



Ecological and morphological relationships of subspecies of *Peromyscus maniculatus* near St. Mary, Montana
by Ronald Jay Glazier

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE in Zoology
Montana State University
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Abstract:

For a period of five months between June 22 to September 7, 1967 and from June 27 to September 5, 1968, a live trapping study was undertaken near the St. Mary region, Glacier National Park, Montana, to determine the ecological distribution and analyze morphological variation of two subspecies of *Peromyscus maniculatus*, *P. m. artemesia* and *P. m. osgoodi*. Morphological measurements were taken on adult mice only. Mean lengths of tail, ear, hind foot and skull are significantly greater in *P. m. artemesia* than *P. m. osgoodi*. Body length, nasal length and mastoid breadth are not reliable measurements for distinguishing between individuals of populations of the two subspecies, Nine individuals of intermediate measurements are classified as suspected hybrids.

Three general habitats are found in the study area, grassland, aspen groveland and coniferous forest. Allopatric *P. m. osgoodi* populations are found in the grasslands and meadows and disturbed areas of the aspen groveland. Allopatric *P. m. artemesia* populations are found in the coniferous forest and the meadows in that forest. The sympatric area corresponds roughly to the narrow groveland-coniferous forest ecotone. Regardless of general habitat the mice are found in those areas where ground vegetation is light but places for concealment are abundant. Although contact was found between the subspecies in three areas, contact in general appears to be limited by the dense vegetation along the sympatric contact line. Hybrids may occur, but they are limited in number. Isolating mechanisms other than habitat selection may be involved.

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ECOLOGICAL AND MORPHOLOGICAL RELATIONSHIPS OF SUBSPECIES
OF PEROMYSCUS MANICULATUS NEAR ST. MARY, MONTANA

by

RONALD JAY GLAZIER

A thesis submitted to the Graduate Faculty in partial
fulfillment of the requirements for the degree

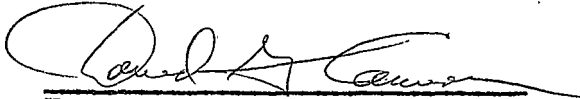
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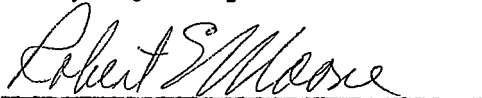
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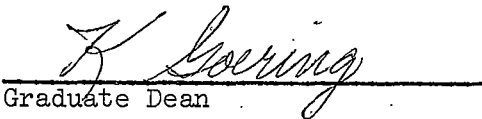
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Abstract

For a period of five months between June 22 to September 7, 1967, and from June 27 to September 5, 1968, a live trapping study was undertaken near the St. Mary region, Glacier National Park, Montana, to determine the ecological distribution and analyze morphological variation of two subspecies of Peromyscus maniculatus, P. m. artemesia and P. m. osgoodi. Morphological measurements were taken on adult mice only. Mean lengths of tail, ear, hind foot and skull are significantly greater in P. m. artemesia than P. m. osgoodi. Body length, nasal length and mastoid breadth are not reliable measurements for distinguishing between individuals of populations of the two subspecies. Nine individuals of intermediate measurements are classified as suspected hybrids.

Three general habitats are found in the study area, grassland, aspen groveland and coniferous forest. Allopatric P. m. osgoodi populations are found in the grasslands and meadows and disturbed areas of the aspen groveland. Allopatric P. m. artemesia populations are found in the coniferous forest and the meadows in that forest. The sympatric area corresponds roughly to the narrow groveland-coniferous forest ecotone. Regardless of general habitat the mice are found in those areas where ground vegetation is light but places for concealment are abundant. Although contact was found between the subspecies in three areas, contact in general appears to be limited by the dense vegetation along the sympatric contact line. Hybrids may occur, but they are limited in number. Isolating mechanisms other than habitat selection may be involved.

Introduction

When the end populations of a circular chain of intergrading subspecies overlap and become sympatric without interbreeding, speciation has been demonstrated (Mayr, 1963). These circular overlaps have been used as evidence for "speciation by distance". Although genetic divergence may be achieved through distance (Wright, 1943), gene flow and genetic homeostasis tend to limit the amount of genetic divergence. In most of the well-analyzed cases of circular overlap the populations are not continuous but have major gaps in the chains or at least show evidence for the former existence of such gaps (Mayr, 1963). The deer mouse, Peromyscus maniculatus, has also been cited as an example of circular overlap (Dicé, 1931 and Mayr, 1942).

In the northern part of lower Michigan two subspecies, P. m. gracilis and P. m. bairdii, are sympatric without showing evidence of interbreeding. This occurs because the two continue to remain ecologically separated; gracilis lives in dense mixed forests of beech, maple, yellow birch and associated trees, while bairdii prefers prairies, open fields and lake beaches (Hooper, 1942). Reproductive isolation was most likely originally accomplished by the extrinsic means of a geographic barrier but now is maintained in areas of sympatry by habitat isolation (Mayr, 1963 and Meehan, 1961):

The ranges of two other subspecies, P. m. artemesiaae and P. m. osgoodi, overlap along the eastern edge of Glacier National Park. Morphological evidence collected by Osgood (1909) and Murie (1933) suggests no hybridization. The subspecies artemesiaae is a long-tailed forest form

while osgoodi is a short-tailed grassland form, each being closely restricted to their respective habitats (Murie, 1933). Knowledge of the overlap in Glacier National Park was originally based on data from Osgood (1909), who states that P. m. artemesia intergraded to the south with P. m. sonoriensis, which is theoretically connected genetically to the east with P. m. rufinus, and finally with P. m. osgoodi.

Murie (1933) based his conclusion that no hybridization occurred from the data collected on a small area, most of which lies in or near the sympatric area. Murie gave no information on either the pattern of morphological variation among individuals of populations of mice or the local distribution of mice in specific habitats in the area.

For a total of five months during the summers of 1967 and 1968, I conducted a live-trapping study of P. maniculatus near St. Mary, Montana. The objectives were (1) to measure morphological variation of each subspecies trapped from a series of populations extending across the sympatric zone, and (2) to determine the ecological distribution of the subspecies artemesiae and osgoodi in allopatric and sympatric areas near the St. Mary region.

Methods

All mice used in this study were captured in Sherman live-traps. Trapping was conducted from June 22 to September 7, 1967, and from June 27 to September 5, 1968. The trapping sites were located in the diverse habitats of the St. Mary and Swiftcurrent drainages and on the prairie south of Duck Lake. These areas included the sympatric zone and adjacent allopatric areas of the two subspecies of mice. Mice were collected for morphological comparisons from eight sites within the major habitats in the area, grassland, aspen groveland and spruce-fir forest. In each of these collection sites an attempt was made to obtain twenty mice for morphological comparisons. However, if after 400 trap-nights less than fifteen mice were captured, trapping at that site was discontinued.

The criteria used in assigning mice to either of the two subspecies were those morphological measurements of tail and ear lengths as used by Osgood (1909) in his revision of the genus Peromyscus. Individuals whose tail and ear length measurements were intermediate of those described for the two subspecies were tentatively classified according to the classification of the population in which they were trapped.

In addition to the eight areas sampled specifically as collection sites, other habitats were sampled to determine the local distribution of each subspecies and to delineate the sympatric zone. The traps were placed so as to sample as many habitats in each area as practicable. Trap lines were extended, wherever possible, across the forest-grassland ecotone. A relative index of subspecies found in each habitat was

computed as a percentage based on the number of mice caught per 100 trap nights.

Each habitat trapped was examined qualitatively and then described according to general vegetation cover and community type with reference to Habeck (1968), Kirkwood (1922) and Lynch (1955). Scientific names for plants follow Booth and Wright (1962) and Booth (1950) and for animals, Hall and Kelson (1959).

Mice used for morphological comparisons were maintained in a laboratory at Montana State University for at least eight months, the minimum age for adult classification (Sheppe, 1963).

Standard measurements of total length, tail length, right hind foot and right ear length were recorded to the nearest 0.5 mm. All measurements were taken from dead animals. Skins and skulls were prepared as museum specimens. Greatest length of the skull, nasal length and mastoid breadth (Hoffman and Pattie, 1968) for each skull were measured twice to the nearest .05 mm using a dial caliper. These measurements have possible value in distinguishing subspecies.

A modification of Duncan's new multiple range test was used to test differences in means of samples with unequal size (Kramer, 1956).

Description of Study Area

General Area

The study area was located in the St. Mary and Swiftcurrent drainages on the eastern side of Glacier National Park, Montana, and on the prairie south of Duck Lake (Fig. 1). St. Mary and Swiftcurrent valleys extend from the continental divide to the edge of the mountain range twenty miles to the east and are glacially carved. Both are relatively narrow with the surrounding mountains rising to 9,000 feet. At the eastern park boundary the St. Mary valley widens, turns northward and is bounded on the east by a lateral moraine known as the St. Mary Ridge (Fig. 1). This ridge rises steeply approximately 1,500 feet above the 4,500 foot elevation of the valley. The eastern slope of the moraine gives way gradually to the rolling hills of the Great Plains. Duck Lake is approximately three miles east of Babb and lies in a depression in the St. Mary Ridge.

The topography of the park is attributed largely to the action of glaciers. During the Pleistocene the park, except the summits of the highest peaks, was completely covered by glaciers. These glaciers completely removed the forest from the park area. It has been only in the last 9,000 years that the area has been revegetated (Dyson, 1960) and the invasion and establishment of animal populations has taken place.

Three major vegetation types are found within the study area. The grassland community of needlegrass (Stipa) and fescue (Festuca) south and east of Duck Lake is a western extension of the Great Plains. Aspen groveland (Lynch, 1955) consisting of a narrow zone of grove-grassland mosaic between the forested eastern front of the mountains and the Great

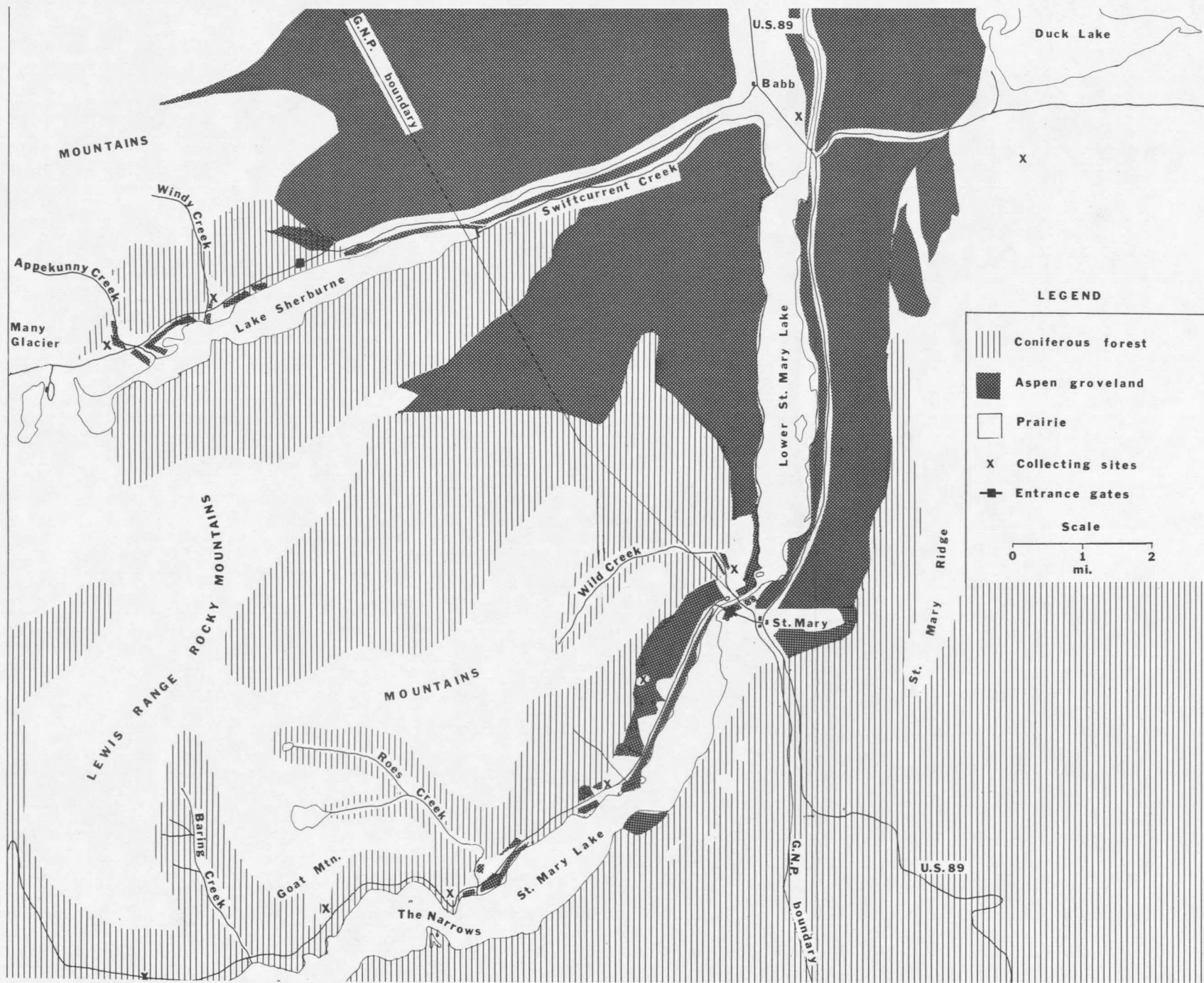


Fig. 1 Map of the study area

Plains is found along both sides of Lower St. Mary Lake. It continues along the west side of St. Mary Lake for three and one-half miles. Isolated stands of aspen groveland are found farther up the valley (Fig. 1). This zone is relatively narrow along St. Mary Lake, extending not more than one mile from the lake edge. A similar condition exists on the north side of Swiftcurrent Creek and Lake Sherburne in the Swiftcurrent drainage. Quaking aspen (Populus tremuloides) is the dominant tree; black cottonwood (P. trichocarpa) and narrowleaf cottonwood (P. augustifolia) are also present. The latter species is restricted to the edges of streams. Grasses, shrubs and forbs make up a very dense undergrowth in the aspen groves, particularly in mesic sites. Buffaloberry (Shepherdia argentea), western serviceberry (Amelanchier alnifolia), shrubby cinquefoil (Potentilla fruiticosa) and chokecherry (Prunus virginiana) are the dominant shrubs in this area. Bluebunch wheatgrass (Agropyron spicatum), bluestem (A. smithii) and bluebunch fescue (Festuca idahoensis) are common grasses found in the grassland adjacent to aspen groves. Lynch (1955) lists rough fescue (Festuca scabrella) as the climatic climax grass of the groveland. Conifers associated with the groveland are relatively unimportant except along the western border and on St. Mary Ridge where the groveland meets montane coniferous forest. Here Engelmann spruce (Picea engelmanni), Douglas fir (Pseudotsuga menziesii) and lodgepole pine (Pinus contorta) are scattered through the aspen stands and adjacent grasslands.

At higher elevations (4,800 ft.) the aspen-groveland is replaced by

the coniferous forest. Two zones characterized by Daubenmire (1943) are represented here, the Douglas fir zone and the spruce-fir zone. In the study area the dominant trees are Douglas fir and lodgepole pine along with some limber pine (Pinus flexilis) on exposed ridges. Above approximately 5,500 feet and in favorable sites the dominant trees are Engelmann spruce and alpine fir (Abies lasiocarpa). The forest in most of the study area appears to be a seral stage forest with the young growth being mostly Engelmann spruce and alpine fir. However, on some of the more exposed areas Douglas fir and lodgepole pine are replacing themselves.

Collection sites

Duck Lake: Most of the trapping was conducted along a ridge approximately one mile south of Duck Lake (Fig. 1). However, some trapping was done on the prairie between the ridge and Duck Lake. Along the ridge crest is an old road bed which is raised slightly above the surrounding ground. A narrow strip of ground along the road bed is covered with rocks and a few small shrubs (Fig. 2). By contrast, the surrounding prairie has very few rocks on the surface and only an occasional shrub. Shrubby cinquefoil is the common shrub along the road bed. The prairie grass is mostly needlegrass (Stipa spp) but bluebunch fescue is also present. However, downy chess brome (Bromus tectorum), meadow foxtail (Alopecurus pratensis) and barley (Hordeum spp) are dominant along the disturbed edges of the road bed. These grasses are commonly found in wastelands (Booth, 1950).

Babb: This site is just north of U.S. 89 approximately three-quarters of a mile southeast of Babb (Fig. 1). The trapping area encompasses an abandoned gravel pit and the surrounding field. The gravel pit consists of outwash gravel covered by grasses and low shrubs. Bluebunch fescue and bluestem are the dominant grasses in the gravel pit and nearby field. Common snowberry (Symphoricarpos albus) is a common shrub in the field. Showy point vetch (Oxytropis splendens), wavyleaf thistle (Cirsium undulatum) and spotted knapweed (Centaurea maculosa) are important weeds in the gravel pit. Some shrubby aspen is scattered across the gravel pit.



Fig. 2 Road bed at Duck Lake



Fig. 3 Disturbed aspen groveland at Windy Creek

Although the surrounding fields are grass covered, about one half of the ground cover consists of forbs.

Windy Creek: West of Babb, 1.4 miles west of the park entrance on the road to Many Glacier is a large clearing on the north side of the road (Fig. 1). This clearing lies in the aspen groveland but has been disturbed by periodic flooding of Windy Creek (Fig. 3). The many dry rocky stream channels which cut through the area give evidence to the alternate disturbance and partial stabilization of the area. A field layer of bluebunch wheatgrass, bluebunch fescue, bryophytes, lichens and sepetose forbs is covered with a discontinuous patch work of low shrubs. Shrubs comprise approximately 50% of the ground cover. Chekecherry, buffaloberry and western serviceberry are the most prevalent shrubs. Small clumps of quaking aspen are interspersed throughout the area with black cottonwood growing along the stream channels. The few scattered conifers are lodgepole pine and limber pine. The area has not been recently disturbed and was in a stable condition during the study period.

Appekunny Creek: Three miles west of the Many Glacier park entrance, north of the highway and immediately west of Appekunny Creek (Fig. 1), is another trapping site similar to Windy Creek in appearance. However, this site has fewer dry stream channels and more subsurface water than the Windy Creek site, as indicated by the heavier vegetation and the presence of more aspen and fescue grass. Coverage of shrubs ranges from about 50% to 100% along the stream bank.

St. Mary Lake: This area is a relatively narrow strip of aspen-groveland and groveland-forest ecotone that parallels the west shore of St. Mary Lake (Fig. 1). The zone extends from the north side of Wild Creek southwest three and three-quarter miles along the west shore of St. Mary Lake. At that point the aspen-groveland is replaced by the Douglas fir forest. There are several large meadows in this section (Fig. 4) which are separated, in the poorly drained areas by bands of quaking aspen. The grass in the meadows is predominately bluebunch fescue and bluebunch wheatgrass. However, some timothy (Phleum pratense) has been planted in some of the meadows. Serviceberry, buffaloberry and snowberry are common shrubs found in the meadows, particularly along the margins. Shrubby cinquefoil, silky lupine (Lupinus sericeus), arrowleaf balsamroot (Balsamorhiza sagittata) and several other composites comprise the major forbs. Douglas fir and lodgepole pine are the dominants in the coniferous forest which has approximately a 75-90% canopy cover. Rocky mountain maple (Acer glabrum), some quaking aspen, cowparsnip (Heracleum lanatum) and western thimbleberry (Rubus parviflorus) constitute the major understory. The ground cover is very heavy near the edges of the meadows and thins out in the forest away from the meadows. The groveland-forest ecotone is sharp throughout the area.

The beach in this area is narrow, approximately ten to twenty feet wide and very rocky. The bank along the beach ranges from about two feet to over ten feet in height. There is relatively little vegetation on the beach, but driftwood is abundant.

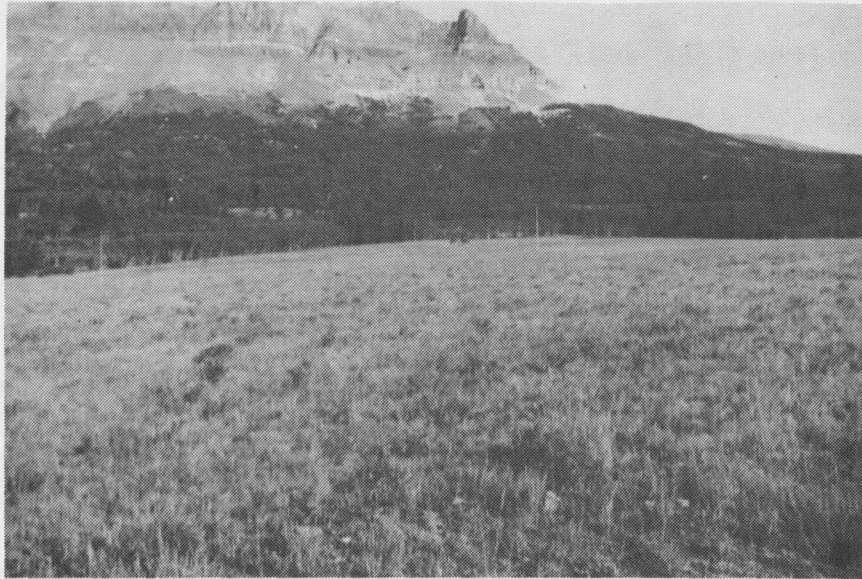


Fig. 4 Aspen groveland meadow, St. Mary Lake

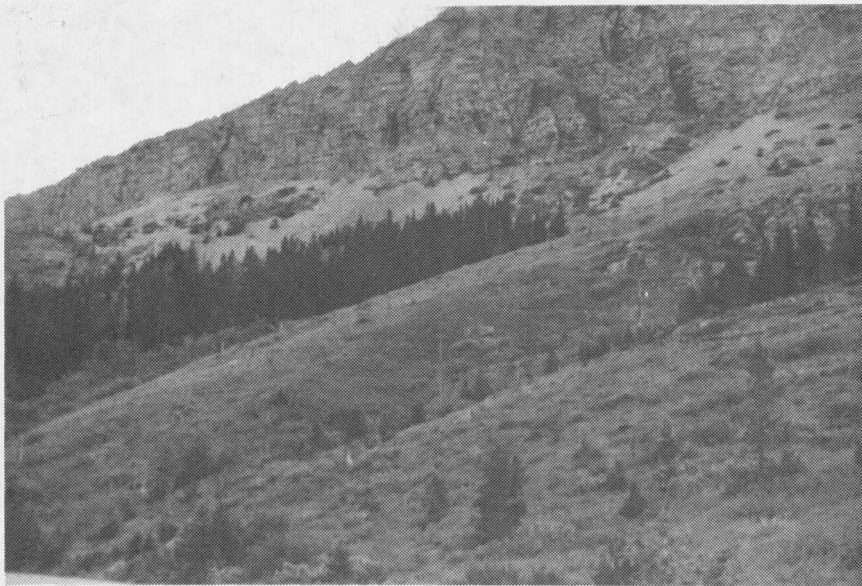


Fig. 5 Meadow in spruce-fir forest at Goat Mountain

The Narrows: A rocky ridge which projects into St. Mary Lake west of Roes Creek forms a constriction in the lake known as the Narrows (Fig. 1).

Deer mice were trapped on the ridge on the north side of the lake.

Douglas fir and lodgepole pine are the dominant trees but some limber pine is found on the exposed rock outcrops of the ridge. There is a sparse reproduction of Douglas fir and lodgepole pine, and the vegetation appears fairly stable. Since the ridge is in an exposed position, the westerly winds have probably prevented the establishment of a spruce-fir forest on this area. The conifers form a 75-80% canopy cover with wheatgrass and fescue grass being found in the open spaces. Snowberry and creeping juniper (Juniperus horizontalis) are scattered throughout the trapping site but only contribute to 10% or less of the ground cover.

Goat Mountain: Three and one-half miles west of the Roes Creek bridge on the Going-to-the-Sun highway is the Goat Mountain site (Fig. 1). This site is on a rocky ridge extending a few hundred yards from the highway to the base of the cliffs of the mountain (Fig. 5). The lower slope is covered with a few very old deadfalls. The upper slope is covered with bluebunch fescue, bluebunch wheatgrass, Montana polemonium (Polemonium parvifolium), serviceberry, buffaloberry and shrubby cinquefoil which constitutes about a 50% ground cover. The rest of the ground is comprised of rocks and rock outcrops. The area has apparently remained unchanged in recent years.

Baring Creek: The trapping site is located 1.4 miles west of Baring Creek (Fig. 1) and extends on both sides of the highway. The forest is a mature seral stage forest and Douglas fir and lodgepole pine are the dominant conifers with Engelmann spruce and alpine fir being found only as the young growth (Fig. 6). There are numerous deadfalls throughout the area. Rocky Mountain maple, cowparsnip and western thimbleberry are very dense throughout the area and contribute to the heavy ground cover in most places.



Fig. 6 Seral stage Douglas fir forest at
Baring Creek site

Results

Morphological Variation

The mean measurements for tail length, hind foot length, ear length and greatest length of the skull (TABLES I and II) are all highly significantly larger ($P < 0.01$) for P. m. artemesia than for P. m. osgoodi (TABLES III, IV and V). Means of body lengths are not necessarily correlated with subspecies; however, P. m. artemesia is generally larger. The longer skull of P. m. artemesia is most apparent in the snout, the nasal bones accounting for 61% of the increased length. Although the skulls of individual P. m. artemesia are larger, there are only slight increases in width, as measurements for mastoid breadth show. The mean nasal lengths of P. m. artemesia are all highly significantly larger than those of P. m. osgoodi with three exceptions which exhibit significant differences ($P < 0.05$) (TABLE V).

A separation of populations by subspecies cannot be made in all cases by using body length or mastoid breadth. Populations of P. m. artemesia at the Narrows and Goat Mountain are significantly or highly significantly larger in both measurements than all P. m. osgoodi populations with only one exception. There are no significant differences in means of body length between the Narrows population and the Babb population (TABLE VI). The population of P. m. artemesia at Appekunny Creek has a significantly larger mean body length than the P. m. osgoodi from St. Mary Lake. No other significant differences in body length occur among the P. m. artemesia and P. m. osgoodi populations. While there are some significant differences in mean mastoid breadth between the two

TABLE I. Means and ranges of body measurements of population samples of
Peromyscus maniculatus osgoodi and Peromyscus maniculatus artemesiaae

measurements in mm						
Area	No. of osgoodi	No. of artemesiaae	Body length	Tail length	Hind foot length	Ear length
Duck Lake	28		96.4 (91-105)	76.6 (60-85)	20.6 (19-22)	16.6 (15-18)
Babb	26		97.0 (89-107)	81.1 (71-92)	20.9 (20-22)	16.9 (16-18)
Windy Creek	22		95.5 (89-101)	83.9 (77-91)	21.0 (20-22)	17.4 (17-19)
Appekunny Creek		6	97.7 (93-109)	106.1 (94-119)	22.8 (22-23)	18.8 (19-20)
St Mary Lake	12		92.7 (86-99)	81.3 (78-89)	20.8 (19-22)	17.6 (16-18.5)
St Mary Lake		20	95.8 (86-101)	101.3 (91-110)	22.3 (21-23)	18.8 (18-20)
Narrows		16	100.0 (94-105)	105.0 (96-117)	22.6 (21-23)	19.8 (19-21)
Goat Mtn.		14	101.6 (94-117)	102.9 (96-110)	22.6 (21-24)	20.9 (18-20)
Baring Creek		11	94.8 (91-108)	102.8 (93-112)	22.5 (21-24)	18.9 (18-20)

TABLE II. Means and ranges of skull measurements of population samples
Peromyscus maniculatus osgoodi and Peromyscus maniculatus artemesia

measurements in mm (+0.05 mm)

Area	No. of osgoodi	No. of artemesiae	Greatest length of the skull	Nasal length	Mastoid breadth
Duck Lake	26		25.74 (24.75-26.93)	10.45 (9.99-11.11)	10.95 (10.40-11.35)
Babb	26		26.09 (25.07-26.92)	10.60 (9.69-11.55)	11.09 (10.58-11.68)
Windy Creek	20		25.73 (25.02-26.95)	10.42 (9.06-11.71)	11.02 (10.75-11.27)
Appekunny Creek		6	26.84 (26.02-28.05)	11.22 (10.70-11.74)	11.25 (11.00-11.64)
St. Mary Lake	12		25.64 (24.68-27.72)	9.95 (9.00-10.72)	10.96 (10.68-11.25)
St. Mary Lake		22	26.40 (24.80-27.95)	10.90 (10.05-11.74)	11.13 (10.55-11.64)
Narrows		16	27.06 (25.51-27.75)	11.17 (10.43-11.75)	11.32 (10.81-11.88)
Goat Mtn.		15	26.94 (25.54-27.90)	10.77 (10.04-11.43)	11.27 (10.78-11.77)
Baring Creek		11	26.55 (25.65-27.70)	11.14 (10.50-11.68)	11.17 (10.98-11.40)

TABLE III. Results of the modified Duncan new multiple range test showing significant differences between population sample means of tail lengths and hind foot lengths.

		<u>P. m. osgoodi</u>				<u>P. m. artemesiaie</u>				
		Duck Lake	Babb	Windy Creek	St. Mary Lake	St. Mary Lake	Narrows	Goat Mtn.	Baring Creek	Appekunny Creek
<u>P. m. osgoodi</u>	Duck Lake	T	t	T	t	T	T	T	T	T
	Babb		T			T	T	T	T	T
	Windy Creek			T		T	T	T	T	T
	St. Mary Lake				T	T	T	T	T	T
<u>P. m. artemesiaie</u>	St. Mary Lake	F	F	F	F	T				
	Narrows	F	F	F	F		T			
	Goat Mtn.	F	F	F	F			T		
	Baring Creek	F	F	F	F				T	
	Appekunny Creek	F	F	F	F					T

T,t-Tail length
F,f-Hind Foot length

Capital letter-highly significantly different (P<0.01)
Lower case letter-significantly different (P<0.05)
Blank-no significant differences

TABLE IV. Results of the modified Duncan new multiple range test showing significant differences between population sample means of ear length.

		<u>P. m. osgoodi</u>				<u>P. m. artemesiaae</u>				
		Duck Lake	Babb	Windy Creek	St. Mary Lake	St. Mary Lake	Narrows	Goat Mtn.	Baring Creek	Appekunny Creek
<u>P. m. osgoodi</u>	Duck Lake			e	e	E	E	E	E	E
	Babb					E	E	E	E	E
	Windy Creek					E	E	E	E	E
	St. Mary Lake					E	E	E	E	E
<u>P. m. artemesiaae</u>	St. Mary Lake						E	E		
	Narrows							E	E	E
	Goat Mtn.								E	E
	Baring Creek									
	Appekunny Creek									

E,e-Ear length

Notations are the same as listed in TABLE III.

TABLE V. Results of the modified Duncan new multiple range test showing significant differences between population sample means of the greatest length of the skull and nasal length.

		<u>P. m. osgoodi</u>				<u>P. m. artemesiaie</u>				
		Duck Lake	Babb	Windy Creek	St. Mary Lake	St. Mary Lake	Narrows	Goat Mtn.	Baring Creek	Appekunny Creek
<u>P. m. osgoodi</u>	Duck Lake	S				S	S	S	S	S
	Babb		S	S		S	S	S	S	S
	Windy Creek			S		S	S	S	S	S
	St. Mary Lake	N	N	N	S	S	S	S	S	S
<u>P. m. artemesiaie</u>	St. Mary Lake	N	n	N	N	S	S	S	S	S
	Narrows	N	N	N	N	S		S		
	Goat Mtn.	N	n	n	N	n	S			
	Baring Creek	N	N	N	N			S		
	Appekunny Creek	N	N	N	N	n				S

S,s-Greatest length of the skull
 N,n-Nasal length

Notations are the same as listed in TABLE III.

TABLE VI. Results of the modified Duncan new multiple range test showing significant differences between population sample means of body length and mastoid breadth.

		<u>P. m. osgoodi</u>				<u>P. m. artemesiaie</u>					
		Duck Lake	Babb	Windy Creek	St. Mary Lake	St. Mary Lake	Narrows	Goat Mtn.	Baring Creek	Appekunny Creek	
<u>P. m. osgoodi</u>	Duck Lake	■			b		b	B			
	Babb		■		b			B			
	Windy Creek			■			B	B			
	St. Mary Lake				■		B	B		b	
<u>P. m. artemesiaie</u>	St. Mary Lake	m				■	b	B			
	Narrows	M	M	M	M	m	■		B		
	Goat Mtn.	M	m	M	M			■	B		
	Baring Creek	m							■		
	Appekunny Creek	m		m	m					■	

B,b-Body length
M,m-Mastodi breadth

Notations are the same as listed in TABLE III.

subspecies, there are no significant differences between seven combinations of P. m. artemesiaae and P. m. osgoodi populations.

Although the intersubspecific differences in morphological measurements are generally greater than within each subspecies, some significant intrasubspecific differences also exist. The mean tail length of the P. m. osgoodi Duck Lake population is significantly smaller than the means of the St. Mary Lake and Babb populations. In addition the mean tail length of the Duck Lake population is highly significantly smaller than the mean of the P. m. osgoodi from Windy Creek (TABLE III). The Windy Creek, Babb and St. Mary Lake populations are not significantly different with respect to mean tail lengths. No significant differences in tail length occur among the P. m. artemesiaae populations.

There is only slight intrasubspecific variation in hind foot length (TABLE III). The only significant difference found among either P. m. artemesiaae or P. m. osgoodi populations is that the P. m. osgoodi from Windy Creek have a significantly larger mean for hind feet than the P. m. osgoodi from Duck Lake.

The P. m. osgoodi population from Duck Lake has a significantly shorter mean ear length than the P. m. osgoodi from Windy Creek and St. Mary Lake (TABLE IV). No other P. m. osgoodi populations show significant differences. The P. m. artemesiaae populations vary considerably in ear length. Although there are no significant differences in means among the deer mice from St. Mary Lake, Baring Creek and Appekunny Creek, all other P. m. artemesiaae populations show highly significant differences

in means.

The greatest length of the skull measurements vary, and several highly significant differences occur among subspecific populations (TABLE V). The Babb population of P. m. osgoodi has a highly significantly smaller mean skull length than all of the other P. m. osgoodi populations. The P. m. artemesiae populations from St. Mary Lake and Baring Creek have significantly or highly significantly smaller mean skull lengths than all other P. m. artemesiae populations.

The nasal measurements do not vary as much within a subspecies as the skull lengths. The mean nasal length of P. m. osgoodi from St. Mary Lake which is highly significantly smaller than those of all other P. m. osgoodi populations is the only difference among P. m. osgoodi populations. The mean length of nasals of P. m. artemesiae from the Narrows are significantly shorter than means of the P. m. artemesiae from the Goat Mountain and Appekunny Creek.

Means of body sizes do exhibit some intrasubspecific variation (TABLE VI). The P. m. osgoodi from St. Mary Lake have a significantly shorter mean than those of deer mice from Duck Lake and Babb. The P. m. artemesiae from Baring Creek have a highly significantly shorter mean body length than the P. m. artemesiae from the Narrows and Goat Mountain. Similarly the mean for P. m. artemesiae from St. Mary Lake is significantly and highly significantly shorter than the means for deer mice from the Narrows and Goat Mountain respectively.

The only significant intrasubspecific difference for mastoid breadth

occurs between the narrower skull width of the P. m. artemesiaae from St. Mary Lake and the deer mice from the Narrows.

Comparisons made between two means of different measurements within one subspecies cannot necessarily be made within the other subspecies. If the P. m. osgoodi populations are ranked with respect to increasing means for body length the same ranking is not obtained for any other external measurements taken. The P. m. artemesiaae populations show the same ranking for means of tail lengths and foot lengths but not for means of body length and ear length.

Means of skull measurements exhibit more consistent ranking, but these measurements serve to show that the comparisons made for one subspecies cannot always be made for the other subspecies. Populations of P. m. artemesiaae exhibit the same ranking for greatest length of the skull and mastoid breadth but not for nasal length. On the other hand, P. m. osgoodi populations have the same ranking for the greatest length of the skull and nasal length but not for mastoid breadth.

Nine individuals which may indicate hybridization between the two subspecies were collected (TABLE VII). Some, but not all, morphological measurements of each suspected hybrid mouse are intermediate with respect to means of the two subspecies.

TABLE VII. Selected body and skull measurements of suspected hybrids

Area	Tail	Hind Foot	Ear	Greatest length of the skull	Nasal
Babb					
1.	92	21	18	26.46	10.47
2.	90	22	18	25.77	10.45
mean for Babb population (<u>osgoodi</u>)	81.1	20.8	16.7	26.09	10.60
St. Mary Lake					
3.	91	21.5	19	24.80	10.17
4.	94	22	18.5	25.74	11.11
5.	89	22	18	26.35	10.20
mean for St. Mary Lake population (<u>osgoodi</u>)	81.3	20.8	17.6	25.64	9.95
mean for St. Mary Lake population (<u>artemesiae</u>)	101.3	22.3	18.8	26.40	10.90
Windy Creek					
6.	91	21	19	26.22	10.30
7.	91	21	17	26.07	10.85
mean for Windy Creek population (<u>osgoodi</u>)	83.9	21	17.4	25.73	10.40
Appekunny Creek					
8.	94	23	18	26.02	10.70
mean for Appekunny Creek population (<u>artemesiae</u>)	106.2	22.8	18.8	26.84	11.27
Baring Creek					
9.	93	21	18	25.65	10.69
mean for Baring Creek population (<u>artemesiae</u>)	102.8	22.5	18.9	26.55	11.14
mean for all <u>osgoodi</u>	80.4	20.8	17	25.83	10.43
mean for all <u>artemesiae</u>	103.1	22.5	19.2	26.77	11.00

Ecological Distribution

The two subspecies are represented by approximately equal population densities in the favorable habitats. The subspecies artemesiae was trapped with a 7.0% success as opposed to a 7.2% success for the subspecies osgoodi (TABLE VIII).

The allopatric areas include Duck Lake, Babb and Windy Creek, for P. m. osgoodi, on the north and east, and the Narrows, Goat Mountain and Baring Creek, for P. m. artemesiae, on the south and west of the study area. The sympatric area lies along the forest-groveland ecotone including the west shore of St. Mary Lake and Appekunny Creek in the Swiftcurrent drainage.

In the allopatric area P. m. osgoodi was trapped on prairie grassland and in disturbed aspen groveland. Trapping success in the prairie sites was better in disturbed areas (road bed and gravel pit) than in the surrounding prairie. In the disturbed aspen groveland at Windy Creek P. m. osgoodi was trapped near shrubs, brushpiles, rock piles and along the edge of the dry rocky stream channels that cut through the area.

In the allopatric area of P. m. artemesiae mice were trapped in a meadow at Goat Mountain and the Douglas fir-lodgepole pine forest at the Narrows and Baring Creek. At Goat Mountain and the Narrows the preferred habitat of the mice appeared to be rock outcrops, and, in addition mice at the Narrows were trapped near brushpiles and juniper bushes around the clearings in the scattered Douglas fir forest. Most of the mice in the mature forest at Baring Creek were caught along the dry rocky wash or

TABLE VIII. Overall trapping success for the two subspecies in each area sampled. The totals include those mice used for morphological measurements.

Allopatric	Area	Habitat type	No. traps	No. mice	%
<u>P. m. osgoodi</u>	Duck Lake	prairie	100	3	3.0
		road bed	525	40	7.6
	Babb	prairie gravel pit	25 100	3 28	12.0 28.0
	Windy Creek	disturbed aspen groveland	575	58	10.1
<u>P. m. artemesiaae</u>	Narrows	stable Douglas fir	575	40	7.0
	Goat Mtn.	meadow	350	40	11.4
	Baring Creek	Douglas fir forest	225	24	10.7

TABLE VIII. (continued) Overall trapping success for the two subspecies in each area sampled. The totals include those mice used for morphological measurements.

Sympatric	Area	Habitat type	No. traps	No. mice	%
	Appekunny Creek	disturbed aspen groveland	400	26 art. 1 osg.	6.8
		aspen groves	100	0	0.0
		Douglas fir forest	75	1 osg.	1.3
		meadows	250	8 osg.	3.2
	St. Mary Lake	aspen groves	200	1 osg.	0.5
		meadows	225	14 art. 6 osg.	8.9
		Douglas fir forest	275	9 art.	3.3
		scattered conifers	725	26 osg.	3.6
		beach	75	7 art. 5 osg.	16.0
		Total <u>P. m. osgoodi</u>	2587	186	7.2
		Total <u>P. m. artemesiaae</u>	2213	155	7.0

near brushpiles and logs. The areas of dense undergrowth appeared to be avoided.

Although the sympatric zone is narrow, a variety of habitats are found within it. At Appekunny Creek, the trapping success was not as high as at Windy Creek. Only one P. m. osgoodi was trapped at this site out of twenty seven mice caught.

All three major vegetative habitats of the study area are found at the St. Mary Lake site. P. m. osgoodi was trapped in the meadows or in the scattered conifers near the edges of meadows while the subspecies artemesiae was found in the coniferous forest west of the aspen grove-land. However, in many places where the undergrowth in the coniferous forest was dense no P. m. artemesiae were caught. Both subspecies were concentrated in rocky and disturbed areas.

At Appekunny Creek and at two locations near St. Mary Lake contact between the two subspecies is definitely made. Both subspecies were trapped along the eroded beaches of St. Mary Lake from a point two and one-quarter miles from the outlet of the lake southwest along the shore for one and one-half miles. Also both subspecies were collected from a rocky, grassy ridge which projects from the coniferous forest into the most westerly meadow at St. Mary Lake. Of the nine intermediate mice trapped, one was caught at Appekunny Creek, one from the beach at St. Mary Lake, and two from a dumpground at the edge of the Douglas fir forest near the rocky ridge where both subspecies were trapped. Three other mice caught in the dumpground were P. m. artemesiae.

The intermediate types collected at Babb and Windy Creek were trapped in areas where P. m. artemesia was not found. However, at both trapping sites possible habitat for P. m. artemesia is near by. At Babb, the banks of the St. Mary River and Lower St. Mary Lake and the coniferous forest at Windy Creek provide the suitable habitat. On the other hand, the intermediate form caught at the Baring Creek site was trapped several miles from the nearest known suitable habitat of P. m. osgoodi.

Discussion

One of the best studied and most widely distributed species of Peromyscus is P. maniculatus, which is distributed over most of North America except for the states of the southeast and the far arctic regions. Hall and Kelson (1959) described this species as consisting of a long series of intergrading populations. In some cases, subspecies with adjoining geographic ranges do not intergrade directly but theoretically intergrade circuitously through other subspecies.

The deer mice in the study area can be separated into two distinct morphological types which supports the current classification of mice in that area. The means of tail length, hind foot length, ear length, greatest length of the skull and nasal length are all significantly or highly significantly larger for P. m. artemesiaae than for P. m. osgoodi. The measurements for tail length and ear length exhibited little overlap in range, and they are the most reliable morphological criteria for distinguishing between subspecies. The hind feet of P. m. artemesiaae are generally longer than those of P. m. osgoodi but the difference is often difficult to distinguish. It is possible to separate the skulls of P. m. artemesiaae from those of P. m. osgoodi with reasonable accuracy without measuring them although the mean difference in greatest length of the skull is less than 2 mm. Although the mean difference is small, it is highly significant. The body length of P. m. artemesiaae, while averaging larger than P. m. osgoodi, cannot be used as a good diagnostic characteristic. The mean difference in body size is small and some populations of P. m. osgoodi have larger body size measurements than some of the P. m.

artemesiae populations. Similarly, mastoid breadth cannot be reliably used to distinguish between subspecies. Also P. m. artemesiae has in general a darker pelage than P. m. osgoodi. However, this characteristic was not used since pelage color reflects the climatic belts of the area and the color of the surface soils (Dice, 1939).

The longer tails and hind feet of P. m. artemesiae are probably an adaptation to their semiaboreal life in the woodland habitat (Horner, 1954). On the other hand, the shorter tails and hind feet of P. m. osgoodi probably reflect the cursorial life in a prairie habitat. Dice (1944) states, however, that there is no evidence to prove that tail length or ear size is actually an important factor in the survival of either form.

The change in morphological variation is abrupt in the study area. Populations and most individuals of different subspecies adjacent to the sympatric zone are easily distinguished by morphological features such as tail length and ear length. The abruptness of the morphological variation is related to the narrowness of the sympatric zone which is limited to the forest-groveland ecotone and may be due to the lack of significant hybridization in that narrow zone. There is an apparent cline of morphological measurements of each subspecies on either side of the sympatric zone. This is particularly noticeable when tail lengths are used as an example (Fig. 7).

There appears to be little hybridization across the sympatric zone. Only nine individuals trapped in the study area were of intermediate

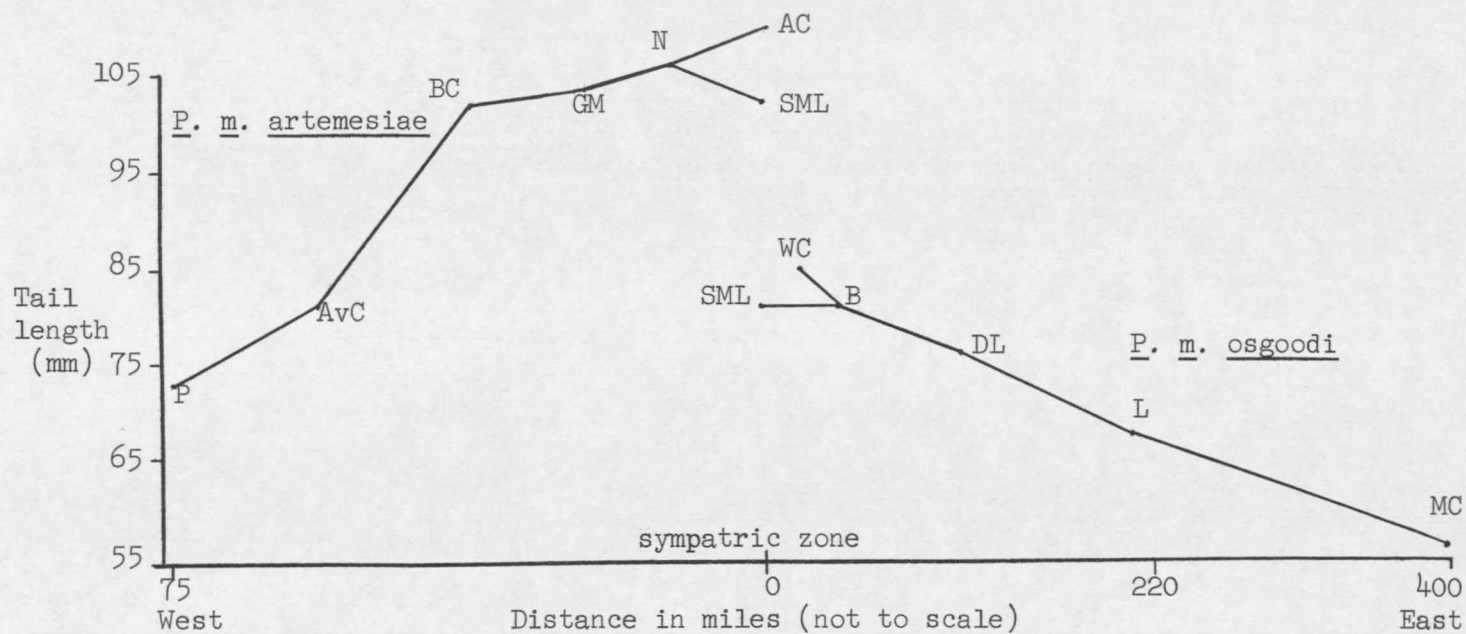


Fig. 7 Geographic variation in means of tail lengths of P. maniculatus across Montana

SML, St. Mary Lake; AC, Appekunny Creek; N, Narrows; GM, Goat Mtn.; BC, Baring Creek; WC, Windy Creek; B, Babb; DL, Duck Lake

P, Polson, Montana; AvC, Avalanche Creek, Glacier National Park; L, Lewistown, Montana; MC, Miles City, Montana From Dice, 1944.

size in some measurements (TABLE VII), and assignment to a particular subspecies was tentative. These nine mice may be hybrids or may represent extreme variants within the populations. Eight of the mice were caught in areas where contact between the two subspecies either was observed or was possible. The mouse trapped at Baring Creek, however, was trapped well outside the recognized sympatric area.

Intrasubspecific variation exists among populations, and some significant and highly significant differences do exist in some measurements. Variation would be expected as individual characters are seldom uniform throughout the whole range of any species or subspecies, even in areas with relatively homogenous environments (Dice, 1940).

In mammals variability of morphological characters is not due primarily to a direct influence of the environment but is based on hereditary variations (Dice, 1940). Blair (1950) states that a major factor in geographic differentiation of Peromyscus is the selection of genotypes by the environment. In regions of general environmental uniformity differences among populations may be expected to be small and in regions of environmental diversity interpopulation variation is likely to be large. The habitat found in the study area is variable and may account for some of the variability between and within populations.

Although Peromyscus is widely distributed in North America, they are chiefly inhabitants of woodlands, brushlands and pioneer stages of grassland development (Baker, 1968). The large geographic range of Peromyscus maniculatus reflects the variety of habitats to which the species is

morphologically, behaviorally and physiologically adapted.

Although P. m. osgoodi is classified as a grassland form and P. m. artemesiaae as a woodland form, both subspecies were usually trapped in or near rock piles, brushpiles and fallen trees, often in early seral stages. Mice of the subspecies artemesiaae are not limited to forest habitats; they were found in meadows within the forest zone where appropriate cover exists. Mice were not caught in areas of heavy ground cover such as in the mature aspen groves; in three hundred trap nights only one mouse, a P. m. osgoodi was caught.

The allopatric P. m. osgoodi inhabited two general habitats in the study area, the grassland and the aspen groveland. However, P. m. osgoodi were caught in the scattered coniferous trees that were found adjacent to the aspen groveland at Wild Creek. The allopatric area for P. m. artemesiaae lies within the coniferous forest zone.

The sympatric area lies along the aspen groveland-coniferous forest ecotone and includes the St. Mary Lake and Appekunny Creek sites. The area of overlap between the two subspecies is limited and is restricted to a contact where the coniferous forest meets the meadow of the groveland. Contact between the two subspecies occurs infrequently because of separation of suitable grassland and forest habitats in many places by bands of dense aspen groves or coniferous forests with dense undergrowth, neither of which provide favorable habitat for the mice. All three specific areas of contact found between the subspecies are small. However, St. Mary Lake road cuts, stream and lake banks and dump-

grounds in the sympatric zone offer avenues of potential contact between subspecies.

Selection for a specialized habitat in P. maniculatus does not seem to be accounted for by a food difference (Cogshall, 1928; Williams, 1959) or by temperature selection (Stinson and Fischer, 1963). Murie (1961) speculated that habitat selection may be related to physical structures of the habitat and Harris (1952) demonstrated habitat selection in highly artificial laboratory environments. Genetic and behavioral factors are apparently involved in habitat selection (Wecker, 1963). Competition may also be important in the distribution of closely related species of Peromyscus (McCarley, 1963).

For a circular overlap to exist the end-populations of a chain of interbreeding populations must meet but fail to interbreed due to isolating mechanisms. In the study area the failure of interbreeding may be attributed largely to the lack of contact between the two subspecies due to (1) somewhat different habitat requirements, and (2) to a buffer of heavy vegetation along the groveland-coniferous forest ecotone where relatively few mice are found. However, contact is made in some places, and some possible evidence of limited hybridization was found. In areas where separation of subspecies due to habitat preferences breaks down, behavioral differences probably contribute to reproductive isolation of the two subspecies.

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