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The Distribution of Three Taxa of Peromyscus in Central Washington

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THE DISTRIBUTION OF THREE TAXA OF *Peromyscus* IN CENTRAL WASHINGTON

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THE DISTRIBUTION OF THREE TAXA OF *Peromyscus* IN CENTRAL WASHINGTON

By G. H. Engelsen

INTRODUCTION

Washington is especially rich in habitat types and biotic diversity. Of the seven Merriam's Life Zones, only the Lower Sonoran zone is absent. According to Dalquest (1948) five taxa of *Peromyscus* are variously represented in the habitats of Washington including the crater of Mount Rainier (Finley, 1933), elevation 14,107 feet, Figure 1.

Two species of *Peromyscus* are represented in the state of Washington. The most widely distributed is *P. maniculatus* of which four recognized subspecies are found in the state. The other species, *P. oreas*, is found in the coastal lowlands, the Olympic Mountains and throughout the Cascade Mountains of Washington north to Rivers Inlet, British Columbia (Hall and Kelson, 1959).

Three taxa of *Peromyscus* are present in central Washington. Except for *P. m. hollisteri* of the San Juan archipelago, *P. m. austerus* Baird (1855) is the sole representative of the genus in the Puget Basin from the Columbia

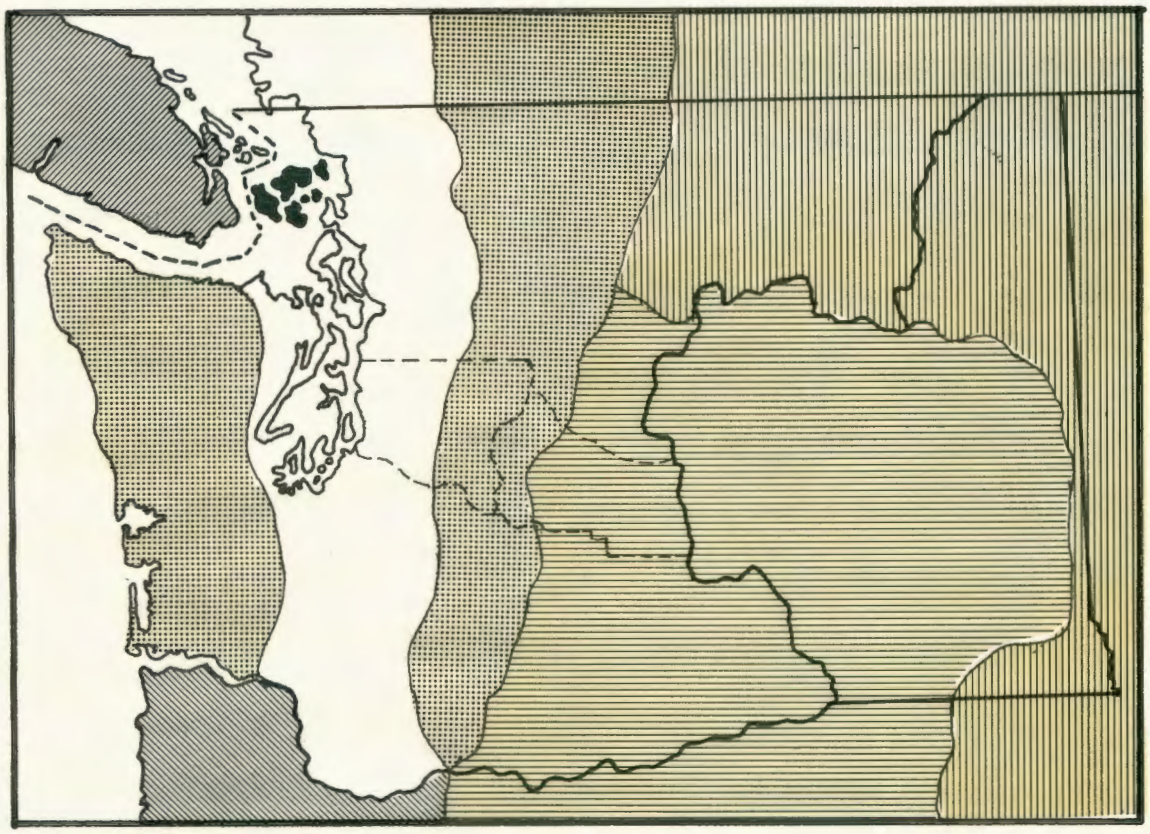

FIGURE 1

DISTRIBUTION OF Peromyscus IN THE PACIFIC NORTHWEST
(Hall and Kelson, 1959)

- P. m. hollisteri
- P. m. angustus
- P. m. austerus
- P. m. rubidus
- P. m. artemisiae
- P. m. gambeli
- P. oreas

River in the south, northward to Kingcome Inlet, British Columbia (Cowan, 1956). This mouse is intermediate in size between P. m. gambeli and P. oreas. The means of 62 adult animals taken in the study areas are: total length 177 mm.; tail length 90 mm.; hind foot length 21.3 mm. and ear length 18.5 mm.

The smallest mouse, P. m. gambeli Baird (1858) is found east of the Cascade Mountains nearly to the Idaho border, north to Lake Chelan, and south into California. The mean measurements of 93 adult specimens taken in the study area are: 157 mm., 69 mm., 19.9 mm., 17.0 mm.

When first described by Bangs in 1898, P. oreas was considered a subspecies of P. maniculatus. Peromyscus oreas is the largest representative of the genus native to Washington. The mean measurements of 102 adult mice from the study area are: 197 mm., 106 mm., 22.8 mm., 19.2 mm.

Results of studies by Liu (1954), experimentally cross breeding P. oreas with P. maniculatus, suggest that P. oreas is genetically isolated from P. maniculatus. An extensive study by Sheppe (1961) based on traditional measurements, ecology and breeding experiments provided conclusive evidence that P. oreas is, indeed, a distinct species. In spite of this, Murray L. Johnson (personal communication, 1963) was

unable to separate the two species on the basis of plasma proteins using paper electrophoresis.

While collecting P. oreas, an animal of intermediate characteristics between P. oreas and P. m. gambeli was consistently encountered on the eastern slopes of the Cascade Mountains in Central Washington. Existing range maps indicated that the ranges of P. oreas and P. m. gambeli do come into contact, but no hybrid zone was described. The problem then became to determine whether or not P. oreas and P. m. gambeli were cross breeding and had established a hybrid zone between the two populations, or whether an undescribed taxon of Peromyscus occupies this habitat in sympatry with P. oreas and P. m. gambeli. To explain this phenomenon a two part study was begun. One aspect of the study was to define the present ranges of all types of Peromyscus in the study area; the other to determine the extent of interfertility of the groups.

THE STUDY AREA

The study area is approximately 120 miles long. It extends from Puget Sound, King County, eastward through Kittitas County to the Columbia River. The crest of the Cascade Mountains marks the boundary between King and Kittitas Counties.

The most striking feature of the study area is the remarkable progression of habitat types in such a limited geographic area. Typical of the Puget Sound region is a dense forest of Western Red Cedar (Thuja plicata), Douglas Fir (Pseudotsuga taxifolia), and Western Hemlock (Tsuga heterophylla). The lowland forests merge with those of the mountains where White Pine (Pinus monticola), Western Hemlock, Mountain Hemlock (Tsuga mertensiana), Douglas Fir and Noble Fir (Abies procera) predominate.

The western and eastern segments of the study area are connected at Snoqualmie Pass, elevation 3,010 feet. Twenty miles east of the pass the humid forest merges with a drier Yellow Pine (Pinus ponderosa) forest that yields to the bunchgrass zone of Rabbitbush (Chrysothamnus nauseosus), Sagebrush (Artemisia tridentata) and Greasewood (Sarcobatus vermiculatus) of the semi-arid Kittitas Valley. From Ellensburg, elevation 1,500 feet, to the Columbia River, elevation 500 feet, floral composition is relatively stable even though Saddle Mountain, elevation 2,800 feet, is crossed.

Most of the precipitation in the study area falls west of the Cascade crest. Rainfall in the Puget Sound region averages about 50 inches annually. Moving eastward up the Cascade slopes the precipitation gradually increases

to more than 100 inches at the crest, much of which is snow. On the leeward slopes precipitation decreases rapidly to less than 20 inches in the Yellow Pine forest and to less than 15 inches annually from Ellensburg to the Columbia River. Figure 2 shows the general physiography and associated floral distribution. A detailed description of Washington's physiography and flora are found in Dalquest (1948) and Lyons (1960).

MATERIALS AND METHODS

Field work was begun with the spring thaw in March, 1966, at the Columbia River. Museum Special snap traps and Havahart live traps were used. Instead of the usual line or grid patterns of setting traps, sets were made in areas of high trapping success potential, such as holes, along or under logs and stumps, brush piles and thickets and field edges. This procedure is more time consuming than straight line setting, but results in higher trapping success. Greater success may result in part from the fact that this technique covers a larger area per number of traps, thereby increasing the probability of crossing the home ranges of more individuals.

From the Columbia River the field work followed the snow melt westward. By May 26, when trapping was suspended

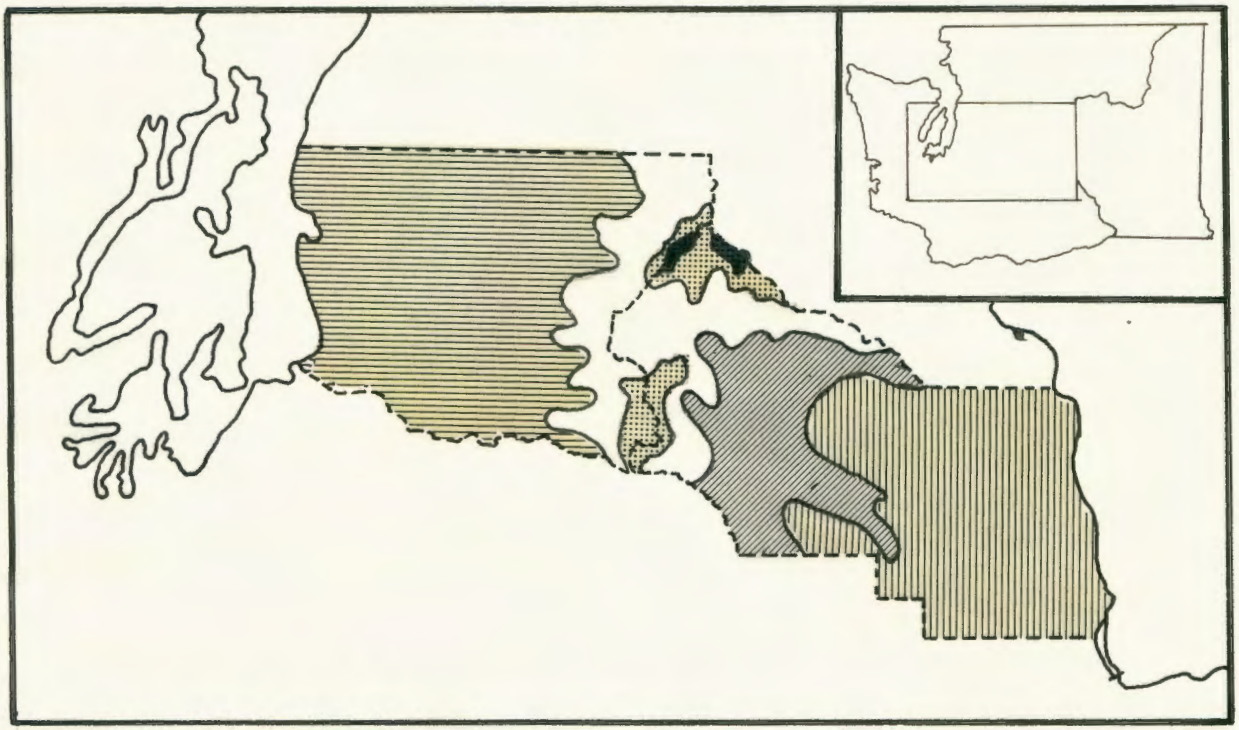

FIGURE 2

FLORAL DIVERSIFICATION IN THE STUDY AREA

Coast Forest

Mountain Forest

Sub-Alpine Forest

Alpine

Yellow Pine Forest

Bunch Grass and Sagebrush

for the summer, the snow had cleared to an elevation of 3,000 feet in some places. Field operations were resumed in October and continued until December, when weather conditions caused suspension of trapping. During the autumn, Snoqualmie Pass and eastern King County were heavily trapped.

Snap-trapped animals were measured on the day of capture to avoid errors resulting from dehydration during storage. Only measurements from animals in adult pelage were recorded for statistical purposes. From these mice a large number of skins flattened on 5" by 8" cards was preserved. A representative collection of study skins, skulls and bacula were also prepared.

Breeding cages of wood and hardware cloth measuring 8 x 10 x 18 inches were provided with nesting cotton and kept outdoors. Two animals, a male and female, shared each unit. A diet of chicken scratch, dog food, fruit and water was liberally supplied. In addition, nuts, table scraps, cooked and raw meats, poultry, fish and insects often supplemented the standard diet. No food item was rejected by the mice and loss of individuals was negligible.

Field data were processed in an International Business Machines 1620 computer.

RESULTS

A total of 246 Peromyscus was trapped during the study period. From Puget Sound to the base of the Cascade Mountains, elevation 500 feet, only P. m. austerus was captured. From the base of the mountains to Snoqualmie Pass 21 P. m. austerus and 33 P. oreas were collected. East of the Pass to the Yellow Pine forest 35 P. m. austerus, 47 P. oreas and 18 P. m. gambeli were captured. At Salmon la Sac all three taxa were taken in one trap line. From the Yellow Pine forest to the Columbia River P. m. gambeli is the sole representative of the genus, Figure 3. Peromyscus population structure, by per cent in areas of sympatry, is shown in Table 1.

Trapping in the mountains consistently yields P. m. austerus and P. oreas at each trapping station, indicating that the eastern and western populations of P. m. austerus are joined at least through Snoqualmie Pass. Even the highest trapping station, Quartz Mountain at an elevation of 6,200 feet, produced both taxa.

Using tooth wear as the criterion of age (Dunmire, 1960), representatives of all three taxa were examined. All eight animals of intermediate size between P. m. austerus and P. oreas were less than 38 days old and therefore proved

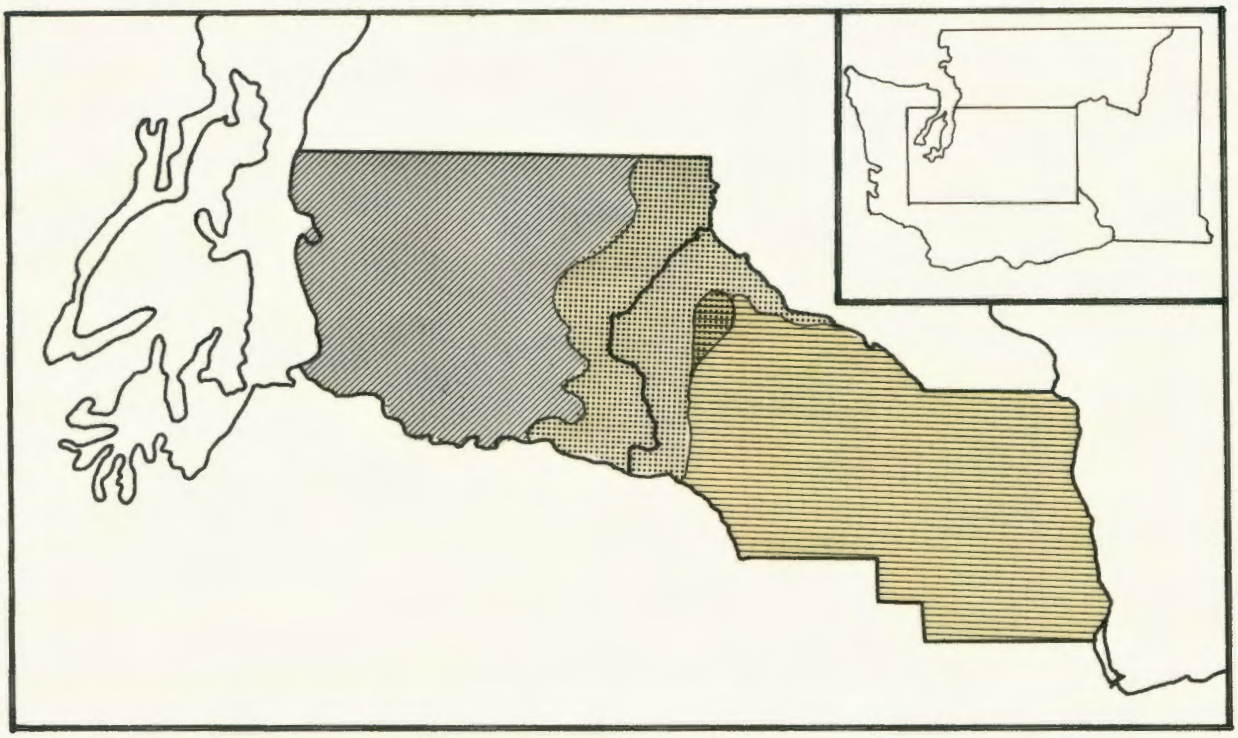

FIGURE 3

DISTRIBUTION OF *Peromyscus* IN THE STUDY AREA

P. m. austerus

P. m. austerus and *P. oreas*

P. m. austerus, *P. m. gambeli* and *P. oreas*

P. m. gambeli

TABLE 1

POPULATION STRUCTURE OF *Peromyscus* IN SYMPATRIC AREAS OF THE CENTRAL CASCADE MOUNTAINS IN WASHINGTON

WESTERN CASCADE MOUNTAINS	
Peromyscus maniculatus austerus	38.8%
Peromyscus oreas	61.2%
EASTERN CASCADE MOUNTAINS	
Peromyscus maniculatus austerus	35%
Peromyscus maniculatus gambeli	18%
Peromyscus oreas	47%

to be subadult P. oreas. Svihla (1936) has shown that P. oreas does not reach maximum proportions in less than three months. The three taxa showed a similar population structure by age.

The comparative morphology of animals taken in the study area are presented in Tables 2, 3 and 4. A graphic representation of some of these data is presented in Figures 4, 5, 6 and 7. In these graphs the vertical line represents the mean, the blackened rectangles two standard errors of the mean on either side of the mean, the hollow rectangles one standard deviation on either side of the mean and the horizontal line represents the range of variation of the sample.

Cross breeding experiments during this study have shown P. m. austerus and P. m. gambeli to be interfertile. Peromyscus m. austerus from both sides of the Cascades bred with P. m. gambeli from the Kittitas Valley producing viable hybrids. Peromyscus oreas failed to breed in captivity. Results of these test crosses are shown in Table 5.

Since tail length is a diagnostic character of the taxa of Peromyscus in Washington, it is of interest to note its modification as expressed by hybrids. Eight intermediates from the laboratory stock had tails of the following types:

TABLE 2

MEAN MEASUREMENTS OF THREE TAXA OF *Peromyscus* IN MM.

AUTHOR	SAMPLE SIZE	TAXONOMIC GROUP	TOTAL LENGTH	TAIL LENGTH	HIND FOOT LENGTH
DALQUEST	40	*P. m. gambeli*	160	71	19.8
	50	*P. m. austerus*	180.5	89	21.0
	40	*P. oreas*	202	110	22.6
COWAN	20	*P. m. austerus*	176	89	21.0
	18	*P. oreas*	202	109	23.0
ENGELSEN	93	*P. m. gambeli*	157	69	19.9
	62	*P. m. austerus*	177	90.5	21.3
	102	*P. oreas*	197	106	22.8

TABLE 3

NUMERICAL VALUES OF SEVEN VARIABLES FROM MEASUREMENTS OF *Peromyscus* IN CENTRAL WASHINGTON

I. *Peromyscus maniculatus gambeli*
(Sample size 93)

VARIABLE	MEAN IN MM.	STANDARD DEVIATION	STANDARD ERROR
Total length	156.944	8.315	.86
Tail length	68.978	5.126	.53
Body length	87.801	5.530	.57
Hind foot length	19.908	.935	.09
Ear length	17.026	1.091	.11
Tail/Body	.788	.069	.00
Tail/Foot	3.469	.267	.02

II. *Peromyscus maniculatus austerus*
(Sample size 62)

VARIABLE	MEAN IN MM.	STANDARD DEVIATION	STANDARD ERROR
Total length	177.241	10.666	.97
Tail length	90.506	6.867	.62
Body length	86.716	6.943	.63
Hind foot length	21.312	1.461	.13
Ear length	18.500	1.406	.12
Tail/Body	1.049	.106	.00
Tail/Foot	4.256	.332	.03

III. *Peromyscus oreas*
(Sample size 102)

VARIABLE	MEAN IN MM.	STANDARD DEVIATION	STANDARD ERROR
Total length	196.828	8.663	.84
Tail length	106.000	4.882	.47
Body length	90.904	6.376	.62
Hind foot length	22.852	.756	.07
Ear length	19.252	1.306	.12
Tail/Body	1.171	.099	.00
Tail/Foot	4.644	.283	.02

TABLE 4

LENGTH OF BACULA

TAXON	MEAN IN MM.	STANDARD DEVIATION	SAMPLE RANGE	SAMPLE SIZE
P. m. gambeli	7.93	.0795	6.8-9.0	41
P. m. austerus	7.38	.42	6.1-9.0	18
P. oreas	8.49	.353	6.9-9.7	22

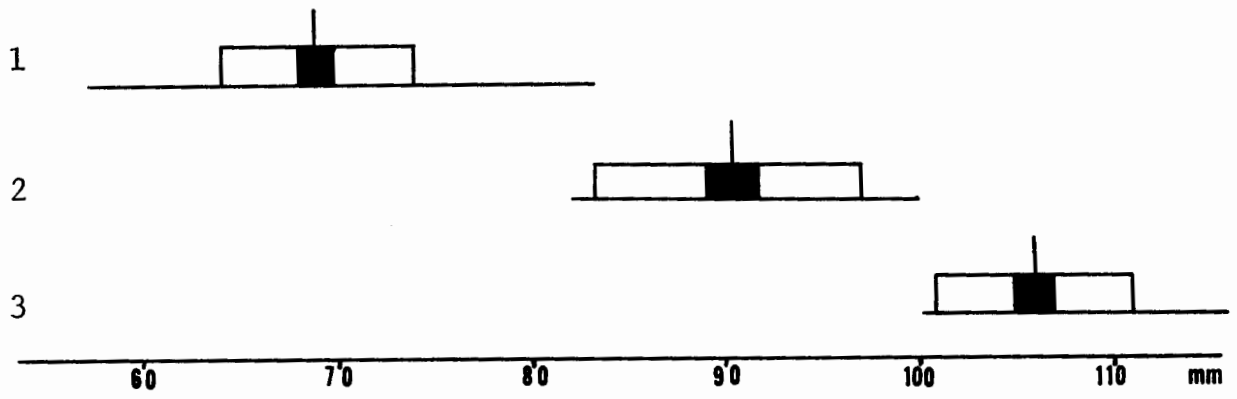

FIGURE 4

TAIL LENGTH

1. P. m. gambeli
2. P. m. austerus
3. P. oreas

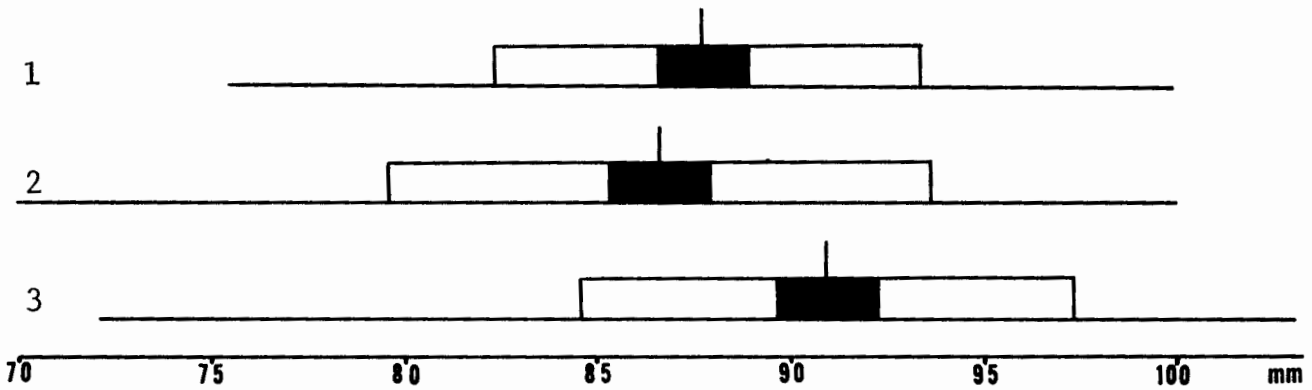

FIGURE 5

BODY LENGTH

1. P. m. gambeli
2. P. m. austerus
3. P. oreas

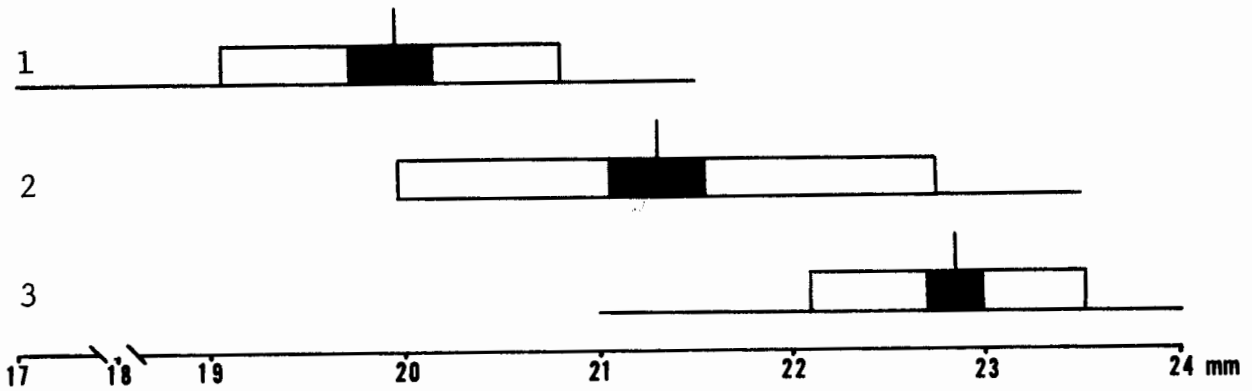

FIGURE 6

HIND FOOT LENGTH

1. P. m. gambeli
2. P. m. austerus
3. P. oreas

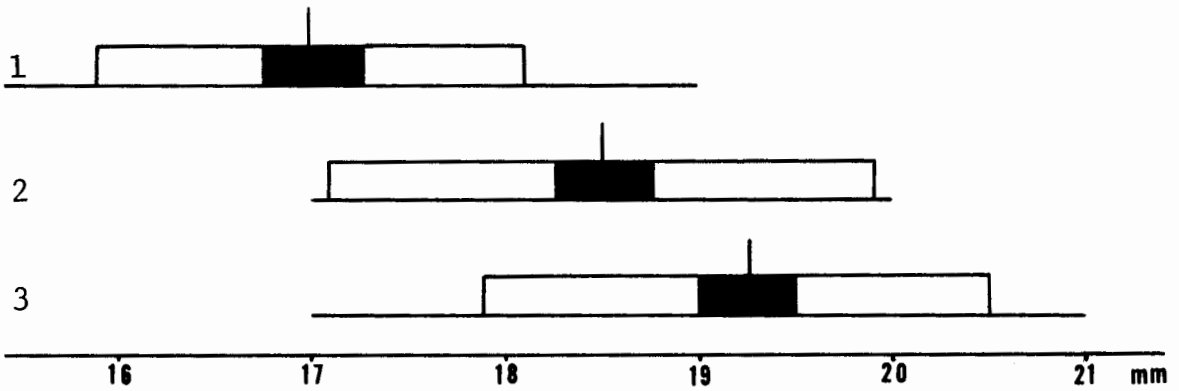

FIGURE 7

EAR LENGTH

1. P. m. gambeli
2. P. m. austerus
3. P. oreas

TABLE 5

RESULTS OF CROSS BREEDING EXPERIMENTS
BETWEEN *P. maniculatus* AND *P. oreas*

MALE	FEMALE	NO. OF LITTERS	LITTER SIZE
P. oreas	*P. oreas*	0	0
P. oreas	*P. m. gambeli*	0	0
P. m. gambeli	*P. oreas*	0	0
P. oreas	*P. m. austerus*	0	0
P. m. austerus	*P. oreas*	0	0
P. m. gambeli	*P. m. austerus*	1	4
P. m. austerus	*P. m. gambeli*	2	5 and 4
P. m. austerus	*P. m. austerus*	1	3
P. m. gambeli	*P. m. gambeli*	1	5

one resembled P. m. austerus, two were of intermediate length and five resembled P. m. gambeli. None of the hybrids had tails exceeding the range limits of the parents. Since most hybrids resemble one taxon or the other, field identification of intermediates is difficult. Perhaps because of this, no clearly defined hybrid zone was found between populations of P. m. austerus and P. m. gambeli. However, of 36 P. maniculatus collected at Salmon la Sac, eight could be construed as being P. m. gambeli x austerus hybrids. This would confirm the subspecific status of these two taxa.

DISCUSSION

In Washington, three taxa of Peromyscus are found to have allopatric populations; two of these taxa are broadly sympatric and the third taxon is in limited sympatry with the others where the ranges meet. How these distributions arose poses a challenging problem. Undoubtedly, the Vashon-Wisconsin glaciation, which reached its maximum 11,000 to 13,000 years ago, and post-glacial events played a vital role in the evolution of Washington's biota as we know it. Five hypotheses are offered to explain the distribution of the three taxa of Peromyscus found in central Washington.

1. Peromyscus oreas is a derivative of a northern form and is replacing P. maniculatus from the mountains of Washington.

There is some evidence to support the northern ancestry of P. oreas. This relationship is suggested by the presence of at least five races of P. maniculatus with morphology similar to P. oreas that are found near the northern end of its range in western British Columbia. Limited evidence based on karyotypes from my work and that of Hsu and Arrighi (1966) indicates that the chromosome morphology of P. oreas is similar to that of P. sitkensis of Admiralty and Baranof Islands of southeastern Alaska. However, when more is known of the karyotypes of Peromyscus in British Columbia, it may be found that a more closely related taxon is more proximal to the present range of P. oreas. In the event that a closely related taxon is not found, then it can be assumed that P. oreas is a relic form of restricted distribution.

If P. oreas is invading Washington from the north, then differentiation either took place since glaciation, or P. oreas found refuge somewhere on the coast of British Columbia during glaciation. It is improbable that P. oreas differentiated from P. maniculatus since glaciation, because geographic isolating barriers have been reduced with the

retreat of the glaciers. The displacement of P. maniculatus from the mountains of Washington as a result of invasion by P. oreas from the north is not likely in view of the disjunction of the two P. oreas populations. In fact, the lack of a connecting population of P. oreas suggests just the opposite; i.e., that P. maniculatus is extending its range into P. oreas habitats.

2. Peromyscus maniculatus is replacing P. oreas in Washington.

Before exploring this hypothesis it is necessary to reconstruct some of the events associated with the most recent glaciation. Present data suggest that during the glacial maximum, P. oreas took refuge in the Willapa Hills region of southwestern Washington, while other forms of Peromyscus, if there were others, were forced from western Washington, Figure 8. With the retreat of the glaciers, P. oreas expanded its range coincident with the development of boreal forests throughout western Washington. During this time, P. maniculatus was excluded from western Washington by barriers of considerable duration--the remnants of the Vashon glacier in the north, the Columbia River in the south, and the montane glaciers in the east.

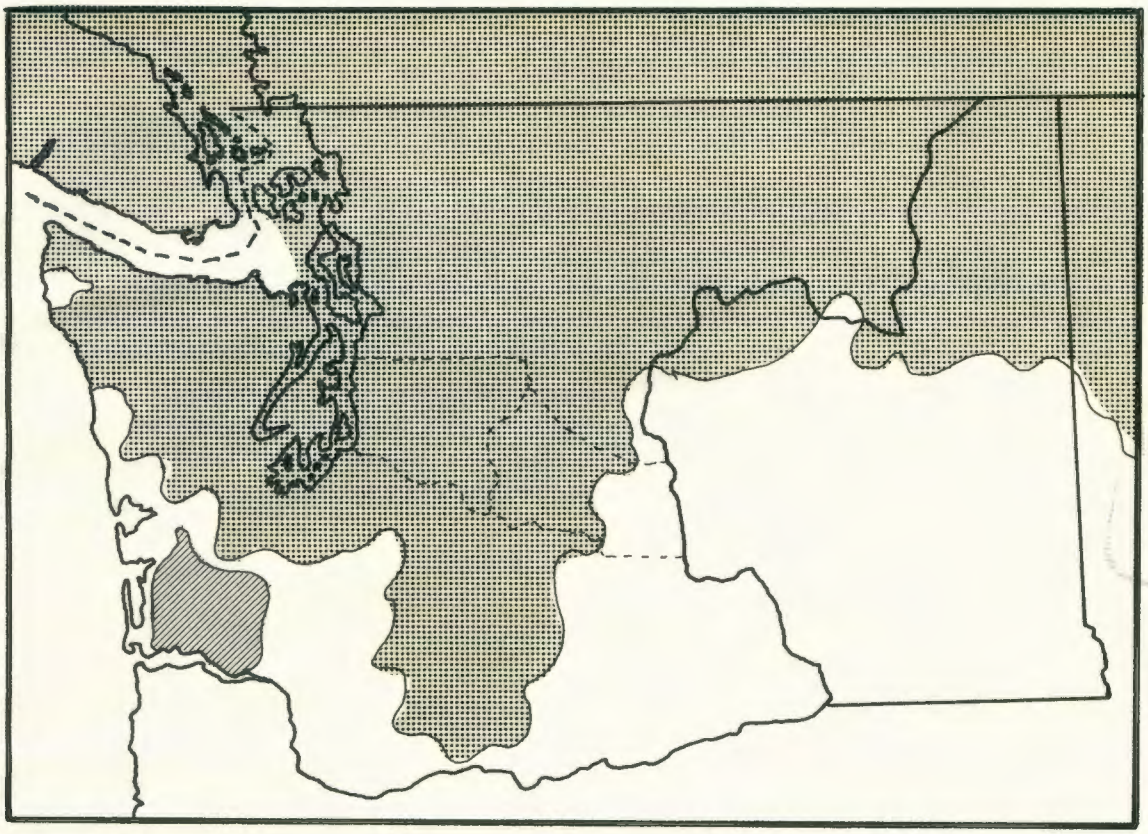

FIGURE 8

GLACIAL MAXIMUM
(Gambs, 1965)

Glaciers

Refuge area of P. oreas

With the development of bunchgrass and sagebrush in eastern Washington, P. m. gambeli invaded from the south. This invasion had little effect upon the distribution of P. oreas since it is not suited to a semi-arid habitat. It was the establishment of a P. m. rubidus-like population in southwestern Washington that had the most profound effect upon the distribution of P. oreas. It should be noted here that P. m. rubidus shows a broad ecological tolerance in Oregon, occupying both coastal and montane habitats and, also, that P. m. austerus is a derivative of P. m. rubidus is strongly suggested by the nearly identical morphology and ecology of these two races and the separation of their ranges only by the Columbia River.

Following the establishment of a P. m. rubidus population in southwestern Washington and its subsequent differentiation to P. m. austerus, a relatively rapid range expansion followed. The most complete inroads were made through the Puget Basin, where competitive exclusion of P. oreas by P. m. austerus occurred, resulting in the division of the range of P. oreas. Invasion into the mountains by P. m. austerus has not resulted in the complete exclusion of P. oreas.

The presence of P. m. austerus in eastern Washington is not unique to Kittitas County. Evidence that P. m. austerus

exists on the eastern slopes of the Cascades of southern Washington was submitted by John Erickson, who collected all three taxa at the 5,400 foot level of Steamboat Mountain, Skamania County. There are two explanations of the occurrence of P. m. austerus in eastern Washington. One explanation is the "end run" theory. It is suggested that P. m. austerus extended its range up the Columbia River Gorge, around the southern end of Washington's Cascades, and then northward along the eastern slopes of the Cascades at least as far as Kittitas County. Range expansion continued on both sides of the Cascades until secondary contact was established between the eastern and western segments of the population through Snoqualmie Pass and probably at other points. The other explanation involves the establishment of a large population of P. m. austerus in western Washington that eventually "spilled over" onto the leeward slopes of the Cascades. Either explanation is supported by my findings and those of Mr. Erickson.

3. Climatic changes of 5,700 years ago strongly influenced the distribution of Peromyscus.

Gambs (1965) has shown that an oak woodland occupied much of western and south central Washington some 5,700 years ago, Figure 9. The present distribution of P. m. austerus

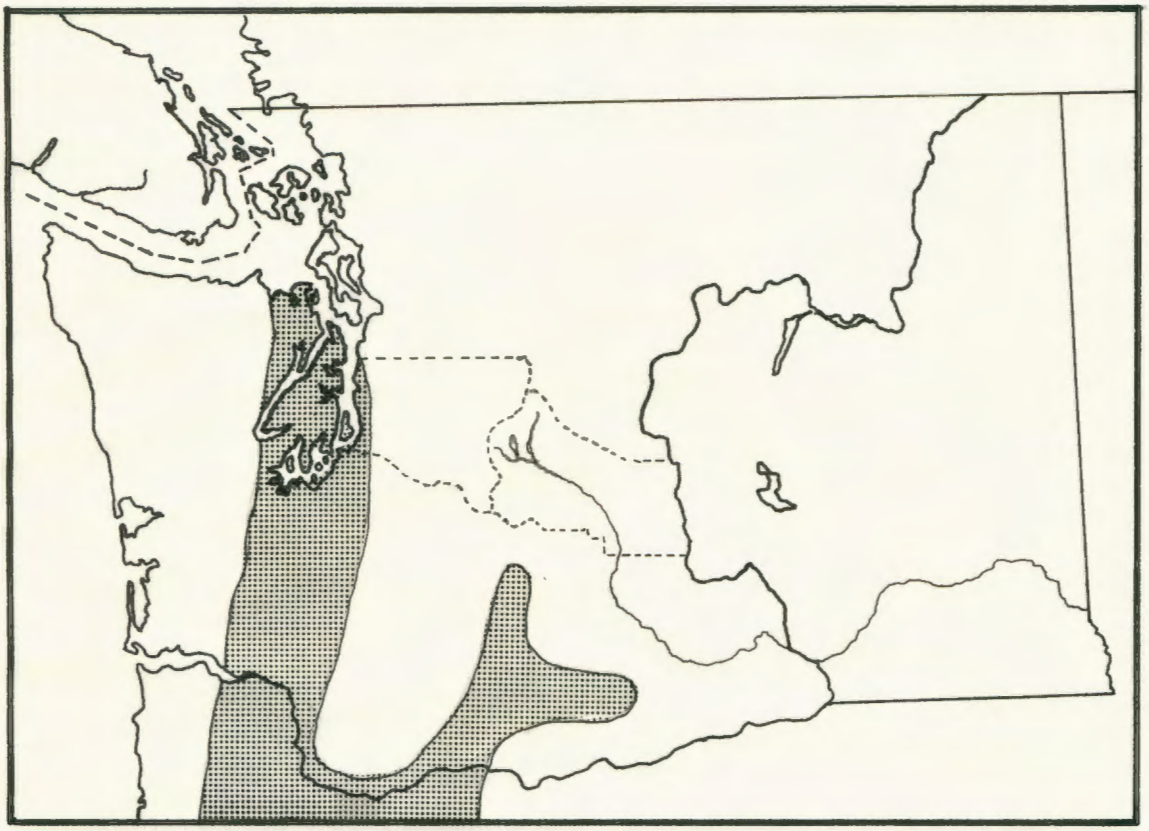

FIGURE 9

DISTRIBUTION OF OAK WOODLANDS IN THE
PACIFIC NORTHWEST 5,700 YEARS AGO
(Gambs, 1965)

Oak Woodlands

shows some correlation with the distribution of the oak woodlands. Conditions associated with this oak woodland, or conditions following its retreat may have affected the distribution of P. oreas and P. m. austerus. The development of these woodlands could be the sole factor in the division of the range of P. oreas. If this is true, then P. m. austerus invaded the Puget Basin in the absence of P. oreas.

4. Niche diversification is great enough that P. oreas is ecologically isolated from P. maniculatus, so neither species is replacing the other.

Evidence supporting this hypothesis is the result of an earlier behavior study. It was noted that the tail is used extensively during climbing. Use of the tail is similar in all three taxa. On horizontal branches the tail has a counterbalance function. In vertical ascent, the tail is pressed firmly against the tree allowing the stiff, ventral, posteriorly-projecting hairs to bear against the bark. When this is done, the tail becomes a tractive device capable of supporting the animal's weight while footholds are gained. A longer tail, then, is an advantage in extending the reach of the animal. From this, it can be argued that tail length is an index to arboreal habits in Peromyscus.

The habitats occupied by the three taxa can be correlated with tail length. Peromyscus m. gambeli, being strongly associated with a semi-arid habitat, has limited climbing facilities. Since forests are conspicuously lacking in semi-arid habitats, climbing by this mouse is restricted to low bushes. The tail length of P. m. austerus suggests semi-arboreal behavior. Throughout much of its range, large amounts of brush and undergrowth are found. A moderate amount of climbing would allow this lower part of the habitat to be exploited. Peromyscus oreas possesses the longest tail and is, perhaps, the most arboreal of the three.

5. The three taxa of Peromyscus have reached their critical distributional limits in Washington.

This hypothesis is a combination of the second, third, and fourth hypotheses. Peromyscus m. austerus has replaced P. oreas in the Puget Basin, but has reached an equilibrium with this species in the mountains where P. oreas is as well or better adapted and can successfully compete. Niche differentiation may be effective only in the mountains. If this is true, then we can expect a continuation of the range extension by P. m. austerus and further limitations of the range of P. oreas in the lowlands, but continued sympatry in the mountains.

SUMMARY

The range of P. m. austerus is shown to include not only the Puget Sound Lowlands, but also to extend into the central Cascade Mountains where it is sympatric with the mountain species, P. oreas. Both P. m. austerus and P. oreas are in limited sympatry with the semi-arid form, P. m. gambeli near the eastern limit of their range. Evidence that the distribution of Peromyscus in the study area is not unique to that region is also presented.

Some evidence of interbreeding between P. m. gambeli and P. m. austerus was found in areas of sympatry. This supports laboratory findings that these two taxa are interfertile and confirms their subspecific status.

Since P. oreas failed to breed in the laboratory and no hybrids were found during the course of the field work, it is concluded that this taxon constitutes a valid species, as has been shown by other investigators.

ACKNOWLEDGEMENTS

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