

1975

The Distribution of the Deer Mouse, *Peromyscus maniculatus*, on the Oregon Side of the Columbia River Gorge

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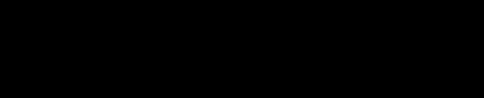
AN ABSTRACT OF THE THESIS OF Ronald P. Neilson for the
Master of Science in Biology presented 6 June 1975.


Title: The Distribution of the Deer Mouse, *Peromyscus
maniculatus*, on the Oregon Side of the Columbia
River Gorge

APPROVED BY MEMBERS OF THE THESIS COMMITTEE:


Richard B. Forbes, Chairman


Robert O. Tinnin


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Quentin Clarkson

A study of the biogeography of *Peromyscus maniculatus* was undertaken in order to ascertain a few of the environmental parameters important in defining the distribution of this species and how the species in turn has adapted to these parameters. The Columbia Gorge was chosen as it presents a climatic gradient from maritime to continental with very little elevation gain. Changes along this gradient in topography, soils and vegetation community structure are discussed. It was found that in the winter in the absence

of *Sorex trowbridgii*, *P. maniculatus* populations correlated loosely, yet in a positive direction with the rainfall pattern. *S. trowbridgii* populations, however, were found to correlate more rigidly in a positive direction to the rainfall pattern. In the presence of *S. trowbridgii* in the spring and summer, the distribution of *P. maniculatus* became more complicated. On the basis of these data, a hypothesis is presented suggesting that *P. maniculatus* is a generalist with respect to habitat and *S. trowbridgii* is a specialist with respect to habitat. It is suggested that both species prefer the more moist sites and are competing for these habitats. Since *S. trowbridgii* is the specialist it is able to dominate the preferred sites, restricting the populations of *P. maniculatus* to the more xeric, peripheral habitats.

No correlation was found between *P. maniculatus* or *S. trowbridgii* distributions and percent cover or individual plant species distributions. Both species probably correlate to complex biological communities. Multiple regression analysis suggests that the brush layer may be more important in defining these communities than either the canopy or ground layers. Evidence is presented suggesting that slope angle may also be an important factor in determining the distribution of *P. maniculatus* in the winter, decreasing in importance into the summer.

The distribution of subspecies of *P. maniculatus* was also investigated on the basis of tail length. *P. m. rubidus* was found in the moist *Pseudotsuga menziesii*

forests and *P. m. gambelii* was found in the more xeric *Quercus garryana* and *Pinus ponderosa* forests. A zone of intergradation is apparent at Mitchell Point which is also the region of the sharpest climatic change in the Columbia Gorge.

THE DISTRIBUTION OF THE DEER MOUSE,
Peromyscus maniculatus, ON THE
OREGON SIDE OF THE
COLUMBIA RIVER GORGE

by

RONALD P. NEILSON

A thesis submitted in partial fulfillment of the
requirements for the degree of

MASTER OF SCIENCE

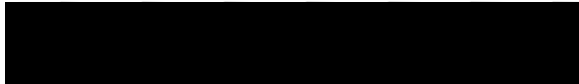
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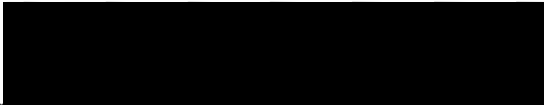
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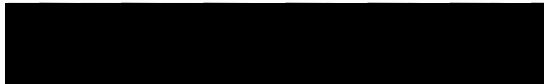
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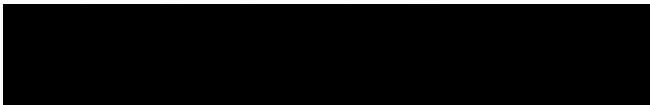
TO THE OFFICE OF GRADUATE STUDIES AND RESEARCH:

The members of the Committee approve the thesis of
Ronald P. Neilson presented 6 June 1975.



Richard B. Forbes, Chairman

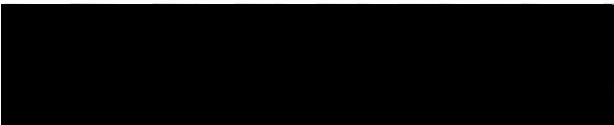

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INTRODUCTION

The distributions of plants and animals are of interest to biologists, insofar as they provide a basis for the study of related ecological and physiological principles. The two main approaches in studying these principles are 1) to investigate the distributions of plants and animals over an environmental gradient and 2) to investigate how these distributions change over time. Changes through time may be thought of in two senses, short term (annual) and long term. With regard to distributional phenomena, the Columbia River Gorge in Oregon is of interest because it bisects a mountain range and presents a strong climatic gradient along a very shallow elevational incline. The gorge extends along approximately 55 miles of the Columbia River as it transects the Cascade Mountains. On the Oregon side Troutdale marks the west portal and The Dalles the east portal (Figure 1). The general features of the gorge, described adequately elsewhere (Lawrence 1939; Baldwin 1966; Lynott 1966; Detling 1958, 1966; Gordon 1966; Storm 1966) will not be discussed here.

Peromyscus maniculatus is the most widely distributed small mammal in North America, both geographically and climatically, and occupies the full length of the gorge. More is known about this native mammal than any other. King (1968) presents an extensive survey of the pertinent literature about the genus *Peromyscus*. Although *P. maniculatus*

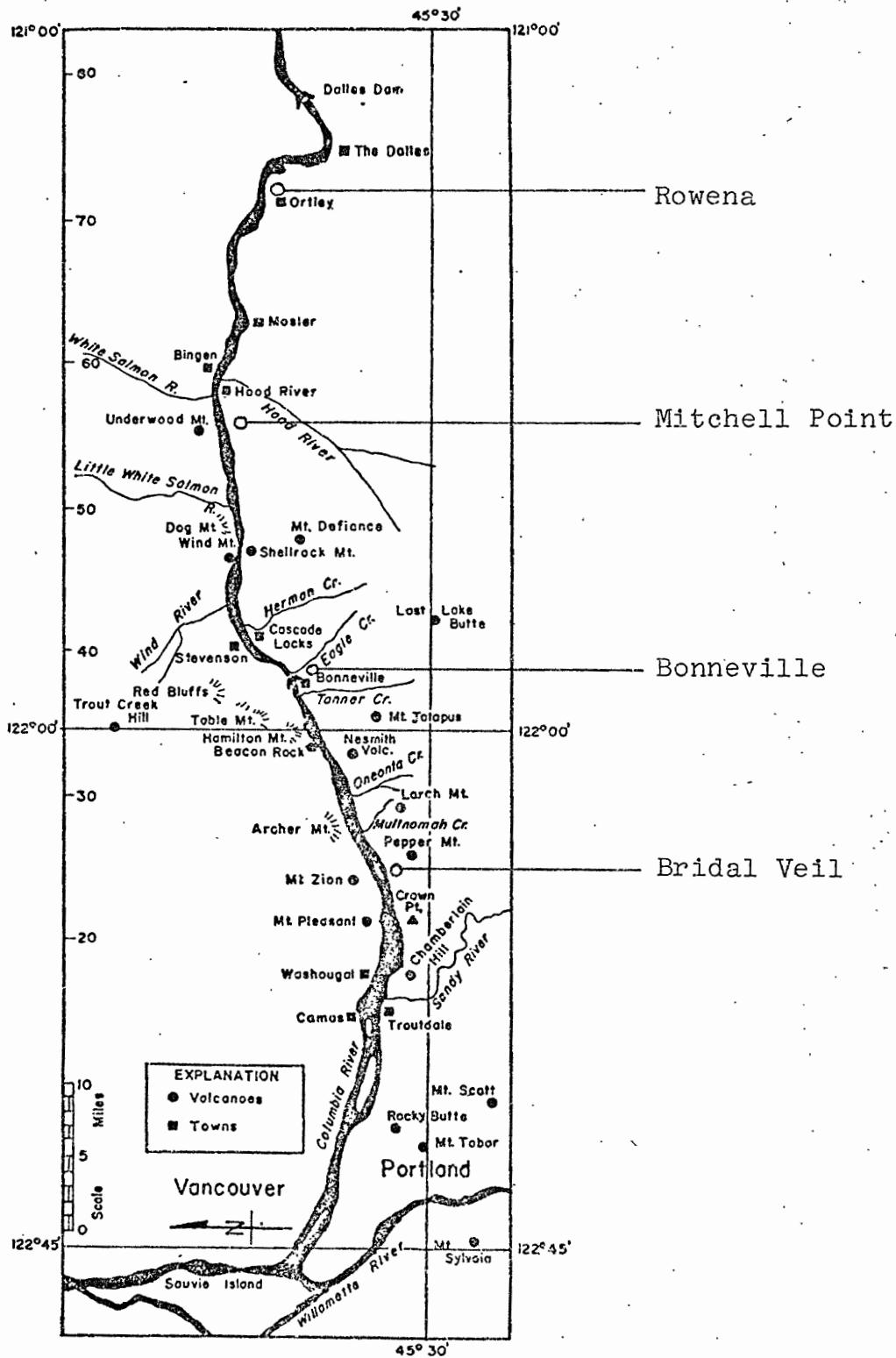


Figure 1. Map of Columbia River Gorge (Baldwin 1964).

is a generalist with respect to habitat and climate, it is my contention that there are discernible constraints upon the distribution of its populations.

The present study seeks to combine the two main analytical approaches in an investigation of some of the constraints upon the distribution of *P. maniculatus* through the Columbia Gorge. The concentration is upon short term changes through time, and on distributional changes over an environmental gradient. However, some data are compared to data from Dice's (1949) study.

MATERIALS AND METHODS

Site Selection

The study area I chose comprised a 44 mile section of the gorge on the Oregon side. Four study sites were selected at nearly equal distances along this range. Since the gorge contains many varied habitats, it was necessary to limit the study to those most prevalent. The site selections were based on the following criteria: 1) each site had to be accessible from the highway, 2) each had to face the river, 3) overall slope angle (from the top of the gorge to the bottom) had to be between 25° and 30° , and 4) the representative area had to be approximately 350 m long by 50 m wide. These criteria dictated the following locations within the gorge: Bridal Veil (T.1N., R.5E., sec. 36), Bonneville Dam (T.2N., R.7E, sec. 22), Mitchell Point (T.3N., R.9E., sec. 36), and Rowena (T.2N., R.12E., sec. 12).

Three square plots 80 m on a side were chosen within each site. The plots were arranged linearly 50 m apart and at least 20 m off the road. Thirty-two trap stations, 10 m apart, were arranged around the periphery of each plot. The capture data were grouped around every fourth trapping station and at these stations various vegetational parameters were assessed and slope angles and aspects were measured. This gave a total of twenty-four data points within three plots at each sampling site.

Site Descriptions

Topography. At Bridal Veil the slope faces N 35° W. The slope, as measured at the twenty-four data points ranges from 13° to 40° with a mean of 21°. The overall configuration of the slope is that of a very broad and uniform face, sloping down at an angle of about 30° and tapering off at the bottom. The sample plots were positioned along the area of tapering.

The slope at Bonneville faces approximately N 40° W and is steeper than that at Bridal Veil. The angle ranges from 22° to 48° with a mean of 34°. Again, this is a very broad, uniform slope, tapering off at the bottom. It was in this lower portion that the sample plots were situated. Both Bridal Veil and Bonneville represent very old, broad talus slopes with a moderately well-developed soil.

Mitchell Point shows some differences in its topography relative to that at Bonneville. The slope faces N 30° W with slopes ranging from 7° to 39° and a mean of 25°. The structure of the slopes, however, is much more complicated than at the first two sites. Again, there are broad talus slopes; however, they appear to have been formed more recently than at the Bridal Veil and Bonneville sites. This may be due to the fact that Mitchell Point is just east of the crest of the Cascades and is consequently much drier than the previous two sites, thus slowing down geomorphic processes. As a result, large ramparts of rock

are projecting up through the talus, dissecting the uniformity of the slope. The tops of the ramparts represent the interfaces between successive layers of Columbia River basalt. The two specific ramparts with which I was concerned are horizontally in line with each other and represent remnants of the same basalt layer. The tops of these ramparts are relatively flat, exposed and xeric, and the fronts are nearly vertical with the entire rampart being surrounded by talus. Consequently, the plots had to be arranged with respect to these ramparts. Two of the squares ran completely around and over the top of the two ramparts and a third was placed between the two ramparts on a relatively uniform, gentle slope. Mitchell Point represents a transition between the moist west end of the gorge and the dry east end of the gorge. The portions of the plots extending over the tops of the ramparts sampled the xeric habitats; all the rest of the data points sampled the more mesic talus slopes. Because this site represents a transition with respect to vegetation, the xeric and mesic subsites represent different habitats. The two habitats were sampled with respect to each other in the approximate proportions in which they occur so as not to weight one habitat over the other.

The site at Rowena is also topographically more complex than either Bridal Veil or Bonneville, although in a different manner than Mitchell Point. Again, this

complexity is partially due to the drier climate. The slope faces approximately N 15° E and ranges in steepness from 6° to 37° with a mean of 15°. The lower portion of the slope (the portion utilized in this study) is composed of three distinct terraces approximately 100 m wide which correspond to successive layers of Columbia River basalt. This area represents a younger stage in geomorphic evolution than Mitchell Point. The talus cones which result from drastically eroded basalt terraces in the more westerly sites are in their barest beginnings at Rowena. Erosion has left moderate slopes at the base of each terrace creating a relatively protected, mesic habitat. However, the front, or "nose", of each terrace is very exposed, windswept and xeric. Again, these two habitats were sampled in approximately the proportions in which they occur. The slopes for the four sites are summarized in Table I.

Climate. Climatic data for the Columbia Gorge were obtained for the four weather stations nearest the study sites - Troutdale, Bonneville, Hood River and The Dalles (Figure 1). Although the data will not be exactly the same for the study sites, trends should be apparent. Averages were obtained for a ten-year period from 1956 to 1965 (Climatological Handbook Columbia Basin States 1969). Monthly means of precipitation and temperature were computed from data collected at each weather station in 1973. These were compared to the ten-year averages for all four sites.

TABLE I

MEAN SLOPE, SLOPE RANGE, AND ASPECT
AT THE FOUR STUDY SITES

	Bridal Veil	Bonneville	Mitchell Point	Rowena
Mean Slope	21°	34°	25°	15°
Slope Range	13 - 40°	22 - 48°	7 - 39°	6 - 37°
Aspect	N 35° W	N 40° W	N 30°W	N 15° E

The differences were negligible.

The climate of the Columbia Gorge is complex. Figures 2, 3 and 4 reveal the interplay between temperature and precipitation from one end of the gorge to the other. The west end of the gorge is wetter and has smaller daily and annual temperature fluctuations than the east end of the gorge. The daily temperature range at each of the four sites is negatively correlated with the mean monthly precipitation. This allows one to rank the four sites in the gorge on a climatic scale ranging from maritime to continental in the following order: Bonneville, Troutdale, Hood River and The Dalles.

Soils. The soils of the gorge are primarily influenced by the climate, the source material, and to some extent the vegetation. There are three major soil groups in the gorge as outlined by the U.S.D.A. Soil Conservation Service for Oregon (OR-SOILS-1). The soils present at my study sites are derived from basalt and range in the U.S.D.A. texture classification from cobbly loam to very cobbly loam.

The Bridal Veil and Bonneville sites both fall into the Wyeth soil series. These have a water supplying capacity of 16 to 20 inches and an effective rooting depth of 40 to 60 inches.

Mitchell Point, as before, represents a complication. The previously described mesic habitats fall into the Wyeth

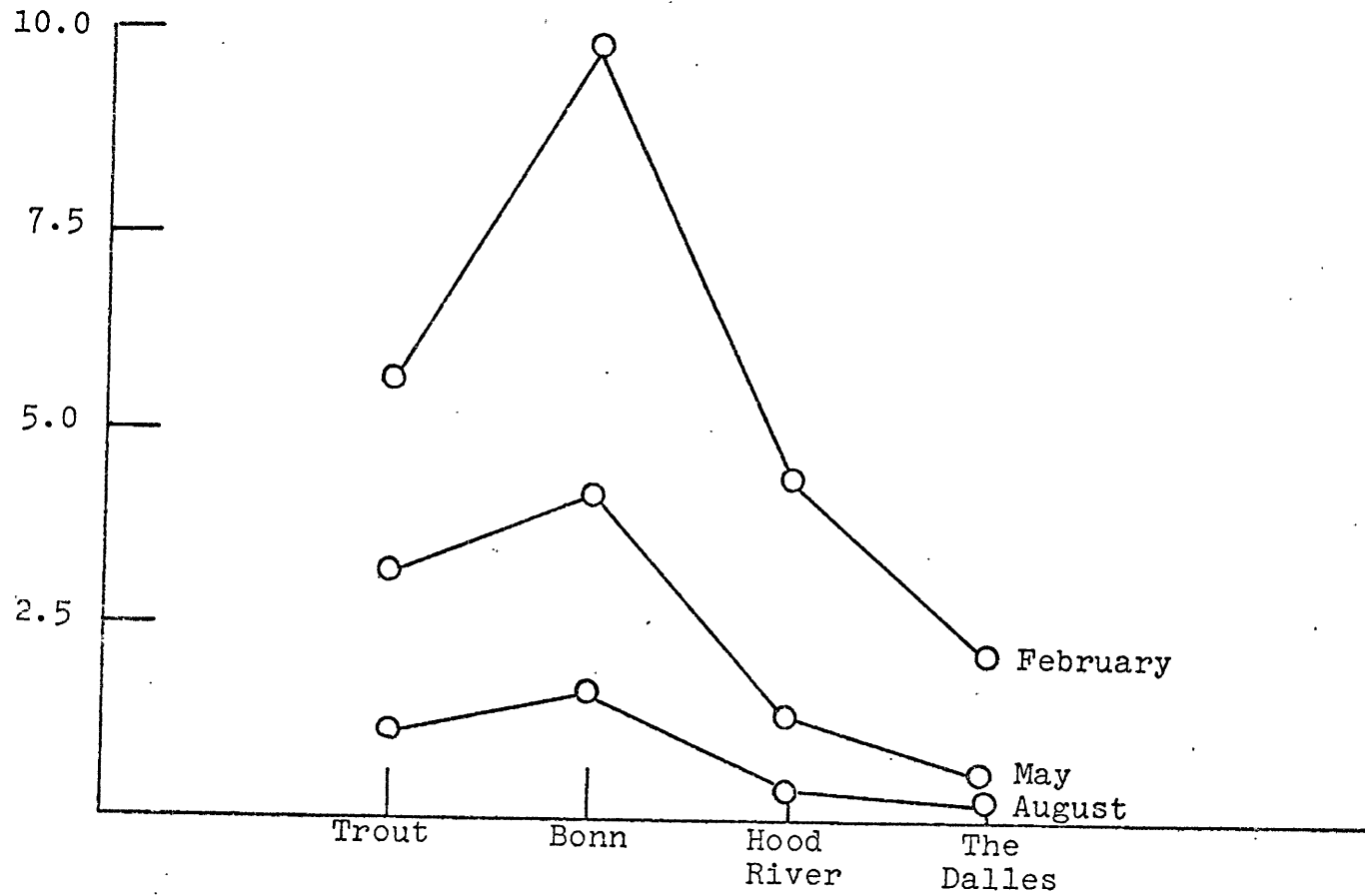


Figure 2. Mean monthly precipitation per 3 month season. The three month seasons were centered around February, May and August, 1956-1965.

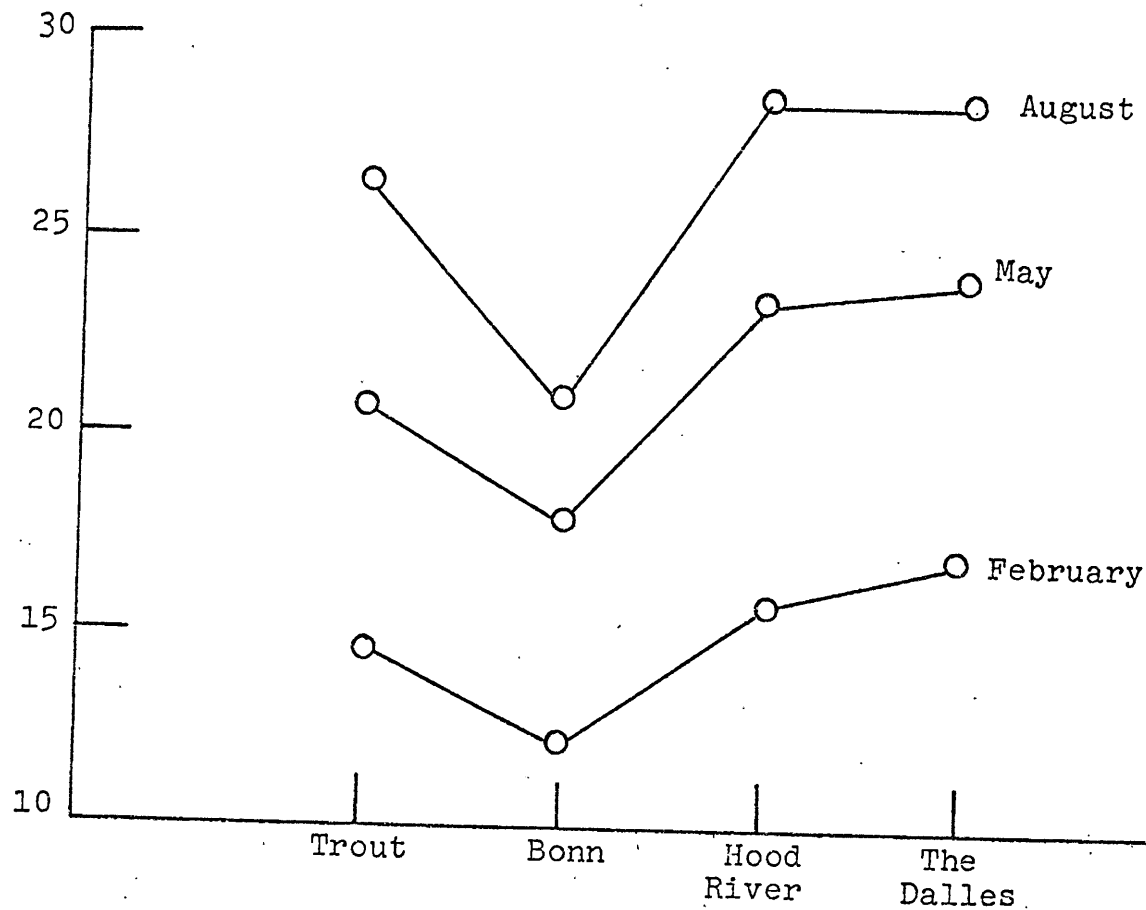


Figure 3. Mean temp. range per day per 3 month season. The three month seasons were centered around February, May and August, 1956-1965.

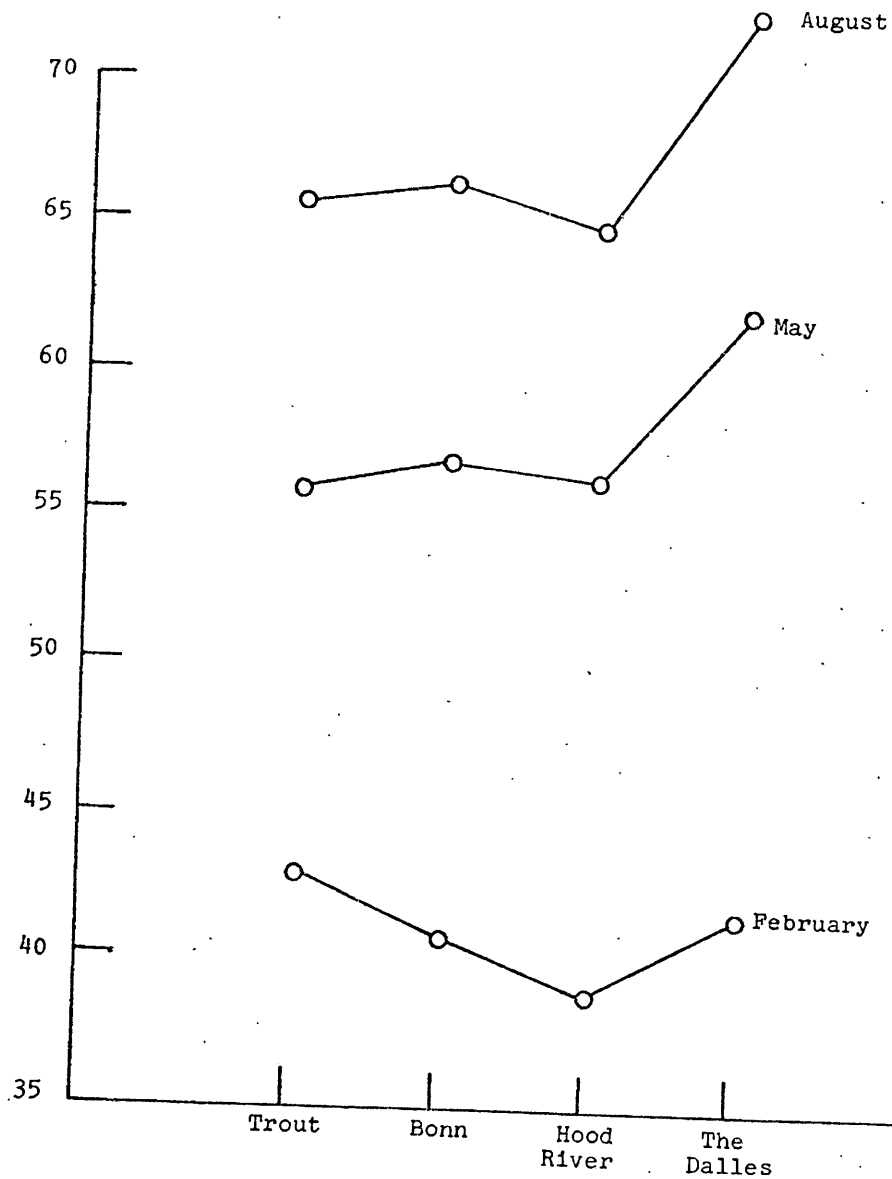


Figure 4. Mean Temp. per 3 month season.

The three month seasons were centered around February, May and August, 1956-1965.

series. The xeric sites, however, fall into the Bald soil series. These have a water supplying capacity of 12 to 15 inches and an effective rooting depth of 20 to 40 inches.

Rowena exhibits a further step in the trend from mesic to xeric sites. The previously described mesic habitats are represented by the Bald series. The xeric habitats at Rowena are characterized by the Bodell soil series. These have a water supplying capacity of 4 to 7 inches and an effective rooting depth of 12 to 20 inches.

Vegetation. Climatic conditions have played a considerable role in determining the vegetational distribution within the gorge (Detling 1958, 1966). A brief study of the flora at the four study sites presents some interesting considerations about the overall habitat at each site. The forest was arbitrarily divided into three vertical layers. From the soil up to one meter was defined as the ground layer; from 1-5 m was defined as the shrub layer; everything above 5 m was defined as the canopy.

The biotic parameters assessed consisted of the percent cover of each of the three layers in the forest and the major vegetational associations within each layer in the forest. The method utilized in this assessment was that of Braun-Blanquet as described by Mueller-Dombois and Ellenberg (1974). Percent cover for each layer was estimated on a broad scale ranging from 0 to 5. Zero corresponded to solitary individuals, one to less than 5%, two

to 5-25%, three to 26%-50%, four to 51%-75% and five to 76%-100% of total plant cover. Since the percent cover from the canopy to the ground should have an additive effect relative to the amount of light reaching the forest floor, the indices for each layer were summed for a total percent cover. This new index would then range from 0 to 15. Means and standard deviations over the twenty-four data points for each of the three layers and overall percent cover were calculated.

Abundance of a plant species was defined as the total number of data points within each site in which the plant occurred. The major plants of each area are listed in Table II in descending order of abundance. Some species were found in more than one layer.

All community designations follow the names given by Franklin and Dyrness (1973). The forest communities residing on the Wyeth soils are very similar and will be considered together. The *Pseudotsuga Acer* forests at Bridal Veil and Bonneville presumably represent seral stages in the *Tsuga heterophylla* zone. Several features indicate that Bridal Veil is in an earlier seral stage than Bonneville. The forest is much younger, as represented by overall size of the *Pseudotsuga menziesii* trees. Also, the presence of *Prunus emarginata* and the absence of *T. heterophylla* and *Gaultheria shallon* at Bridal Veil point to an earlier stage. The *Pseudotsuga Acer* forest at Mitchell

TABLE II

DOMINANT PLANT SPECIES IN DESCENDING ORDER OF ABUNDANCE
(from Hitchcock and Cronquist, 1973)

	Bridal Veil	Bonneville
Canopy	<i>Pseudotsuga menziesii</i> <i>Acer macrophyllum</i> <i>Prunus emarginata</i> <i>Cornus nuttallii</i> <i>Alnus rubra</i>	<i>Pseudotsuga menziesii</i> <i>Acer macrophyllum</i> <i>Cornus nuttallii</i> <i>Alnus rubra</i> <i>Tsuga heterophylla</i>
Shrub	<i>Acer circinatum</i> <i>Corylus cornuta</i> <i>Symphoricarpos albus</i> <i>Osmaronia cerasiformis</i> <i>Cornus nuttallii</i>	<i>Acer circinatum</i> <i>Cornus nuttallii</i> <i>Corylus cornuta</i> <i>Philadelphus lewisii</i> <i>Holodiscus discolor</i> <i>Rosa gymnocarpa</i> <i>Symphoricarpos albus</i> <i>Vaccinium parvifolium</i>
Ground	<i>Achlys triphylla</i> <i>Similacina racemosa</i> <i>Vancouveria hexandra</i> <i>Rubus parviflorus</i> <i>Actaea rubra</i>	<i>Polystichum munitum</i> <i>Berberis nervosa</i> <i>Achlys triphylla</i> <i>Vancouveria hexandra</i> <i>Dicentra formosa</i>

TABLE II (Continued)

	Bridal Veil	Bonneville.
Ground (Cont)	<i>Polystichum munitum</i> <i>Disporum smithii</i> <i>Hydrophyllum tenuipes</i>	<i>Adiantum pedatum</i> <i>Symphoricarpos albus</i> <i>Rubus parviflorus</i> <i>Gaultheria shallon</i> <i>Smilacina racemosa</i>
	Mitchell Point (mesic)	Mitchell Point (xeric)
Canopy	<i>Pseudotsuga menziesii</i> <i>Acer macrophyllum</i> <i>Quercus garryana</i>	<i>Quercus garryana</i> <i>Pseudotsuga menziesii</i>
Shrub	<i>Acer circinatum</i> <i>Corylus cornuta</i> <i>Rosa gymnocarpa</i> <i>Holodiscus discolor</i> <i>Symphoricarpos albus</i> <i>Philadelphus lewisii</i>	<i>Viburnum edule</i> <i>Holodiscus discolor</i> <i>Amelanchier alnifolia</i> <i>Quercus garryana</i>
Ground.	<i>Rhus diversiloba</i> <i>Polystichum munitum</i> <i>Berberis nervosa</i> <i>Trientalis latifolia</i> <i>Smilacina racemosa</i> <i>Symphoricarpos albus</i> <i>Rubus parviflorus</i> <i>Rubus laciniatus</i>	<i>Rhus diversiloba</i> <i>Lupin</i> <i>Balsamorhiza deltoidea</i> grasses <i>Vicia americana</i> <i>Symphoricarpos albus</i>

TABLE II (Continued)

	Rowena (mesic)	Rowena (xeric)
Canopy	<i>Quercus garryana</i> <i>Pinus ponderosa</i>	<i>Quercus garryana</i> <i>Pinus ponderosa</i>
Brush	<i>Symphoricarpos albus</i> <i>Ceanothus integerimmus</i> <i>Berberis nervosa</i> <i>Amelanchier alnifolia</i> <i>Holodiscus discolor</i>	<i>Ceanothus integerimmus</i> <i>Symphoricarpos albus</i> <i>Holodiscus discolor</i> <i>Quercus garryana</i>
Ground	<i>Rhus diversiloba</i> grasses <i>Vicia americana</i> <i>Achillea millefolium</i> <i>Galium echinospermum</i>	grasses <i>Achillea millefolium</i> <i>Rhus diversiloba</i> <i>Galium echinospermum</i> <i>Vicia americana</i> Lupin

Point is difficult to place. It has characteristics of both the *T. heterophylla* zone and the *P. menziesii* zone and probably represents a transition.

The understory species of the three *Pseudotsuga/Acer* forests are indicative of the climate through the gorge. *Polystichum munitum* is dominant in the wet sites at Bonneville and subdominant at Bridal Veil and Mitchell Point. *Cornus nuttallii* prefers moist sites and is consequently absent from Mitchell Point. *Rhus diversiloba*, however, prefers more xeric habitats and is dominant only from Mitchell Point eastward.

The three remaining habitats at Mitchell Point and Rowena represent the *Pinus ponderosa* zone. The Mitchell Point site is again complicated and probably represents the very narrow band of *Quercus* residing between the *Pseudotsuga* and *Pinus* zones of eastern Oregon and Washington. The forests at Rowena are more characteristic of the *Pinus/Symphoricarpos* association. The major difference, aside from topography and soils, between the two habitats at Rowena is one of vegetation density, with the mesic habitat being more dense than the xeric habitat.

Climatic differences between these latter three forest communities are again implicit in their plant compositions. *Amelanchier alnifolia* occurs in the higher rainfall area of Mitchell Point and in the mesic habitat of Rowena. *Viburnum edule* is present at Mitchell Point and absent from Rowena.

Differences are also apparent between the habitats represented in the subsites at Rowena. *Berberis nervosa* is present in the mesic habitat and not the xeric habitat. *Ceanothus integerimmus* is dominant in the xeric habitat and subdominant in the mesic habitat. The vegetation in the gorge reflects the previously described climatic scale from maritime to continental.

Trapping Methods

Three Museum Special Rodent Traps were set within a radius of one meter at each of the 96 trapping stations per site, for a total of 288 traps at each site. Trapping was done during the months of February, May and August 1974, so as to sample during three seasons. Each week a different site was trapped, thereby requiring four weeks to trap all four study sites. The traps were run for three nights during each census, giving a total of 864 trap nights per census. The trapping data were grouped around every fourth trapping station, shrinking the 96 trapping stations at each site to 24 data points per site.

Two subspecies of *Peromyscus maniculatus* are known to occur within the range of the present study (Fox 1948, Dice 1949). *P.m. rubidus* occurs on the west side of the Cascades and *P.m. gambelii* occurs on the east side. Dice (1949) found that the Hood River and The Dalles mice differed strikingly from each other in body dimensions and in

pelage color. The Hood River subspecies was assigned to *rubidus*, and The Dalles subspecies to *gambelii*. Dice concluded that the only important evidence of intergradation toward *gambelii* by Hood River mice was their somewhat shorter tail as compared to most of the Oregon *rubidus*. In order to gain a clearer understanding of the intergradation and habitat preference of these two subspecies, tail lengths were measured from mice from each of the four sites. The range, mean and standard deviation were calculated for each group.

Statistical Techniques

The physical and biotic parameters were grouped around the twenty-four data points and entered into two statistical programs on the Honeywell 6040. The plant species were grouped into the arbitrary classification of canopy, shrub and ground layers for computer analysis in order to investigate the possible importance of one layer over another in determining the *P. maniculatus* and *S. trowbridgii* distributions. As the plant composition of the canopy was virtually uniform over the study area, this layer was not considered in the analysis. The shrub and ground layers should be indicators of the microhabitats within the *Pseudotsuga/Acer* forest. Each plant within these layers was treated as a separate variable and the entire group of variables was regressed separately to the

P. maniculatus and *S. trowbridgii* data using the UCLA Multiple Regression package BMD03R (Dixon 1970). The analysis was performed only at the Bridal Veil site for the summer data in order to gain some idea as to the effectiveness of the method.

The Factor Analysis package BMD08M (Dixon 1970) was utilized to obtain the correlation matrix for all the possible pairs of variables at each of the four study sites. This was done in order to obtain possible correlations between the trapping data and any of the assessed physical or biotic parameters.

RESULTS AND DISCUSSION

The mammal capture data are summarized in Table III. The only two species trapped in abundance were *Peromyscus maniculatus* and *Sorex trowbridgii*. The capture data for these two species are presented in Table IV. The February sample of *P. maniculatus* is correlated positively with the rainfall data shown in Figure 2. If, in fact, the mouse populations are responding solely to variations in rainfall, one might expect a large drop in the mouse population at Mitchell Point relative to that at Bonneville. Yet, in February there was 65% less rainfall at Mitchell Point than at Bonneville, while the mouse population at Mitchell Point was only 16% less than at Bonneville. However, edaphic factors can serve to modify a given environmental system as compared with what might otherwise be expected under given macroclimatic conditions. Mitchell Point is a complex site composed of two very different habitats, both of which are subject to the same rainfall conditions. The overriding feature in this case seems to be the presence of the *Pseudotsuga/Acer* forest. A closer examination of data from the twenty-four sample points at Mitchell Point indicates that in February 2.53 mice were caught per sample point in the *Pseudotsuga/Acer* habitat, whereas only 0.5 mice were caught per sample point in the *Quercus* habitat. The high number of *P. maniculatus* at this site seems to indicate a wide range of tolerance of this species to climatic factors such as rainfall. A similar conclusion was obtained by Johnson

TABLE III

SPECIES CAPTURED IN THE COLUMBIA GORGE DURING
THREE SEASONS IN 1974

	Bridal Veil			Bonneville			Mitchell Pt			Rowena		
	Feb	May	Aug	Feb	May	Aug	Feb	May	Aug	Feb	May	Aug
<i>Sorex trowbridgii</i>		1	4		10	50			3		1	
<i>Sorex vagrans</i>						4						
<i>Neurotrichus gibbsii</i>					1	1						
<i>Eutamias townsendii</i>		2	1									
<i>Peromyscus maniculatus</i>	18	63	35	61	36	21	51	52	55	4	1	6
<i>Neotoma cinerea</i>			1						1			
<i>Mus musculus</i>											1	
<i>Zapus trinotatus</i>			1									

TABLE IV

TRAP DATA FOR THE FOUR STUDY SITES

	Bridal Veil		Bonneville		Mitchell Pt		Rowena	
	P.m.*	S.t.**	P.m.*	S.t.**	P.m.*	S.t.**	P.m.*	S.t.**
February	18	0	61	0	51	0	4	0
May	63	1	36	10	52	0	3	0
August	35	4	21	50	55	3	6	0

* *Peromyscus maniculatus*

** *Sorex trowbridgii*

(1926), who found that *P. maniculatus* correlates to major climatic changes which define biotic communities.

At Bridal Veil there was a winter low in the population of *P. maniculatus*, a spring high and a summer decline. This seems to be the normal pattern for western Oregon (Gashwiler 1959, Sheppe 1963). *S. trowbridgii*, however, was first captured in the spring; captures increased into the summer. *S. trowbridgii* breeds in the spring and summer, which accounts for the buildup at that time (Ingles 1965). Bonneville, however, showed a constant decrease in *P. maniculatus* density from a winter high. *S. trowbridgii* showed the opposite trend, a rise from winter to summer. At Mitchell Point the *P. maniculatus* population was virtually constant through the seasons, while only a few *S. trowbridgii* appeared in the summer. Rowena, too, remained constant with respect to *P. maniculatus*. Only one *S. trowbridgii* was captured.

The populations of *S. trowbridgii* from west to east exhibit a very close positive correlation with precipitation (Figure 1). This is not unexpected, as shrews seem to prefer moist habitats (Williams 1955). However, other factors could also contribute to this distribution. Jameson (1955) found that the habitat of *S. trowbridgii* does not seem to vary much through the range of that species. It generally prefers mature coniferous forests with abundant ground litter for foraging. The forest at Bonneville is a

more mature forest than that at Bridal Veil and although the litter was not quantitatively assessed, it appeared to be most abundant at Bonneville. Increased litter would also be expected at Bonneville, as higher precipitation should produce greater plant growth. These data suggest that *S. trowbridgii* is less tolerant with respect to its habitat preference than is *P. maniculatus*. It was in the preferred habitat at Bonneville that the population of *S. trowbridgii* increased dramatically and that of *P. maniculatus* decreased.

In the light of these considerations, I present the hypothesis that *P. maniculatus* and *S. trowbridgii* are competing with respect to habitat preference in the Columbia Gorge. *S. trowbridgii*, being more specialized with respect to habitat requirements, is able to dominate the habitat at Bonneville. *P. maniculatus*, being more generalized with respect to habitat preference, has a wider range of distribution.

It is possible that the trapping data taken from the gorge are merely artifacts of the sampling procedure. For example, the trapping in one season could affect the populations in the next. However, Stickel (1946) presents evidence which seems to refute this possibility. There is apparently extensive rehabilitation of an area by immigration after trapping. Another possibility is that the mouse population at one end of the gorge is fluctuating in a

manner which is out of phase with the mouse population at the other end of the gorge. However, populations of *P. maniculatus* are generally fairly stable, showing the lowest fluctuations when compared with other small mammals. Populations outbreaks are rare (Terman 1966). It is possible, however, that the mouse population at Rowena, which is in a different habitat, could be somewhat out of phase with those populations in the *Pseudotsuga/Acer* habitat. Trapping over a period of years would be necessary in order to elucidate further the relationships between these two major habitats.

The data for tail length are presented in Table V along with Dice's (1949) data from Hood River and The Dalles. The mice measured in the present study were taken in the summer and represent mice of all ages. The ranges of tail length, therefore, are complicated by the presence of juveniles. The Rowena mice, although few in numbers, belong to the *gambelii* subspecies (Dice 1949). The Bridal Veil and Bonneville mice are of the *rubidus* subspecies, although the mean tail lengths are somewhat less than those given by Dice. If one examines only the data from the present study, the mice at Mitchell Point are clearly intermediate between *rubidus* and *gambelii* with respect to tail length. Again, Mitchell Point stands out as a transition zone.

Pelage coloration was not quantitatively assessed;

TABLE V

Peromyscus maniculatus TAIL LENGTHS IN MM.
(Partially adapted from Dice 1949)

	Mean Tail Length	Range	Standard Deviation	Sample Size	Subspecies
Bridal Veil	80.6	69 - 90	4.637	25	<i>rubidus</i>
Bonneville	82.6	74 - 90	4.857	13	<i>rubidus</i>
Mitchell Pt.	76.3	69 - 84	3.805	25	<i>rubidus</i>
Rowena	69.7	69 - 71		3	<i>gambelii</i>
Hood River Field Mice	87.00	73 - 103	7.49	17	<i>rubidus</i>
Hood River 1 yr. mice	87.68	77 - 98	4.35	84	<i>rubidus</i>
The Dalles 1 yr. mice	75.95	65 - 81	3.81	99	<i>gambelii</i>
The Dalles 2 yr. mice	75.68	68 - 85	4.73	32	<i>gambelii</i>

however, the Rowena mice were distinctly more brown than the Bridal Veil or Bonneville mice, which were clearly black. Mitchell Point revealed mice of both colors as well as intermediate colorations. Thirteen of the 25 mice sampled were clearly black. Eleven of these 13 possessed tails which were longer than the mean tail length of the sample. Four of the mice were brown; three of the four possessed tails shorter than the mean tail length of the sample. The remaining eight mice were intermediate in coloration and tail length. Four possessed tails longer than the mean tail length and four possessed tails shorter than the mean tail length. These data suggest an intergradation of *rubidus* and *gambelii* at Mitchell Point.

There is, nevertheless, a remarkable difference in tail length between Dice's Hood River mice and the Mitchell Point mice. Mitchell Point mice should have tail lengths at least as great as those at Hood River, four miles to the east. There are several possible explanations for this result. The mice were measured by two different investigators, possibly using slightly different techniques. This, however, is likely of low importance as the two means are so divergent, 10.7 mm. A high percentage of juveniles in the present study could have shifted the range in tail length. Data from Table V support this possibility. Another explanation would be a shift in the intergradation zone during the period from 1949 to 1974. It seems likely that such a

zone would not remain absolutely stationary.

The mean tail length at Mitchell Point is very close to that found by Dice at The Dalles, which would place the mice in the subspecies *gambelii*. Yet, the data from this study and the physical location of the mice at Mitchell Point suggest that the mice belong to the subspecies *rubidus*. Fox (1948) found a mean tail length for *gambelii* of 73 mm and for *rubidus* of 95 mm. Fox's data are much closer to those of Dice than to the data from the present study. If there has not been a shift in the intergradation zone, then perhaps there has been an evolutionary change in the tail lengths of *P. maniculatus* during the course of 25 years. It is, however, apparent that Mitchell Point represents a transition zone for many physical and biotic factors, all of which are ultimately a function of significant climatic changes caused by the presence of the Cascade Mountains.

In order to understand more clearly the relationships between the animals under consideration and the environment, a closer examination of each habitat is necessary. The main approach to this problem is assessment of the importance of the physical and biological parameters measured. The first step in this approach is to construct a simple correlation matrix which plots the correlation coefficients between all possible pairs of variables. In this case the occurrence of each plant in each of the

three layers on the forest is considered as a separate variable. Thus, one is able to look for correlations between the capture data and any of the physical or biological parameters which were assessed.

The correlation coefficients between *P. maniculatus* and slope are presented in Table VI. The data for Rowena are not included since there were not enough animals captured for satisfactory statistical analysis. Aside from the winter correlation coefficient at Bridal Veil, there seems to be a decreasing dependence of *P. maniculatus* on slope from winter to summer. Since the correlations are negative, the data indicate that the mice preferred the flatter regions during the winter and tended to spread out over the entire slope as the year progressed. The possible reasons for this distribution pattern are so numerous that speculation on them in light of the present data would not be edifying at this time.

The seemingly anomalous coefficient at Bridal Veil in the winter could reflect several factors. The coefficient is based on data from only 18 mice and the mean slope is more gentle than on the other two sites considered. The former of the two factors is probably the most important, since the low number of mice is approaching the lower limit for satisfactory analysis.

The data are too few to show any correlation between *S. trowbridgii* and slope. The correlation coefficients

TABLE VI

CORRELATION COEFFICIENTS BETWEEN *P. maniculatus* AND SLOPE

	Bridal Veil	Bonneville	Mitchell Point
February	0.19916	-0.41437	-0.46055
May	-0.45105	-0.19694	-0.22638
August	-0.06416	-0.16736	-0.05053

range from -0.30186 to 0.17413 with no discernible pattern. The shrews were caught over most of the slope in both the spring and summer.

Percent cover is here considered as a physical parameter. Although cover is a function of the presence of vegetation, it is presumably an indirect indicator of the amount of light that penetrates the forest. Percent cover can also be an indirect indicator of other physical parameters such as nutrient availability, temperature, soil depth and soil porosity. The correlation coefficients within each site do not indicate any significant correlation between percent cover and either *P. maniculatus* or *S. trowbridgii* densities. These data are in agreement with Verts (1957) who found no correlations between the distribution of *P. maniculatus* and percent bare ground, annuals, grasses, woody vegetation, perennials, biennials and stems per square meter.

The correlation coefficients between the capture data and the occurrence of individual plants revealed no statistical correlation. This finding, again, is in agreement with Verts (1957). The correlation coefficients between the plants were also very low. These results are consistent with those of del Moral (1974) in lending support to Whittaker's (1965) hypothesis

...that distributional patterns in plants result from evolutionary processes that produce habitat differentiation such that the mode of each distribution with respect to particular environmental

gradients is displaced with respect to potential competitors.

The structure of plant communities is filled with such complexity that one would, in fact, not expect much correlation between animal populations and the distribution of any one plant.

The *S. trowbridgii* data were too few to permit satisfactory statistical analysis with multiple regression. The multiple correlation coefficient for the shrub and ground layers combined, when regressed to the *P. maniculatus* data was 0.9102. However, this represents a considerable number of variables. When considered separately, the shrub layer revealed a multiple correlation coefficient of 0.7668 and the ground layer 0.4363. These coefficients taken together indicate the relative importance of each layer in determining the distribution of *P. maniculatus*. It is not surprising that the shrub layer is more important than the ground layer. The habitats within the forest are determined by the composition of the canopy which is a function of climatic and edaphic factors. The complement of shrubs will be determined by the canopy and climate; the distributions of the shrubs will be determined by microhabitats. The distributions of the ground species will be determined to a large extent by the shrubs, insofar as the shrubs modify and create microhabitats which are suitable or unsuitable for the ground species. *P. maniculatus* is a generalist with respect to habitat selection. It is, therefore, not

surprising to find that *P. maniculatus* can live in a wide range of microhabitats defined by the ground layer, as indicated by the low correlation coefficient for this layer. Yet, *P. maniculatus* is more restricted to the more general microhabitats defined by the shrub layer, as indicated by the higher correlation coefficient for this layer. What, then, is the nature of the microhabitats in which the mice reside?

Johnson (1926) found no correlation between the distribution of wild mice and such microclimatic features as temperature, humidity and air movement. He did find that mouse populations were correlated with the major climatic changes which define different biotic communities. Johnson's conclusions are in agreement with my finding that *P. maniculatus* prefers a *Pseudotsuga/Acer* forest to a *Quercus/Pinus* forest. Johnson thought that the mouse populations were correlated with very complex biotic communities. The results from the simple correlation analysis and the multiple regression analysis also point toward this conclusion. The nature of these communities, however, is not easy to elucidate.

Most approaches to the community problem aim at clustering the vegetational units into communities thought to be biologically meaningful. The actual success of many of these approaches is questionable. One method, however, which might come closer to the desired result than most is

that of del Moral (1975). He describes a nonhierarchical, divisive, iterative and polythetic method based on Euclidean distance which would produce communities that are at least moderately interpretable biologically. Like most other methods, this one allows the investigator to produce communities at many levels. That is, one may define communities based solely upon canopy species, as is often done (Franklin and Dyrness 1973). Likewise, one may define communities at lower levels including both shrub and canopy species. As the distributions of mice in this study appear to be most affected by the composition of species in the shrub layer, this should be the level first investigated for the presence of communities with which mouse populations might be correlated. Unfortunately, I have not been able to undertake such investigations.

CONCLUSIONS

Peromyscus maniculatus is only loosely associated with rainfall patterns. In the absence of *Sorex trowbridgii*, *P. maniculatus* prefers the higher rainfall area near Bonneville Dam. In the presence of *S. trowbridgii*, *P. maniculatus* is more restricted to the drier sites at Bridal Veil and Mitchell Point. The area near Bonneville Dam appears to be the primary habitat for both species. Since *S. trowbridgii* is more specialized with respect to habitat, it dominates the Bonneville site. Since *P. maniculatus* is more generalized with respect to habitat it is more capable of tolerating the peripheral sites at Bridal Veil and Mitchell Point.

The subspecies *rubidus* and *gambelii* of *P. maniculatus* are distributed with respect to gross climatic changes. The climates on the east and west sides of the Cascades are different enough for both subspecies to exist, *rubidus* on the west and *gambelii* on the east. The zone of intergradation of the two subspecies occurs near Mitchell Point. I speculate that this zone has either shifted over time or an evolutionary change has taken place with respect to tail lengths over time.

The distribution of mice within one subspecies is more subtle than the distribution of mice between subspecies. In general, *rubidus* prefers the more moist habitats. However, upon searching for correlations between these mice and physical and biotic parameters, I conclude

that *rubidus* is distributed relative to complex biological communities which reflect the physical and biological attributes of the microhabitats. The shrub species are probably the most important in defining these communities. However, in the winter slope angle is also an important indicator of preferred microhabitats, decreasing in importance into the summer. A method is suggested for the further elucidation of the nature of these communities.

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