mojave Desert had the smallest proportion of dark hairs; those from the Oregon coast had the highest. "Wear" in the sense of abrasive loss of substance from or breakage of the hair was nil. There seemed to be a differential between the rate of loss of light-banded hairs and dark overhairs. The light-banded hairs were lost more often than the dark overhairs.

During the years 1932-1950, Dice published a series of papers dealing with variation in Peromyscus. These papers and the works of his students on the same subject constitute one of the most complete studies available of the progress and direction of selection and speciation in a mammalian species.

Dice began his work in 1932 with a paper describing the variations among three stocks of the prairie deer mouse, P. m. bairdi. The results of this study are similar to the results in many of the later studies. The color of the pelage was found to be correlated with the color of the soil. The body dimensions differed significantly between the races. The size or proportions of all characters measured tended to increase in the more western stocks. This clinal variation appears to be wide-spread in the prairie and plains populations. Dice raised young mice from birth in the laboratory and killed them at specified ages so that age and environmental factors were eliminated. The

mice attained nearly their adult size within three months but continued to grow slowly until two years of age. The methods initiated in this study were used in all subsequent studies.

P. m. rufinus from different altitudes in Colorado and New Mexico also differed significantly in pelage color and body dimension, but meaningful trends in the latter were difficult to discern. In this study, Dice compared differences between age and sex classes within the same stocks. No difference in pelage color was found between the one year and two year classes. The hind feet of males averaged longer than those of females and males were also heavier. There were no apparent differences in color between the sexes (Dice, 1933).

Eleven stocks of mice from the Columbia river basin exhibited differences in pelage correlated to the aridity of the habitat and paleness of soil. Stocks from comparable habitats on opposite sides of the Snake river, which forms a nearly complete barrier to gene exchange, resembled each other in pelage characters more than they resembled stocks from the same side but from more humid sites. There were differences in skeletal dimensions and other body proportions but there was no visible correlation with conditions of habitat (Dice, 1939).

Variation in the deer mice of Nebraska followed a clinal pattern with respect to skeletal dimensions.

These stocks come from an area between the smaller P. m. bairdi and the larger P. m. osgoodi. Size increased from eastern stocks to western stocks with no apparent relationship to environment. However, coat colors varied with soil conditions (Dice, 1941).

Several stocks of mice representing three mainland races and two island races were collected from the Oregon coast, California coast, California islands, and California deserts. Color comparisons showed that the desert stocks averaged palest, those from the California coast were intermediate, and those from the Oregon localities were darkest. The last also had the longest tails. Stocks of the two subspecies, P. m. gambeli and P. m. sonoriensis, varied only in color. The island stocks displayed several variants (Dice, 1941).

Six stocks of mice from localities in the Black Hills and Bad Lands of South Dakota and Wyoming differed in pelage color according to the vegetation type where they lived. The gradient pattern in skeletal dimensions shown by Nebraska and North Dakota stocks was also apparent here. The size increased without respect to elevation from east to west. Pelages averaged darkest in mice from the dense forests of the highest Black Hills, lightest in the Bad Lands stocks, and intermediate in stocks from the lower slopes of the mountains (Dice, 1942).

Ten stocks representing three subspecies of P. maniculatus from Idaho, Wyoming, Utah, and Montana were

measured. There were important differences in average ear and tail length, apparently associated with the habits of the subspecies. Color of pelages, again, were related to vegetative types (Dice, 1944a).

Variation in nine stocks of P. maniculatus from New Mexico is of interest because of the small compass of the area. The most distant stocks were from localities only fifty miles apart, yet significant differences in pelages and dimensions were demonstrated. There was no discernible trend in differences in body dimensions. No stock ranked consistently large or small in all dimensions. The color of pelages appeared linked to the density of vegetation at the original habitats (Dice, 1944b).

Using an artificial "jungle," Dice (1947) attempted to measure the effectiveness of selection against mice whose coat color contrasted with the background. Owls consistently took greater numbers of mice with contrasting coats.

Lerass, a student under Dice and using the techniques of Dice, found no correlation between body proportions and vegetational type in stocks of mice from different elevations in the Uintah Mountains of Utah. Though his stocks varied significantly in several measurements, the variation had no discernible trend. Coat colors, however, decreased in lightness as the vegetative cover became more dense (Lerass, 1938).

Blair (1947a) determined that two allelic genes control the pelage colors of buff and gray in the geo-

graphic race, P. m. blandus, but that their expression is modified by undetermined numbers of minor genes.

The frequencies of the genes for buff and gray colors from areas of differently colored soils in the Tularosa Basin of New Mexico were found to vary with the soil color (Blair, 1947b).

Horner (1954) forced several semi-arboreal and terrestrial types of Peromyscus to climb on cylinders and rods of many textures and forms. She scored their efforts by counting errors such as slipping. The semi-arboreal forms made significantly higher scores than the terrestrial forms. The tails of some mice were amputated. Loss of the tail was more of a handicap for semi-arboreal types than for terrestrial mice, since the number of errors increased proportionately more for the former.

Harris (1952), another student of Dice, constructed artificial habitats with forms resembling tree trunks and grass tufts. Semi-arboreal, forest dwelling P. m. gracilis consistently were found in the forest side. P. m. bairdi, a terrestrial, prairie-living race was found more often in the simulated grassland. Habitat preferences shown in this experiment are an important illustration of the ecological differences thought to maintain the separateness of these two races, whose ranges are contiguous.

A paper by Cook and Hannon (1954) is of special interest because it is a report of an investigation of physiologic differences found among different strains of the same

species. Oxygen consumption, a function of metabolic rate, was experimentally determined in three strains of P. m. rubidus from varying altitudes. Cook and Hannon obtained the mice from Berkeley (elev. 1000), Tule Lake (elev. 4000), and White Mountains (elev. 13,000), California. The tested individuals were wild-caught specimens acclimated to laboratory conditions by a two month period of captivity. Relative percentages of oxygen consumed by males per gram of body weight using White Mountain mice as the standard were White Mountain 100 per cent, Tule Lake 112 per cent, and Berkeley 116 per cent. Females exhibited similar requirements.

Foster (1959) compared the responses made by two subspecies of deer mice when they were exposed to similar situations. P. m. bairdi appeared more cautious and tense than P. m. gracilis. The latter moved more deliberately but with less inhibition and exhibited fewer evidences of nervous tension. In disturbing situations P. m. bairdi responded frequently by "freezing", that is, refusing to move. In the same situations, P. m. gracilis were apt to attempt flight or defensive action.

Dunmire (1960) studied reproduction in Peromyscus maniculatus on the slopes of White Mountain in California. The reproductive rate was greatest for lowest altitudes and increased with elevation. The higher populations apparently produced larger but fewer litters. The decreased reproduction in populations at higher elevations appeared to be offset by reduced losses to predation.

Jameson (1953) presents evidence that larger litters occur more frequently at the seasons when breeding activity is at a peak. The number of young in a litter has a relationship also to the age and size of the mother. Jameson compares those data with results obtained by Scheffer (1930). The average litter size in the Sierra Nevada (Jameson) was 4.6 ± 0.11 compared to 5.1 ± 0.16 for Scheffer's mice from Washington.

Coventry (1937) found an average litter size of 5.04 ± 0.08 in P. leucopus novaboracensis caught in Ontario while Svilha (1932) recorded average litter size of 4.36 in Michigan populations.

The average home range for P. maniculatus in several vegetational associations as computed by Blair is shown in Table A.

Table A.--AREA OF HOME RANGE IN ACRES.

Subspecies	Habitat	Males	Females	Source
<u>P. m. gracilis</u>	woodland	2.3 ± 0.27	1.39 ± 0.16	Blair 1942
<u>P. m. bairdi</u>	grassland	0.77 ± 0.06	0.63 ± 0.07	Blair 1942
<u>P. m. blandus</u>	mesquite	4.66 ± 0.33	4.10 ± 0.39	Blair 1943

Williams (1955) used Blair's methods to calculate home ranges for P. m. rufinus in a Ponderosa pine community. The home ranges averaged 0.81 acres for males and 0.62 acres for females.

Howard (1951) set up a number of nest boxes on a Michigan prairie. He marked all P. m. bairdi born in the boxes and recorded their subsequent movements. The maximum distance traveled by a mouse before reproducing was 3,300 feet. Of 675 young studied, 30 per cent of the males and only 15 per cent of the females moved over 550 feet before reproducing. Howard estimates that four to ten per cent of 186 litters observed were the product of parent-offspring or intra-sibling matings (Howard, 1949). Blair, (1942) in the same area as Howard's study found average densities of deer-mice fluctuated from none to a maximum of 9.2 per acre.

Tevis (1956) compared small rodent populations on adjoining tracts of cut-over and virgin douglas fir. A tract that had been timbered twenty years before yielded twenty-eight P. maniculatus compared with twenty-four from virgin timber. A tract that had been cut over six years before yielded sixty-one P. maniculatus compared with fifteen from virgin timber.

McCabe and Blanchard (1950) offer the opinion, "In this area (California), Peromyscus, in short, is a creature of the chapparal edge even more truly than the large forest mammals are actually creatures of the forest edge." Murray (1957) says that McCabe and Blanchard consider any trail or break an "edge". Murray, using recapture data from three lines paralleling a definite sage-grassland interface, found no significant increases in numbers trapped along the edge.

Williams (1958) compared small mammal densities in different ecological types at eight to ten thousand feet elevation in Colorado. The highest densities for Peromyscus were recorded in an open ponderosa pine stand, along a power line cut through lodgepole pine, and in a burned-over area with young trees less than six feet tall. The lowest densities were recorded in mature lodgepole pine and a grazed meadow. Williams concluded that P. maniculatus in that region were associated with the early successional stages.

Quast (1954) compared rodent numbers in ungrazed and grazed chaparral range in California. P. maniculatus were found in greatest numbers in heavily grazed swales away from the canopy of the blue oak and digger pine. They were found in limited numbers in moderately grazed snow brush but did not occur in the dense stands of these plants.

Chapter III
METHODS AND MATERIALS

Selection of study areas.

Figure 1 shows the locations in North-Central Colorado where the mice used in this study were trapped. Originally, six principal stations, typical of several diverse habitats and easily accessible were chosen at approximately twelve-mile intervals along an east-west line. A seventh, Sulzer Gulch, was chosen for its environmental similarity to Rist Canyon thus serving as an added control of the distance factor. Barriers hindering free movement of mice, such as large streams and busy roads, were not present within a site. Several other areas were trapped for reasons other than those of this study. Information from these incidental sites has been included because it seemed pertinent to an understanding of the community relationships of P. maniculatus.

Field Notebook.

A field notebook was kept. Observations pertinent to the study included weather, animal and plant species seen on the sites, location of the traps, plants occurring within a radius of one foot of each trap, success or failure of each trap, species and sex of mice caught, fate of each specimen

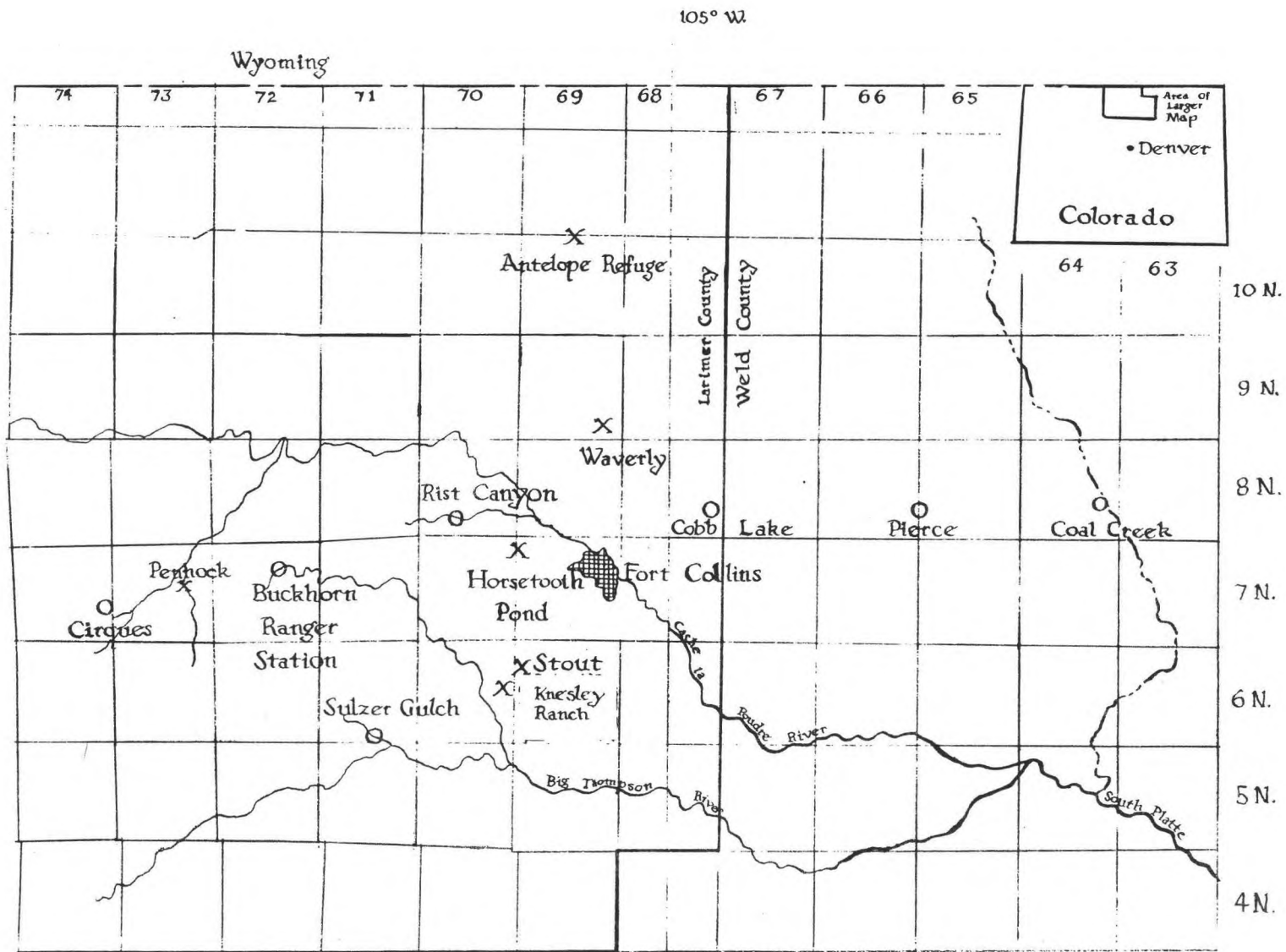


Figure 1. Map showing location of trapping sites.

trapped, and behavior of the living captives. Plants, mammals, and birds were identified by use of Harrington (1954), Palmer (1954), and Peterson (1941).

Trapping techniques.

The mice were taken in live traps modified from the Michigan trap (Blair, 1941). They were small sheet metal boxes 2 3/4" x 2 1/2" x 7 1/2" with a trap door closed by a treadle arrangement. Rolled oats was the usual bait.

The traps were set out in irregular lines at about five yard intervals. Bushes, holes, rocks, brush piles, were favored trapping sites. The traps were checked each morning, collected, and re-set in new locations each day. Trapping continued at each site until sixty to seventy specimens had been captured and processed. Beginning with Coal Creek, the trapping sequence progressed westward through the Pierce, Cobb Lake, Rist, Sulzer, Buckhorn, and Cirques sites. An interval of less than seven weeks separated the times of capture of the first-and last-caught mice considered in the analysis, excepting laboratory specimens. These had been captured the previous summer and were killed and prepared in June, 1958.

Plant censusing technique.

The area within a radius of one foot of the trap may be considered to be a small quadrat for purposes of

plant censusing. From the total occurrence of a species in the trapping record, a frequency can be calculated which is probably positively biased for shrub and weed species because of personal prejudice for setting traps near such cover.

Other censusing methods used were the line strip method (Woodin and Lindsey, 1954) and the random pairs method (Cottam, 1949).

Morphological measurements.

Eleven anatomical characters were measured and compared. They were the length of the body, tail, hind foot, ear (from notch), femur, mandible, nasals, upper molariform tooth row, condyle-zygomatic distance, and condyle-premaxillar distance, as well as the width of the skull at the bullae. The first eight measurements are described in Dice, 1932. The last three are described in Cockrum, 1955. Precedent determined the choice of these particular characters from the many possibilities.

The measurements were taken with a rule or vernier calipers. One person made all the measurements of any character.

Method of ageing specimens.

Four factors were considered in assigning the specimens to either of two age classes, adult or subadult. They were sexual maturity, total length, hair texture, and

Table 1.--CRITERIA USED FOR CLASSIFICATION OF MICE BY AGE.

Stage of maturity	Reproductive organs	Total length	Hair texture	Presence of juvenal molt pattern
adult male	testes over 6 mm. long	over 145 mm.	coarse	absent
subadult male	testes under 6 mm. long	less than 145 mm.	fine	present
adult female	placental scars, embryo or enlarged uterus	over 145 mm.	coarse	absent
subadult female	no placental scars, embryo or enlarged uterus	less than 145 mm.	fine	present

presence or absence of the juvenal molt pattern. The last feature is marked by blackened areas on the inner surface of the skin at the base of the tail and between the ears accompanied by remnants of the juvenal pelage (Collins, 1923). Length was used only when none of the other criteria seemed conclusive. Only adult mice were considered and compared in this study. Some criteria were regarded as more conclusive than others. Pregnancy alone was sufficient to classify a female as adult while possession of a juvenal molt pattern weighed heavy in the decision to classify a mouse as immature. Hair texture and length were much less definitive but were relied upon when the other criteria were ambiguous.

Pelage reflectance-preparation of skins.

After the external measurements had been taken, the mice were skinned. Each skin was tagged and pinned out flat to dry. Considerable stretching of the skin occurred and the amount was not constant. The dry skins were placed between newspapers to absorb oils and fats and stored in a dark container for a period of one to two years until the summer of 1959.

Measurement apparatus.

A Photovolt photo-electric reflection meter Model 610 was used to measure reflectance. This machine consists essentially of a light source, a photocell, and a galvano-

meter. The photocell is activated by light reflected from the specimen and produces an amount of current which the galvanometer registers. The galvanometer can be calibrated to express the amount of current produced as a percent of the amount produced by light reflected from a standard white enameled plaque. The reflectance of the black top of the instrument case was considered to be zero. A colored glass filter reduces the light source to a narrow spectral band. Tristimulus values corresponding to the Munsell system can be obtained but were not since this study was concerned only with relative values. A black paper washer reduced the normal aperture of the scanner so that only the color of the dorsal or the side stripe affected the reading. The washer added a constant source of reflection which should have reduced the sensitivity of the apparatus except that it also absorbed much of the light that otherwise would have been reflected from the standard plate whose reduced reflectance, nevertheless, was regarded as 100 per cent. The net result was sensitivity approximately equal to that of the unaltered machine, but the readings were no longer similar to the tristimulus value. However, they were adequately accurate for the present study.

Measurement procedure.

All the individuals of one sex were measured at one session. The machine was calibrated with the green filter and a reading for green reflectance obtained from

every skin of that sex. Then the machine was set for the red filter and a red reading taken from every specimen of the sex. Finally, the same procedure was followed for blue. The calibration of the machine was frequently checked against the standards. While there is a satisfactory homogeneity for procedure within sexes, readings are not comparable between sexes.

Collection of soil samples and measurement of soil reflectance.

Ten random samples of surface soil were collected from each locality. Actually the sample included soil to about one-half inch depth. The true surface was not retained. Reflectance of the soil was measured in the same manner as that of mouse skins. A piece of cellophane was taped over the masked aperture. Otherwise, dust worked onto the top of the washer and changed the amount of light reflected by the washer.

Statistical procedures.

Quantitative data used in this study are of both the continuous and discrete type. They require different methods of statistical analysis. Snedecor (1956) discusses the computational procedures.

The X^2 contingency table test was applied to determine the significance of proportional differences in enumerative data such as the size of litters.

Differences between means were compared by the single-way classification analysis of variance. The single-way classification was used in order to avoid the difficulties introduced by unequal numbers of observations among the classes. However, the observations had to be segregated into sex and year groups in order to eliminate from the variance differences due to those factors. Year represents differences in the methods of measurement or, in the case of pelages, unequal periods of storage. There is a separate analysis of variance for every character in each sex group. The single classification within the analysis is locality which represents any number of factors. Among them the most important are environment and heredity.

When the F value obtained from the ratio of the locality mean sum of squares to the residual mean sum of squares was significant (less than one per cent probability), the locality sum of squares was broken down into pre-established portions by the method of individual comparisons in order to find where the differences between means of localities actually occurred.

As a check upon the accuracy of techniques of measurement, ten mice were measured three times at one-day intervals. The reflectances of ten skins were measured three times before and twice after recalibrating the reflectometer. These procedures simulated those followed during the study.

The coefficients of variation among the three measurements of length are shown in Table 2 and those for reflectance in Table 3.

The errors made in measuring the external characters are considerably larger than those for skeletal characters. They are little larger than those for reflectance. The errors in external measurements did not appear to be altogether random for the differences between two successive sets of measurements were nearly all in the same direction. The non-randomness may have resulted because of differences in the attitude of the observer or differences in the condition of the mice. Neither of these factors was controlled during the study. The procedures followed in the study for measuring reflectance and skeletal parts appear to have effectively randomized the errors due to technique. This error, then, should have been removed in the error term of the analyses of variance while that error in the external measurements may have been confounded with the locality component.

Table 2.--AN ESTIMATE OF ERROR IN THE MEASUREMENT OF LENGTH.

	Mean differences	Variance	Coefficient of Variation
Body	+4.5	11.17	12.0
Tail	-3.2	3.83	6.0
Hind foot	+0.27	0.14	0.7
Ear	-0.27	0.18	1.1
Condyle- premaxilla	-0.04	0.08	0.3
Condyle- zygoma	+0.01	0.04	0.2
Nasal	+0.12	0.17	1.5
Bullar width	+0.22	0.12	1.1
Tooth Row	-0.01	0.03	0.9
Mandible	+0.03	0.03	0.2
Femur	-0.02	0.03	0.2

Table 3.--AN ESTIMATE OF ERROR IN THE MEASUREMENT OF PELAGE REFLECTANCE.

Within Calibrations	Green		Red		Blue	
	Side	Dorsal	Side	Dorsal	Side	Dorsal
Mean difference	-0.8	-0.2	-1.2	+0.6	+0.3	-0.4
Variance	1.12	0.19	2.82	1.69	0.77	0.37
Coefficient of variation	6.0	2.0	6.0	4.0	4.0	3.0
Between Calibrations						
Mean difference	+1.0	-0.3	+4.2	+4.1	+2.0	+2.3
Variance	0.87	0.29	9.32	14.13	2.91	1.06
Coefficient of variation	5.0	3.0	20.0	30.0	15.0	8.0

Chapter IV
DESCRIPTION OF THE HABITATS REPRESENTED
AT THE STUDY SITES

Deer mice were very abundant in north-central Colorado during 1957 and 1958. Probably an occasional Peromyscus might have been taken from nearly any quarter-acre plot in Larimer or Weld Counties, which might, then, be considered a continuous population. However, a large proportion of mice, especially in the high mountains and uncultivated plains, were distinctly aggregated in relatively small areas. The distribution of mice in these areas might be compared to beads strung along the threads of the creeks and high ridges. The deer mouse populations of the open plains were clumped in small areas with individuals widely scattered over most of the site. The most even distributions occurred along the foothills and on cultivated lands; these areas were also the regional centers of abundance. Except for the continual disturbance by cultivation, which has apparently created more favorable conditions for the species, the distribution of Peromyscus in the cultivated area would probably resemble the distribution at Coal Creek.

Coal Creek.

Coal Creek is the easternmost site studied. The

vegetational type is short-grass prairie. The important species are: blue gramma (Bouteloua gracilis) 78 per cent, relative basal area, buffalo grass (Buchloe dactyloides) 18 per cent, salt grass (Distichlis stricta) 3 per cent, western wheat grass (Agropyron smithii) blue grass (Poa spp.) and Torrey's muhly (Muhlenbergia torreyi), each less than 1 per cent. Saltbush (Atriplex canescens), prickly pear (Opuntia polyantha), snakeweed (Gutierrezia sarothrae), Eriogonum spp., and rabbitbrush (Chrysothamnus spp.) assume dominant aspects but cover an insignificant area. Common herbs include: scurf pea (Psoralea tenuifolia and P. lanceolata), prairie clover (Petalostemon candida), bull thistle (Cirsium plattensis), skeleton weed (Lygodesmia juncea), mallow (Sphaeralcea coccinea), sunflower (Helianthus spp.), sweet clover (Melilotus spp.) and Russian thistle (Salsola kali).

An intermittent creek runs through the site. Although one might suspect that because of the dry climate mice would be attracted to the water, no mice were captured along the creeks near water. Rather, the greatest numbers of mice were captured along dry gullies lateral to the creeks. As shown in Table 4, the trapping index along dry gullies was three hundred times greater than over the typical plains grassland. The grasshopper mouse (Onychomys leucogaster), a strictly plains species, showed no such localism but was captured in an essentially random distribution.

The dry gullies approached a bad-lands-type terrain. Bare, rounded hummocks and shelving walls characterize the terrain. The typical grassland extends to the very edge of the gullies and sparse weeds penetrate into them.

The elevation of the Coal Creek site is about 5,100 feet. The climate should resemble Greeley's to the south or Grover's to the north (Table 5). Possibly, Peromyscus at this site must face the most extreme conditions of mice anywhere along the transect. The summers are hot and free water is scarce. Blizzards often sweep the area in winter.

The soil at Coal Creek is derived from light colored, predominantly yellow and tan Tertiary sedimentary rocks and Recent gravels. Organic matter in the soil is low. Approximately 63 per cent of the soil surface is exposed.

Important competitors to Peromyscus at this site may include: kangaroo rats (Dipodomys ordi), which were very abundant, spotted ground squirrels (Citellus spilosoma), grasshopper mice, and many seed-eating birds. Predators observed at this site were: coyotes (Canis latrans), badgers (Taxidea taxus), skunks (Mephitis mephitis, and Spilogale putorius) Golden Eagles (Acquila chrysaetos), American Rough-legged Hawks (Buteo lagopus), Marsh Hawks (Circus hudsonius), Short-eared Owls (Asio flammeus), Great Blue Herons (Ardea

herodias), bull snakes (Pituophis catenifer), king snakes (Lampropeltis doliata), and grasshopper mice.

Pierce and Cobb Lake.

Before cultivation, the Pierce and Cobb Lake sites were part of the same ecologic type as Coal Creek. They are now cultivated areas with part of each under irrigation and the rest devoted to raising dry-land wheat. The Cobb Lake site is further denaturalized by two large reservoirs. Along fence rows and in abandoned corners weeds such as summer cypress (Kochia scoparia), wild lettuce (Lactuca spp.), Russian thistle, sunflowers, tansy mustard (Descurainia sophia), ragweed (Ambrosia trifida), and winter grass (Panicum capillare) are the important species. Blue grass, western wheat grass, and cheat grass (Bromus tectorum) are common grasses. Rabbitbrush, willow (Salix spp.), and snakeweed are frequent shrubs. Wheat and alfalfa were the principal crops being grown during the study. In the summer, mice were most abundant in the fence rows and abandoned areas and scarce in the fields.

Predators observed include: Marsh Hawks, Sparrow Hawks (Falco sparverius), Rough-legged Hawks, Short-eared Owls, Long-eared Owls (Asio wilsonianus), Barn Owls (Tyto alba), Horned Owls (Bubo virginianus), skunks, house cats (Felis domestica), raccoons (Procyon lotor), coyotes, grasshopper mice, herons, and bull snakes. The house mouse (Mus musculus) was a common competitive species

at both sites. Harvest mice (Reithrodontomys megalotis), apparently were numerous at Cobb Lake; their remains were found in owl pellets in the ratio of one harvest mouse to three deer mice. Meadow mice (Nicrotus ochrogaster) occurred at both sites. No kangaroo rats were found at either site. Grasshopper mice were taken occasionally at both sites.

The reddish soils at Pierce are of aeolian origin. The soils at Cobb Lake originate from the same sediments as Coal Creek. Both sites have an elevation of about 5,000 feet. Their climate is similar to that of Coal Creek, but is ameliorated by the presence of trees and other windbreaks and the influence of irrigation.

Rist Canyon and Sulzer Gulch.

The Rist Canyon and Sulzer Gulch sites were chosen for their similarities. Both are in east-west canyons in the first range of mountains. The site at Rist Canyon is somewhat higher and the canyon somewhat deeper and narrower and appears slightly more humid than the Sulzer Gulch site. The vegetation of both areas is influenced by every change in aspect and inclination and further complicated by soil accumulation and drainage from cliffs. Mountain mahogany (Cercocarpus montanus) is the principal shrub on open south slopes. The herb stratum under the brush, in order of estimated importance, includes; cheat grass, blue grama, Griffith's wheat grass (Agropyron griffithi), golden buckwheat (Eriogonum aureum), mountain muhly (Muhlenbergia montana), needlegrass

(Stipa comata), sleepy grass (Stipa robusta), Scribner's needlegrass (Stipa scribneri), sideoats grama (Bouteloua curtipendula), and big bluestem (Andropogon gerardi). Yucca, (Yucca glauca) and antelope bitter-brush (Purshia tridentata) are important shrubs, the former, partially so because it seems to afford shelter to P. maniculatus. South facing ravines are choked with plum (Prunus americana), chokecherry (Prunus virginianus and P. pennsylvanicus), skunkbush (Rhus trilobata), poison ivy (Rhus radicans), Virginia creeper (Parthenocissus vitacea) and wild grape (Vitis sp.). Stream bottoms support the same species plus snowberry (Symphoricarpos spp.), gooseberry (Ribes spp.), willow (Salix spp.), ninebark (Physocarpus sp.), shrub birch, (Betula occidentalis), alder (Alnus tenuifolia), and shrub maple (Acer glabrum). Cottonwoods (Populus sp.), blue grass, smooth brome (Bromus inermis), and timothy (Phleum pratense) are other noteworthy streambottom species. The north-facing slopes are densely wooded. At Rist, ponderosa pine (Pinus ponderosa), and douglas fir (Psuedotsuga menziesii) make up the forest. At the Sulzer site only ponderosa pine grows although douglas fir becomes abundant just above the site. Under the trees, the shrub understory consists chiefly of juniper (Juniperus communis), redberried elder (Sambucus pubens), ninebark, and shrub maple. The most frequent herb is Arnica cordifolia. Only needles underlie the densest canopies. The more open pine woods of southern slopes and ridges are underlain by

the shrub and herb stratum of untimbered slopes. An aerial photo of the Rist Canyon area indicates that thirty-seven per cent of the total area is densely wooded, forty-seven per cent is open woods, ten per cent brush land, and six per cent meadow or cropland.

The soils at Sulzer, Rist, and Buckhorn are derived from Pre-cambrian schists and granitic intrusions. The unaltered rocks, themselves, make up a considerable part of the surface. The surface soils range from pale gravels to black loams and red or tan duffs.

The Rist site includes elevations from 5,700 to 6,800 feet. Elevations at Sulzer vary from 5,500 to 6,200 feet. Temperatures are probably more moderate and precipitation higher than at Fort Collins (Table 5). The microclimates of north and south slopes are quite different.

Predators observed at Rist and Sulzer were Red-tailed Hawks (Buteo borealis), Prairie Falcons (Falco mexicanus), Swainson's Hawks (Buteo swainsoni), American Rough-legged Hawks, Golden Eagles, Horned Owls, Screech Owls (Otus asio), Saw-whet Owls (Cryptoglaux acadica), bull snakes, (Crotalus viridis), bobcats (Lynx rufus), weasels (Mustela frenata), skunks (Mephitis mephitis), raccoons, coyotes, and bears (Ursus americanus). Snakes are more numerous at these two sites than at the others. Peromyscus nasutus is common in Rist Canyon. Reithrodontomys megalotis occurs at

Sulzer Gulch. Golden-mantled ground squirrels (Citellus lateralis), and chipmunks (Eutamias sp.), are abundant at Sulzer Gulch. Peromyscus maniculatus may be found at any part of the two sites but they occur in greatest numbers along the stream bottoms, in ravines, and along the higher redges. They appear to be least numerous in the timber and on cheat grass-covered slopes (Table 4).

Buckhorn Ranger Station.

The Buckhorn Ranger Station site lies across the 8,000 foot contours. From an aerial photo it appears that nearly pure stands of lodgepole pine (Pinus contorta) in very high densities, cover 63 per cent of the total area; a mixture of douglas fir, ponderosa pine, and lodgepole pine covers 18 per cent, aspen (Populus tremuloides) 15 per cent, and meadow 4 per cent. The mice of the Buckhorn sample were all taken in, or near, the meadow portion which forms a narrow strip bordering the creek. In this portion of the habitat, willows (Salix spp.), antelope bitterbrush, squaw current (Ribes cereum), flowering raspberry (Rubus strigosus), juniper (Juniperus communis), snowberry kinnickinnic (Arctostaphylos uva-ursi), and bilberry (Vaccinium spp.), are important shrubs. Mountain muhly, blue grass, a marsh grass (Deschampsia caespitosa), nodding brome (Bromus anomalous), and hairy drop seed (Blepharoneuron

tricholepsis), are important grasses. Buffalo pea (Thermopsis spp.), yarrow (Achillea spp.), flea bane (Erigeron spp.), aster (Aster spp.), arnica (Arnica spp.), and numerous others are important herb species. "Slash" from lumbering activity and fallen rail fences were centers of trapping success.

One species of garter snake, Thamnophis elegans, is present at this site. The avian and mammalian predators probably include most of those seen at Rist or Sulzer but animal life, in general, is less obvious at this site. Chipmunks, chickarees (Tamiasciurus hudsonicus), golden-mantled ground squirrels, Richardson's ground squirrels (Citellus richardsoni), and voles (Microtus longicaudus) were all abundant. The last was trapped more often than Peromyscus. The climate of the Buckhorn site probably resembles that at Estes Park to the south (Table 5).

Cirques.

The highest site was the Cirques on the slopes of Comanche Peak. Cirques meadow, at the lower end of the site, has an elevation of 9,800 feet. Mice were caught at Cirques Lakes, which lie at 11,000 feet, and on the east ridge of Comanche Peak at 11,500 feet elevation. Cirques meadow is a swampy sedge and sphagnum meadow interspersed with beaver ponds and surrounded by 160 acres of recently logged lodgepole pine, and Engleman spruce (Picea englemanni).

Between the meadow and timberline is a forest of old stand lodgepole pine, Engleman spruce, and alpine fir (Abies lasiocarpa). The proportion of lodgepole pine decreases with elevation. Sedges (Carex spp.), willow (Salix spp.), dwarf birch (Betula glandulosa), and Senecio spp. are important species in the meadow. Bilberry (Vaccinium spp.), juniper (Juniperus communis), and several species of Arnica make up much of the understory in the surrounding forest. Of these, bilberry covers by far the most ground surface.

Several mice were captured around the meadow. None was taken in the forest proper. Most mice were captured in the Krummholz zone at timberline. In this area low islands of dwarfed and matted spruce, fir, and limber pine (Pinus flexilis), are surrounded by open tundra. Willow and dwarf birch are other "island" forming species. The most important herb species are a sedge (Kobresia bellardi), sandwort (Arenaria sajanensis), clover (Trifolium dachysta-phylum) avens (Geum spp.), spike trisetum (Trisetum spicatum), and bilberry.

From an aerial photograph, the "islands" of spruce and fir appear to cover approximately 12 per cent of the total area within a line joining the most scattered clumps. At least half of the area in the Krummholz zone is bare rock outcrops or talus slopes.

Long-tailed voles were extremely abundant throughout the site in 1957 and common in 1958. Red-backed voles

Clethrionomys gapperi) were caught more often than Peromyscus. The spruce mouse (Phenacomys intermedius) was taken occasionally. Chipmunks and golden mantled ground squirrels were common throughout the forest and above timberline. Chickarees were common in the woods. Pikas (Ochotona princeps) were common among the rocks. Predators observed include coyotes; martens (Martes americana), Red-tailed Hawks, Marsh Hawks, Horned Owls, weasels (Mustela frenata), and bobcats.

This site might seem to have the most rigorous environment of all the areas trapped. Deep snow covers this area from mid-October or November until mid-June or later. Frosts occur frequently throughout the summer and the weather in general is probably comparable to that of Longs Peak, Colorado (Table 5). On the other hand, the matted spruce clumps are quickly covered by snow in the fall, leaving insulated galleries of considerable area under the snow. The short growing season produces an abundant forage and seed crop. There are countless crannies offering shelter in the talus. All summer, water trickles down from the snowdrifts and from springs. Cirque mice may lead the most sheltered existence of all the mice studied.

The soil is chiefly humus, raw duff, or gravels. The duff is gray or reddish. The rocks are pale gray and white gneisses and granites. The rocks are more or less covered with lichens, gray lichens being the most common.

Other trapping sites.

In addition to the seven sites chosen specifically for the purpose of studying variation in the mice, several other areas were trapped for various other reasons. The information on distribution of Peromyscus on these other areas seems pertinent to the discussion of the nature of the role Peromyscus is playing in different environments and therefore is included in the report. Following are short descriptions of the other areas.

Stout, Horsetooth Pond, and the Knesley Ranch are alike in that they all lie in valleys between hogbacks at 5,500 feet elevation. The principal vegetation on the greater part of all three is mountain mahogany, skunk brush, and cheat grass. The same sedimentary deposits are exposed at all three sites. All three sites are being or have been farmed.

The Stout area is divided between wheatland, brushy pasture, and former cropland now set off for resort houses; it is now coming back to grass. The area was once extensively quarried for building stone and piles of rubble are numerous on the hillside. The area was trapped twice. Twelve traps were set around a wheat field in brush and along a fence now bordering on the housing development. Six P. maniculatus were taken. About a month later fifty-two traps were set in a grid fifteen yards on a side in a pure stand of Sporobolus in the resort development. Nothing was caught.

The Knesley ranch lies to the west across a hogback from Stout. The bottom is presently in wheat. It is extensively eroded and the gullies are lined with plum and chokecherry. The traps were set around the edge of the field along a fence row in the chokecherry and plum thickets, along the edges of the gullies, and on a hill in the mountain mahogany. Twenty-seven P. maniculatus were taken in forty-four traps with the highest success along the gullies.

The Antelope Refuge trapping site lies across a low stony ridge. The habitat is predominantly short grass prairie, but a short distance west the ground is broken into hogbacks and buttes on which the foothills associations of plants mingle with the prairie sod. The pasture has been heavily grazed for many years and the sod clumps, by erosion of the intervening bare soil, have come to stand two or three inches higher than the rest of the ground surface. Many holes have been dug into the clumps. Forty-four traps were set and thirty-five Peromyscus were caught. Peromyscus were apparently twenty to thirty times more abundant here than on similar prairie at Coal Creek.

Horsetooth Pond has been disturbed by earthmoving operations during which fill has been removed for a large reclamation project. Two small streams with large gullied beds converge on the pond. Traps set along walls of the stream gullies, which were much tunneled by Microtus, produced the greatest proportion of Peromyscus. Success fell

off sharply across the weedy flats between gullies and pits. This area is especially interesting because the mice trapped there were the most strikingly red-colored seen in the study. The soil of the area is a very deep-red clay derived from Lykins sediments. Understandably, the quarrying operation left a "bad-lands" habitat with a sparse and weedy vegetation.

The Pennock Creek site lies at about 8,400 feet at an old farmstead in a small meadow cleared of aspen and surrounded by lodgepole forest. The cleared aspens were piled in a windrow along one edge of the meadow. Traps set around the earth-matted roots and around the barns produced twenty-one captives in twenty traps. Five mice were captured in twenty-two traps set in lodgepole timber around the edge of the meadow. No mice were taken in twenty traps set in a line uphill through lodgepole pine.

Pawnee Buttes rise two hundred feet above the surrounding countryside in north-eastern Colorado. They are capped with a thin stratum of limey rock and are composed principally of clay sediments. The slopes are steep and eroded into slick, rounded hummocks of badlands character. Vegetation on the slopes is practically nonexistent. A few yucca or blades of grass cling to the protection of chunks of caprock. Mice were very abundant on the barren areas. Twenty-seven were taken from forty-six traps. In the surrounding mixed-grass prairie none was caught in ten traps.

Pingree Park is a meadow about one by one-half mile in diameter in the valley of the Little South Fork of the Poudre River. The elevation is roughly 9,000 feet. It is occupied by ranches, sawmills, summer homes, and the Summer Camp of the College of Forestry of Colorado State University. The information obtained about mice here was gathered by students under the direction of Dr. Harold Steinhoff and Mr. Douglas Gilbert. The camp stands on an east slope in mixed lodgepole pine, aspen, and willow. Fifteen standard Calhoun lines of twenty stations and sixty traps have been set out by students. Each of the fifteen lines is trapped three nights during the summer. These lines lie in meadow, swamp, and timber. The last location has the most lines. The timber is cut by many roads and trails. There is a good relationship between success in trapping Peromyscus and the presence of buildings and roads. The buildings offer shelter and probably forage. Many species of plants, not usually found in the forest, grow along the roads.

Table 4.--COMPARISON OF TRAPPING SUCCESS IN DIFFERENT HABITATS AT SEVERAL LOCALITIES IN WELD AND LARIMER COUNTIES, COLORADO.

	Total trap nights	No. of P. man. captured	Trap-ping index
Coal Creek, more than 25 yds. from cut bank	312	3	.001
Coal Creek, less than 25 yds. from cut bank	346	115	.332
Pierce, fence row	154	56	.364
Cobb Lake, abandoned farm land	424	241	.569
Rist Canyon, more than 50 yds. from creek	199	18	.090
Rist Canyon, less than 50 yds. from creek	431	92	.214
Sulzer Gulch, more than $\frac{1}{4}$ mi. from creek	60	10	.167
Sulzer Gulch, less than 50 yds. from creek	160	67	.419
Buckhorn, more than 50 yds. from creek	374	63	.168
Buckhorn, less than 50 yds. from creek	252	32	.127
Upper Cirques, at timberline	1057	70	.066
Lower Cirques, more than 50 yds. from any significant "break" or edge	76	0	.000
Lower Cirques, less than 50 yds. from any significant break	299	25	.084
*Pingree Park, lodgepole more than 50 yds. from road, edge, building, or stream	1833	15	.008
*Pingree Park, lodgepole less than 50 yds. from road, edge, building, or stream	3375	153	.045
Hogback valleys, several locations in Larimer County	264	118	.446
East of Waverly, abandoned farm land	26	23	.885

*From data supplied by Drs. Steinhoff and Gilbert of the faculty of the College of Forestry, Colorado State University.

Table 5.--METEOROLOGICAL STATISTICS FROM WEATHER STATIONS IN WELD AND LARIMER COUNTIES, COLORADO.

County	Station	Temperature Mean				Killing Frost	
		July	Jan.	Max.	Min.	Last	First
Larimer	Estes Park	61.7	25.1	98	-35	June 9	Sept. 15
Larimer	Ft. Collins	68.9	26.0	102	-38	May 7	Sept. 29
Larimer	Longs Peak	55.5	22.5	94	-41	July 2	Aug. 30
Larimer	Moraine	59.1	25.1	96	-42	June 14	Sept. 10
Weld	Grover	70.4	25.2	105	-37	May 20	Sept. 24
Weld	Greeley	72.2	24.9	107	-45	May 5	Sept. 30

Years recorded	Growing season days	Average precipitation						
		Year	Jan.	Feb.	Mar.	April	May	June
22	98	17.94	0.47	0.89	1.30	2.3	2.09	1.42
40	145	15.2	0.27	0.64	1.08	2.13	2.82	1.56
40	59	21.97	0.71	1.29	2.0	2.92	2.44	1.68
12	88	16.01	0.75	0.93	1.38	2.26	1.61	1.41
27	127	13.57	0.21	0.53	0.54	1.52	2.26	1.70
38	148	12.60	0.21	0.42	0.75	1.52	2.28	1.58

July	Aug.	Sept.	Oct.	Nov.	Dec.
2.75	2.17	1.57	1.33	0.86	0.79
1.64	1.32	1.52	1.17	0.49	0.56
3.48	2.27	1.89	1.52	0.83	0.96
3.32	1.39	1.48	1.23	0.50	0.75
2.32	1.68	1.33	0.65	0.34	1.48
1.69	1.15	1.13	0.98	0.41	1.49

From "Climate and Man", Yearbook of Agriculture USDA, 1941.

Chapter V

RESULTS

A total of 726 Peromyscus was captured during the course of the study. Of these, 528 were retained as specimens. The remaining 198 were either released because they were obviously juvenile or were used for other purposes. A larger proportion of males was captured, which is consistent with the results of several other studies and probably reflects the greater home range of the males (Blair, 1942; Williams, 1955) (Tables 6 and 7).

External measurements.

The measurements of the external characters contained such large errors that they have not been included in the discussion. However, the original observations may be found in the Appendix on file in the library of Colorado State University.

Variation in skeletal measurements.

The measurement of skeletal characters was much more precise. However, no differences of significance in the dimensions of any of the seven skeletal characters were found (Table 8).

Through an error, 158 of the skeletons were destroyed before they could be measured. Because the sample size was

Table 6.--NUMBERS OF P. MANICULATUS OF EACH SEX CAPTURED IN SEVERAL LOCALITIES OF NORTH-CENTRAL COLORADO.

Year	Males	Females	Undetermined
1957	140	109	76
1958	205	152	44

Table 7.--NUMBERS OF P. MANICULATUS OF EACH SEX CAUGHT BY SNAP TRAPS AT PINGREE PARK FROM 1954-1959*.

Males	Females
179	117

$\chi^2_{1df} = 13.0 \quad p < .01$

*From data furnished by Professors Steinhoff and Gilbert of the faculty of Colorado State University College of Forestry.

Table 8.--SUMMARIZED MEASUREMENTS OF P. MANICULATUS FROM WELD AND LARIMER COUNTIES, COLORADO ARRANGED BY LOCALITY AND SEX. MEAN LENGTHS AND STANDARD DEVIATIONS IN MILLIMETERS.

\bar{x} is the mean length, s is the standard deviation, n is the number of mice in the sample.

"Lab." mice were field-caught but retained, for other experimental purposes, in the laboratory for periods from two months (1958 lab. mice) to nearly a year (1957 lab. mice).

Locality of Adult Males		Con- dyle- premax- illa	Con- dyle- zygoma	Femur	Nasal	Bul- lar Width	Tooth Row	Man- dible
Coal Creek 1958	\bar{x}	24.92	17.50	15.60	10.60	11.48	3.84	16.25
	s	0.53	0.48	1.27	0.43	0.51	0.22	0.61
	n	5	5	2	5	4	5	4
Pierce 1958	\bar{x}	24.60	17.25	15.69	10.29	11.40	3.70	15.72
	s	0.82	0.64	0.78	0.63	0.29	0.18	0.51
	n	11	11	9	11	11	11	11
Cobb Lake 1958	\bar{x}	24.66	17.24	16.26	10.46	11.56	3.60	15.58
	s	0.43	0.39	0.70	0.37	0.26	0.009	0.36
	n	15	16	16	15	16	16	15
Rist Canyon 1958	\bar{x}	24.71	17.29	15.82	10.43	11.60	3.64	15.55
	s	0.66	0.46	0.62	0.44	0.38	0.19	0.58
	n	26	27	25	26	27	27	25
Sulzer Gulch 1958	\bar{x}	24.77	17.22	15.62	10.48	11.59	3.68	15.66
	s	0.71	0.45	0.72	0.55	0.38	0.13	0.35
	n	26	26	24	26	26	26	26
Buckhorn Ranger Station 1958	\bar{x}	25.02	17.34	15.76	10.48	11.62	3.70	15.88
	s	0.83	0.57	0.63	0.74	0.40	0.15	0.33
	n	10	10	8	10	10	10	10
Coal Creek Lab 1958+1957	\bar{x}	25.08	17.58	15.72	10.58	11.65	3.54	15.70
	s	0.89	0.54	1.26	0.59	0.26	0.11	0.51
	n	5	5	5	5	4	5	5
Cirques Lab. 1958	\bar{x}	25.16	17.50	15.92	10.70	11.15	3.72	15.56
	s	0.52	0.37	0.84	0.60	0.31	0.09	0.34
	n	7	7	4	4	5	5	5

Table 8.--Continued.

Locality of Adult Males		Con- dyle- premax- illa	Con- dyle- zygoma	Femur	Nasal	Bul- lar Width	Tooth Row	Man- dible
Cirques Lab. 1957	\bar{x} s n	24.45 0.58 4	17.12 0.24 5	15.62 0.90 4	10.74 0.38 7	11.10 0.26 5	3.74 0.18 8	16.19 0.32 7
Locality of Adult Females								
Coal Creek 1958	\bar{x} s n	24.56 0.31 3	17.30 0.36 3	16.05 0.78 4	10.72 0.33 4	11.10 0.20 3	3.47 0.10 4	15.42 0.34 4
Pierce 1958	\bar{x} s n	24.39 0.82 15	17.18 0.57 15	18.81 0.86 15	10.09 0.89 15	11.24 0.29 15	3.56 0.17 15	15.60 0.44 13
Cobb Lake 1958	\bar{x} s n	24.60 0.74 25	17.30 0.40 25	15.95 0.86 18	9.98 0.75 25	11.50 0.30 25	3.55 0.13 25	15.85 0.16 22
Rist Canyon 1958	\bar{x} s n	24.99 0.71 16	17.40 0.45 16	16.34 0.88 16	10.54 0.47 16	11.39 0.50 16	3.63 0.13 16	15.89 0.50 16
Sulzer Gulch 1958	\bar{x} s n	24.94 0.67 16	17.45 0.43 16	16.19 0.83 15	10.64 0.67 15	11.66 0.43 16	3.66 0.11 16	15.86 0.47 15
Buckhorn Ranger Station 1958	\bar{x} s n	24.55 0.45 8	17.01 0.36 8	15.96 0.87 7	10.22 0.40 8	11.39 0.95 8	3.52 0.13 8	15.86 0.43 7
Coal Creek Lab. 1958	\bar{x} s n	25.07 0.35 7	17.61 0.29 7	16.74 0.37 7	10.56 0.65 7	11.32 0.25 6	3.57 0.16 7	16.03 0.30 7
Coal Creek Lab. 1957	\bar{x} s n	25.10 0.87 10	17.47 0.56 10	16.43 0.55 3	10.48 0.65 10	11.14 0.34 8	3.62 0.12 10	15.96 0.61 10

Table 8.--Continued.

Locality of Adult Females		Con- dyle- premax- illa	Con- dyle- zygoma	Femur	Nasal	Bul- lar Width	Tooth Row	Man- dible
Cirques Lab. 1958	\bar{x} s n	24.78 0.93 4	17.30 0.68 4	15.62 1.00 4	10.82 0.74 4	11.38 0.29 4	3.65 0.14 4	15.98 0.82 4
Cirques Lab. 1957	\bar{x} s n	24.57 2.05 7	17.26 0.52 7	15.20 0.54 5	10.74 0.20 7	11.12 0.37 6	3.73 0.13 7	16.27 0.75 7

reduced, a degree of statistical precision was lost. However, there is nothing to indicate that larger numbers of specimens might reveal significant differences.

Variation in pelage coloration.

Peromyscus maniculatus have a sharply bicolored pelage. The feet and underparts are white and the upperparts are red or yellow buffs. A broad band of darker hue, referred to as the dorsal stripe, runs along the spine. A buffier band, the side stripe, runs along each flank. The buff is narrowly edged with clear orange at its juncture with the white at the muzzle and near the base of the tail and sometimes laterally. The tail is well furred and has a dark stripe, or pencillation, dorsally and white fur ventrally. Anterior to the base of each ear is a prominent tuft of hair, the pre-auricular tuft, which is often embellished with white hairs.

The hairs on the dorsal pelage are of two types. The first is an agouti underfur with a dark gray proximal portion, a buffy subterminal band, and a black tip. The second type comprises guard hairs which are pigmented throughout their length.

Visual comparison.

Some skins in each sample closely resemble some skins in each of the other six samples. The lightest individuals of each sample possess a similar deep orange-buff

pigmentation. The presence of sepia pigments intermixed with the orange and the possession of greater proportions of dark hairs produces a dark red, characteristic of the color of many mice from the mountains. When the dark pigments are abundant and the buff pigment is dilute, or qualitatively less intense, the skins are dark brown. Skins of many mountain specimens, especially those from Buckhorn and Sulzer, are this color. The same dilute buff pigments, with less sepia, mark light-brown skins common in all samples. A few skins from Cobb Lake and Coal Creek have abundant but dilute yellows and little sepia. The dorsal stripe is indistinct in a few Rist Canyon and plains mice.

When the skins of each sample were arranged by order of increasing color and brightness, the importance of each of the color variants described above seemed to be as follows: the orange mice constituted one-half or more of the samples from the plains localities, one-third of the Rist sample, one-sixth of the Sulzer sample, one-seventh of the Buckhorn sample, and one-fifth of the Cirques sample. Light brown or gray skins, which do possess some buff pigment but in low proportion, occur in similar proportions except that they make up a lesser proportion of the plains samples. Dark reddish-brown and dark brown skins dominate the Sulzer and Buckhorn samples while one-fifth of Rist and many Cirques mice are this color. The Cobb Lake samples would be nearly identical to the Rist series in color gradation if the

yellow skins of the first locality and the dark red and brown skins of the second area were eliminated.

There were no great differences in color between any of the samples. The individual skins could not be separated into groups corresponding to geographic areas. However, the samples from Sulzer Gulch and Buckhorn Ranger Station resemble each other in possessing proportional numbers of similarly colored skins. The composition of the samples from Coal Creek, Pierce, and Cobb Lake are also alike whereas the differences between the relative composition of the former and latter groups are evident to visual inspection. Rist Canyon and Cirques samples are intermediate in character yet do not markedly resemble each other.

Photometric comparisons.

Table 9 presents the mean reflectance reading for each sample by sex and filter. The reflectance is a percentage of the reflectance of a standard enamel plaque. These values are relative only and cannot be converted to color equivalents. Note that the differences are relatively small.

The results of the analyses of variance in pelage reflectance are shown in Table 10. From this table, it is apparent that the most important source of variance is associated with the mean of all mountain samples. Of twelve separate analyses, only the differences between these

Table 9.--MEAN VALUES OF THE REFLECTANCE OF THE PELAGES OF P. MANICULATUS FROM SEVERAL LOCALITIES IN NORTH-CENTRAL COLORADO. MEAN AND STANDARD DEVIATION EXPRESSED AS A PERCENTAGE OF THE REFLECTANCE OF A STANDARD ENAMEL PLATE.

Locality of Adult Males		Green		Red		Blue	
		Side	Dorsal	Side	Dorsal	Side	Dorsal
Coal Creek 1958	\bar{x}	18.13	12.60	48.67	39.87	19.87	12.67
	s	2.7	3.1	2.7	2.1	2.0	1.2
	n	15	15	15	15	15	15
Pierce 1958	\bar{x}	18.36	10.63	48.86	39.31	18.68	12.72
	s	2.7	2.0	3.2	2.8	1.9	1.7
	n	22	22	22	22	22	22
Cobb Lake 1958	\bar{x}	19.55	11.10	50.05	39.55	19.60	13.15
	s	2.6	1.9	3.9	2.8	2.4	1.5
	n	20	20	20	20	20	20
Rist Canyon 1958	\bar{x}	17.35	8.96	47.61	37.71	17.57	11.54
	s	3.1	1.4	4.2	2.7	2.6	1.3
	n	28	28	28	28	28	28
Buckhorn Ranger Station 1958	\bar{x}	15.80	8.13	42.73	34.86	16.26	10.53
	s	2.1	1.1	4.5	2.4	2.0	1.2
	n	15	15	15	15	15	15
Sulzer Gulch 1958	\bar{x}	15.80	8.69	45.11	36.26	16.54	10.89
	s	2.1	1.6	1.9	2.0	1.6	1.0
	n	26	26	26	26	26	26
Coal Creek Lab. 1958	\bar{x}	19.50	11.00	52.00	40.67	19.30	13.16
	s	1.6	1.7	3.0	3.2	0.1	0.8
	n	6	6	6	6	6	6
Cirques Lab. 1958	\bar{x}	18.11	9.67	47.11	37.22	17.67	12.00
	s	2.2	1.7	2.8	2.6	1.7	1.6
	n	9	9	9	9	9	9
<u>Locality of Adult Females</u>							
Coal Creek 1958	\bar{x}	19.00	10.77	54.22	46.44	25.89	20.22
	s	1.3	1.0	2.4	2.0	1.5	1.0
	n	9	9	9	9	9	9

Table 9.--Continued.

Locality of Adult Females		Green		Red		Blue	
		Side	Dorsal	Side	Dorsal	Side	Dorsal
Pierce 1958	\bar{x}	18.26	10.36	53.47	45.37	25.89	20.42
	s	2.3	1.4	2.4	1.9	1.7	1.1
	n	19	19	19	19	19	19
Cobb Lake 1958	\bar{x}	19.62	11.59	53.15	45.74	26.67	21.25
	s	2.3	1.3	2.8	2.2	1.5	1.2
	n	27	27	27	27	27	27
Rist Canyon 1958	\bar{x}	19.60	10.06	50.53	43.47	25.12	20.12
	s	1.7	1.9	2.3	2.0	1.3	1.2
	n	17	17	17	17	17	17
Buckhorn Ranger Station 1958	\bar{x}	16.75	9.88	50.12	43.62	25.00	20.00
	s	1.0	1.3	3.2	2.5	0.9	1.4
	n	8	8	8	8	8	8
Sulzer Gulch 1958	\bar{x}	16.38	9.06	52.39	45.05	25.16	20.00
	s	1.9	1.3	2.2	1.2	1.6	2.3
	n	18	18	18	18	18	18
Coal Creek Lab. 1958	\bar{x}	19.89	11.67	54.22	46.22	26.77	21.11
	s	3.1	1.6	2.6	2.3	2.2	1.1
	n	9	9	9	9	9	9
Coal Creek Lab. 1957	\bar{x}	20.86	12.60	55.80	47.13	27.26	21.00
	s	3.6	1.6	3.4	2.3	2.5	1.3
	n	15	15	15	15	15	15
Cirques Lab. 1958	\bar{x}	16.78	10.11	51.78	45.33	25.00	20.22
	s	1.8	1.7	2.9	2.6	1.7	1.1
	n	9	9	9	9	9	9
Cirques Lab. 1957	\bar{x}	16.00	10.05	52.72	44.72	24.33	19.61
	s	2.9	2.1	3.3	2.8	2.2	1.2
	n	18	18	18	18	18	18

Table 10.--RESULT OF ANALYSES OF VARIANCE IN PELAGE REFLECTANCE.

Comparison	M A L E S						F E M A L E S						Variance Associated With Comparisons
	Green		Red		Blue		Green		Red		Blue		
	Side	Dorsal	Side	Dorsal	Side	Dorsal	Side	Dorsal	Side	Dorsal	Side	Dorsal	
Coal Cr. Lab. residence vs. Cirques Lab.	20	6	86*	42	10	5							
Lab. res. 1 yr. vs. Lab. res. 3 mo.							1	2	4	0	1	2	
Coal Cr. Lab. Res. 1 yr. vs. Cirques Lab. res. 1 yr.							294*	52*	78	47*	70*	16*	
Coal Cr. Lab. res. 3 mo. vs. Cirques Lab. res. 3 mo.							41	11	7	2	14	3	
Coal Cr. & Cirques sam- ples Lab. res. separated from other samples ¹	5	2	45	6	2	5	1	15	4	19	0	0	
Mtn. origin vs. plains origin	162*	217*	409*	279*	183*	99*	20	50*	115*	59*	33*	3*	
Pierce & Cobb vs. Coal Creek	7	33*	6	3	6	1	0	0	7	6	1	3	
Pierce vs. Cobb	14	1	15	1	8	1	21	16	0	2	7	7	
Rist & Sulzer vs. Buckhorn	7	5	158*	54*	7	6	3	0	13	3	1	0	
Rist vs. Sulzer	33	1	83*	28	15	5	7	2	30	22	4	2	
Between sample m. s.	27.6*	29.4*	89.0*	46.9*	25.6*	13.5*	43.9*	17.2*	28.7*	17.8*	14.6*	5.1*	
Between sample d. f.	7	7	7	7	7	7	9	9	9	9	9	9	
Residual m. s.	6.5	3.4	12.0	6.5	4.3	1.8	5.6	2.4	7.4	4.8	3.2	1.3	
Residual d. f.	131	131	131	131	131	131	139	139	139	139	139	139	

¹A computational step without biological significance.

*The probability is less than 1 in 100 of obtaining by chance an F value as large as the quotient of this value over the residual mean square.

two categories in green reflectance from the side pelage of females are less than significant. There are also significant differences between local samples within each category. For example: the mean red reflectance from the dorsal stripe in skins of males from Rist Canyon is 4.9 per cent greater than that of skins from Sulzer Gulch. However, the differences within either category are smaller and less frequently significant than differences between the combinations.

Effect of captivity.

There is possibly an effect of captivity upon coat coloration since readings from captive mice from Coal Creek averaged higher than wild specimens from Coal Creek and since readings from specimens in captivity one year averaged higher than readings from specimens in captivity three months. However, the reverse relationship was found for Cirques captives; the long-term captives yielded lower readings than the short-term ones. Furthermore, neither the differences between separate Coal Creek samples nor between separate Cirques samples were significant. The effect of captivity, if any, is probably a reflection of the average age of the different samples. Peromyscus maniculatus become buffier up to the age of six months (Collins, 1923). After the year of captivity, all the mice must necessarily have been at least one year old.

Effect of molting.

Molting has an effect on pelage reflectance. For example, note the significant t value for green reflectance (side strip) in Table 11. Sometimes, differences in the color on either side of a molt line were easily apparent. The hair was patchy and dark where the old coat was shedding. The light bands did not cover up as much of the dark portion of hair beneath. The new hairs were usually visible underneath when the patchy hair was lifted forward. Only the more apparent examples entered into the results shown in Table 11.

The differences due to less obvious molts were not estimated but are assumed to be less. Approximately 47 per cent of the adult mice showed some evidence of molt. The proportion of mice molting did not differ significantly among the several samples (Table 12).

Soil reflectance.

Soil reflectance followed more of a gradient pattern than pelage reflectance. The soils appeared consistently darker as the altitude of their origin increased. Cobb Lake soil reflectance was practically identical to Coal Creek reflectance while Pierce had lower mean green and blue reflectance and a higher mean red reflectance than either Coal Creek or Cobb Lake. The soil at all three localities is more uniform over wider areas than at any

Table 11.--DIFFERENCES OBSERVED IN REFLECTANCE VALUES OF PELAGES ANTERIOR OR POSTERIOR OF A VISIBLE MOLT LINE. MEAN AND STANDARD DEVIATION EXPRESSED AS A PERCENTAGE OF THE LIGHT REFLECTED BY A STANDARD ENAMEL PLATE.

		Green		Red		Blue	
		Side	Dorsal	Side	Dorsal	Side	Dorsal
Posterior	\bar{x}	19.6	10.0	52.0	41.1	21.8	15.5
	s	4.1	2.5	2.6	5.0	4.3	3.8
	n	8	9	7	8	7	8
Anterior	\bar{x}	17.2	9.2	46.3	38.4	20.7	14.6
	s	4.1	2.6	6.4	5.4	5.1	5.6
	n	8	9	7	8	7	8
	\bar{d}	2.8	1.0	5.9	4.1	1.4	1.5
	$S_{\bar{d}}$	1.1	0.2	1.8	1.6	0.5	0.7
	$T_{\bar{d}}$	2.5	6.0	3.3	2.0	2.8	2.1
	p		<.01				

Table 12.--COMPARISON OF THE PROPORTION OF SKINS SHOWING EVIDENCE OF MOLT IN THE SAMPLES.

	Coal Creek		Pierce		Cobb Lake		Rist		Sulzer		Buck- horn		Cir- ques Lab.		Coal Creek Lab.		Total	
	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%
Molt	10	42	19	46	19	40	19	42	21	48	13	56	23	61	13	43	137	47
Not Molt	14	58	22	54	28	60	26	58	23	52	10	44	15	39	17	57	155	53
Total	24		41		47		45		44		23		38		30		292	

$\chi^2_{7df} = 7.13 \quad .70 > p > .50$

mountain locality. The Coal Creek and Cobb Lake soils have a definite yellow hue while Pierce soils are dull red. It is interesting that these visually apparent differences were repeated in the photometric results because it thus gives reason to believe that the results of the photometric readings, if distorted, are essentially reliable.

Table 13 presents the mean reflectance of the ten soil samples from the seven localities. The mountain soils are darker. Part of this trend is due to the texture of the soil. The plains samples are chiefly mineral, dry, and dust-fine. The mountain soil samples included a large proportion of litter, were damper, and generally coarse. Porous soils reflect less light, thus reducing the galvanometer reading. However, grinding the soil to a fine powder increased the reflectance most for the few cloddy samples from the plains and scarcely affected the readings obtained from mountain duffs and gravels (Table 14).

The correlation of mean soil reflectance to mean pelage reflectance of mice of the same locality was calculated. The correlation was positive. The r value differed significantly from zero only for the correlation of blue reflectance of the soil to blue reflectance of the side stripe of adult females. There is an indication in the many low

Table 14.--COMPARISON OF REFLECTANCE VALUES FOR COARSELY
GROUND AND FINELY GROUND SOIL SAMPLES.

		Green	Red	Blue
Mean reflectance				
Coarse		12.2	45.2	20.7
Fine		17.3	53.7	25.8
Mean difference	\bar{d}	5.2	9.2	5.2
	$S_{\bar{d}}$	2.8	3.4	1.7
	n	6	6	6
	T	1.9	2.6	3.05
	P	.27p>.1	.057p>.02	.057p>.02

Table 15.--LINEAR RELATIONSHIP OF MEAN PELAGE REFLECTANCE TO MEAN SOIL REFLECTANCE BASED ON DATA FROM TABLES 9 AND 13.

	Green		Red		Blue	
	Side	Dorsal	Side	Dorsal	Side	Dorsal
b_{yx} coefficient of regression of pelage color on soil color-adult females	0.23	0.12	0.17	0.13	0.18	0.08
r coefficient of correlation-adult females	0.02	0.66	0.21	0.56	0.85	0.72
t value	0.05	2.9	0.52	1.6	3.9	2.7
Probability of t	1>p>.95	.05>p>.02	.7>p>.6	.27p>.1	.017p>.001	.057p>.02
b_{yx} coefficient of regression of coat color on soil color-adult males	0.16	0.19	0.34	0.26	0.24	0.11
r coefficient of correlation-adult males	0.64	0.78	0.67	0.75	0.80	0.52
t value	1.9	3.0	2.2	2.6	3.2	1.5
Probability of t	.2>p>.1	.05>p>.02	.1>p>.05	.057p>.02	.027p>.01	.27p>.1
n = 8						

probability values that significance could be achieved with more observations (Table 15).

The regression coefficient is very small. I think it might be increased if the readings were made of the undisturbed surface in all cases. Soils from the high mountains are topped with a thick layer of duff. The surface is often bleached while only a fraction of an inch down decay has blackened the litter. The action of taking the soil sample naturally mingled the dark and the bleached materials. The samples of plains soils are more representative since the soils from the plains sites contain little organic material.

The coloring of the tail stripe, or pencillation, varied from brown through black. The following method was used to group the specimens into five classes of increasingly dark coloration. Two skins; #208 from Pierce, with a representative black pencillation and #531 from Buckhorn Ranger Station, with a representative brown tail, were selected as standards. The remaining tails were compared with these two and assigned to one of five classes.

System of classification of mousetails
according to darkness of pencillation

CLASS	CHARACTERISTICS
1	lighter than #531
2	identical to #531
3	lighter than #208, darker than #531
4	identical to #208
5	darker than #208

All the comparisons were made in one afternoon under natural illumination.

The pencillation of the tail is ordinarily made up of hairs resembling stubby guard hairs. They are black throughout their length. The tails of some mice, however, exhibit many hairs with a banded pattern except that the light portion of the hair often lacks any discernible pigment, yellow or otherwise. In other specimens, the tails are sprinkled with completely white hairs; others have patchy hair so that the light skin shows through. This condition apparently results from injuries, perhaps due to fighting with other mice. These additional factors complicate subjective comparison between tails. Nevertheless, the important factor causing one tail to appear lighter or darker is that its pigments actually appear blacker. Whether this is a qualitative difference or a matter of density of pigment material is not known.

The observations were placed in a X^2 contingency table. The null hypothesis that proportions of tails in each darkness class were the same in all samples was tested. The resultant X^2 has a probability much less than one per cent which refutes the null hypothesis and supports an assumption that there are significant differences in proportions of dark tails among the samples.

Observations of tail color in males previously had been compared to those of females, but no differences in

proportions were found between the sexes. Therefore, all observations of both sexes are included in Table 16.

Increase in litter size with elevation.

The data in the first eleven rows of Table 17 suggested that litters of mice from the high mountains usually contain more young than litters of foothill mice and still more than litters of plains mice. The suggestion was strengthened by the data from Pingree Park supplied by Professors Gilbert and Steinhoff who graciously furnished the data gathered under their supervision over several years by students at the summer forestry camp at Pingree Park. Only counts of embryos are included from those data. Pingree Park lies between the Buckhorn site and the Cirques sites; it is somewhat nearer the latter.

Fall Creek, draining the Cirques, joins the Little South Fork of the Poudre River one-half mile above Pingree Park. Pennock Creek lies midway between the Pingree and the Buckhorn sites. Data from these sites were combined to form the high altitude class in a X^2 contingency table. Similarly, data from Coal Creek, Pierce, and Cobb Lake were grouped together in the low altitude class. The resultant X^2 , 43.17 with 12 degrees of freedom, discounts the null hypothesis that differences observed in the proportion of litters of each size are due to chance alone.

Table 16.--PEROMYSCUS MANICULATUS (BOTH SEXES) FROM SEVEN LOCALITIES CLASSED ACCORDING TO DARKNESS OF THE TAIL PENCILLATION.

Dark- ness Class	Coal Creek	Pierce	Cobb Lake	Rist	Sulzer	Buck- horn	Cir- ques Lab	Coal Creek Lab	Total
1	6	11	10	5	5	2	0	2	41
2	7	14	16	8	5	3	5	6	64
3	6	16	17	22	18	5	8	16	108
4&5	1	4	3	8	15	12	19	5	67
Total	20	45	46	43	43	22	32	29	280

$$\chi^2_{2df} = 74.98 \quad p < .01$$

Table 17.--FREQUENCY DISTRIBUTION OF LITTER SIZES IN
PEROMYSCUS MANICULATUS FROM DIFFERENT ELEVATIONS.

Site	1	2	3	4	5	6	7	8	9	Num- ber of fe- males	Mean lit- ter size	Mean and standard error of body length
Coal Creek		1	5	3	1					10		
Pierce	1	1	2	9	4					17		
Cobb Lake			2	17	9	1				29		
5100-5300'	1	2	9	29	14	1				56	4.3	95.5±0.7
Rist		1	2	8	6	2	3			22		
Sulzer		1	2	10	2					15		
5500-6500'		2	4	18	8	2	3			37	4.4	95.9±0.9
Buckhorn			1	3	1	1		1		7		
Pennock Creek			1	3						4		
Cirques						1	1	1		<u>3</u> 14	5.0	94.2±2.2
Pingree Park	*1		1	6	6	11	5	2	1	33	5.6	
8000-11000'	1		3	12	7	13	6	4	1	47	5.4	

$$\chi^2_{12df} = 43.17 \quad p < .01$$

*From data furnished by Professors Steinhoff and Gilbert of
the Colorado State University College of Forestry.

Chapter VI

DISCUSSION

Philosophical considerations.

The samples differ in pelage reflectance, in pigmentation of the tail stripe, and in average litter size. They do not differ significantly in any skeletal dimension measured.

The validity of this study depends upon the assumption that these samples adequately reflect the characteristics of the natural populations from which they were drawn.

Variation within an animal species originates from three principal sources. First, environment acts directly upon the organism during development to modify the normal genetic response. Previous workers, notably Sumner (1927) and Dice (1932 and subsequent papers) have shown that the characters typifying wild populations distinguish their offspring as well, although the latter have been raised together under uniform conditions often quite unlike their ancestral habitats. The homeostatic responses of mice, as in most mammals, are quite effective in reducing the effects of a variable environment. It has been assumed that in the characters considered in this study differences due directly to environmental influences were negligible. Second, the individual undergoes progressive modification of all characteristics as it develops, matures, and ages. Two

individuals of different ages, even though they possess the same genotype for a particular trait, will not exhibit that character in precisely the same degree. Often the difference in size, for example, will be great. The age of each specimen was estimated so that the observations could be grouped in a manner intended to reduce the effect of this factor. Finally, the frequency in the breeding population of genetic factors controlling a characteristic is changed by one of several ways. Natural selection, mutation, random loss or fixation of alleles, and differential migration are probably the most prominent factors modifying gene frequencies in P. maniculatus.

Evolution is defined as the alteration of gene frequencies. The goal of this study of variation was to observe the present status of evolutionary tendencies in a segment of the species, P. maniculatus. All results have been interpreted in that light.

Variation in pelage colors.

The correlation of pelage coloration to the color of the soil is a phenomenon that has been observed frequently (Sumner, 1932; Dice, 1932 and other publications; Dice and Blossom, 1937; Lerass, 1936; Blair, 1947). The relationship has been assumed to have developed through natural selection of a concealing coloration. The selective agent was considered to be predation. Dice (1949) has demonstrated that mice whose color contrasts with that of the substrate

suffer a higher mortality when subjected to predation by owls in an experimental situation. Others have shown a similar adaptiveness of concealing appearance in other animals (Sumner, 1923).

In the present case, the correlation between colors of soils and pelages, while positive, is not remarkably great. This may indicate that the intensity of selection by predation is too low to overcome the homogenizing effect of genetic migration among the populations studied.

The differing degrees of pigmentation observed in the pencillation of the tail possibly illustrate one device by which changes in coloration have been achieved. The quality of sepia pigment possessed by hairs of the tail is shared also by the dark tips of agouti hairs and the guard hairs. The different aspect of dark red mice and orange-buff mice described above may be due simply to the presence of more or richer sepia pigments.

Variation in litter size.

Dunmire (1960) has noted an association between larger litters and higher elevations. He attributed the differences in fecundity to heredity. Obviously it could be adaptive to produce more young per litter in a region with a short breeding season. However, several factors are known to influence the numbers of offspring in each litter in mammals. Among them are age, nutrition, climate, size, previous breeding history, interval between pregnancies,

lactation at time of conception, and heredity (Asdell, 1946). Jameson (1950) and Davis (1956) have noted the association of season and age and size of mother to litter size. However, the relations of size and fecundity are reversed in the present study. As shown in Table 13, the average body size is smallest, though not significantly so, for the mice with the largest litter size. There is a speculative suggestion that producing large litters is a phenotypic response to a short breeding season. Sows are known to produce significantly more young in a litter when ten months have elapsed since the last litter than when only five months have intervened (Johanssen, 1929 in Asdell, 1946). If the breeding season is short so that fewer litters are born, then the average interval between parturitions is increased.

Regardless of whether the observed differences are attributable primarily to heredity or environment, there are other studies which link fecundity with the length of the season. Jameson (1950) compared the results of his studies on breeding in *P. m. gambeli* in the Sierra Nevada with those of Scheffer (1930) in Washington State. The average litter size was larger in the northern group. Similarly, Coventry (1938) found that both *P. maniculatus* and *P. m. leucopus* from Ontario had larger litters on the average than did their counterparts from Michigan, according to Svilha (1932).

Relationship of distribution and variation.

The lack of skeletal differences between populations

is not unusual. Although Dice (1932 and later publications) and others (Blair, Lerass, Sumner) found significant differences frequently among local stocks, they did not often find any correlation between those differences and any environmental condition. When a significant relationship did appear, the stocks involved were representatives of subspecies with known differences of habit and habitat preference. The opposite inference is that lack of skeletal differences indicate similarity of habit. Unfortunately, the latter is not corollary to the former. Nevertheless, certain similarities between the habitats utilized by P. maniculatus at the several sites (Chap. IV) do lend credence to the latter alternative. Foster (1960) and Harris (1948) have been able to demonstrate differences in behavior and in habitat preference between prairie and forest dwelling races of P. maniculatus. Horner (1954) produced evidence of greater climbing ability in the longer tailed forest forms compared to the short tailed grassland species. No such detailed experiments were made in the present study. However the behavior of several escapees in the laboratory was noted. The plains and mountain mice, alike, would run along the floors with no attempt to climb furniture or walls. The semi-arboreal species, P. trueii, P. boylei, and P. nasutus scampered up walls and furniture without hesitation.

Perhaps a more significant indication in this matter is the pattern of distribution throughout the study area.

The highest indices of population were recorded in cultivated districts where the concentrations of mice occurred along fence rows and abandoned corners. The most uniform indices were obtained in the foothills communities though even there the mice apparently avoided timbered slopes. It seems safe to conclude that the greatest population of deer mice per unit area was found in the habitats of cultivated fields and foothills. Mice in the higher mountains were found exclusively along creeks, open ridges, and disturbed areas within the forest; the bulk of the forest was nearly barren of mice. Forests cover far the largest portion of the total area at the mountain sites. Moreover, the indices of population for the higher sites in no instance were as large as those in the foothills or farm country. The picture presented was that of very low densities over all. The area of high index on the plains did not include over five per cent of the total so that again the average density appeared low. A fair conclusion is that Peromyscus is unable to exploit these regions equally because it has not developed the necessary adaptations.

A widespread, numerous population capable of existing in a wide range of habitats is probably an asset to a species in an unstable environment. Frequent genetic exchange is probably a natural condition of such a situation. By minimizing the influence of selection in the more extreme portions of the range and dispersing its effects throughout the populations, genetic exchange contributes to the maintenance of a general adaptedness (Brown, 1958).

Questions for further study.

In summer, at least, P. maniculatus in north-central Colorado are distributed unevenly through the habitat. In the higher mountains and on the plains, the distributions are very sparse. They appear to be most uniformly distributed and also most abundant in the cultivated lands and in the foothills. The manner in which they are distributed has several important implications for understanding the origin of geographic variations, their present maintenance, and adaptive values. Therefore, a continued study of the distribution of P. maniculatus in this area is desirable.

The distribution of the species is an indication of its preferences and capabilities. Although Peromyscus is probably the best known North American rodent no concise description of its niche even for a small community exists. A further study or studies of distribution would contribute valuable information toward answering these questions.

The mice of different sites do not appear to have developed special structures adapted to those sites. There are, however, certain features of the environment, i.e., atmospheric pressure, which are very different at different sites and which the mice cannot avoid by behavior. A further study should investigate possible differences in food storing and nesting habits, oxygen requirements, cold tolerance, activity rhythms, and determine if these habits and physiological developments are under genetic control.

Chapter VII

SUMMARY

Geographical variation in populations of P. maniculatus from north-central Colorado was studied during the years 1957-1958. Seven hundred mice were collected from seven sites at elevations from 5,000 feet to 11,500 feet. The sites represented several diverse habitat types.

Variation among populations in lengths of the condyle-premaxillar distance, condyle-zygomatic distance, nasal, femur, maxillary tooth row, mandible, and width of the skull at the bullae was insignificant.

The reflectance of the pelage, as measured by photoelectric reflectometer, was greater for plains specimens than for mountain specimens. It was observed that the color of the pencillation of the tail varied from brown to black. The intensity of the color in the pencillation was related to the general darkness of the pelage. Brown tails occurred more frequently in plains mice while black tails predominated in mice from high elevations. The darkness of pelages increased with elevations and was correlated to the darkness of the soil, although not strongly so. The differences in coat color among populations may have resulted through selection by predators.

It was noted also that litters tended to be larger in female mice from the highest localities. The average

litter at 5,000 feet elevation was 4.0 embryos; at 6,000 feet it was 4.6 and at 8,000 to 10,000 feet it was 5.0. The causative factors behind variation in the number of young produced per litter are not known.

In the course of obtaining the specimens observations were made of the patterns of distribution of Peromyscus maniculatus through the environment. At all sites the mice were found more abundantly in some portions of the habitat. The distribution of mice, as a result, is dendritic or discontinuous, which may have had important effects in evolution of differences among populations.

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ABSTRACT OF THESIS

VARIATION IN DEER MICE FROM
DIFFERENT ELEVATIONS

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In partial fulfillment of the requirements
for the Degree of Master of Science
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Fort Collins, Colorado
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