NUMBER 270 JULY 1, 1933

OCCASIONAL PAPERS OF THE MUSEUM OF ZOOLOGY

UNIVERSITY OF MICHIGAN

ANN ARBOR, MICHIGAN THE UNIVERSITY OF MICHIGAN PRESS

THE ECOLOGICAL RELATIONSHIP OF TWO SUBSPECIES OF *PEROMYSCUS* IN THE GLACIER PARK REGION, MONTANA[1]

BY ADOLPH MURIE

INTRODUCTION

THE species of deer-mouse, *Peromyscus maniculatus,* found over a large part of North America, is made up of a number of subspecies or geographic races, which are assumed to intergrade either directly or indirectly. In general, the exact relationships existing between the subspecies in the field is unknown, for few detailed studies have been made to determine the ecological and genetic relationships where subspecies meet. Conditions existing where two subspecies meet are especially significant from the viewpoints of taxonomy, distribution, and evolution.

At St. Mary, in Glacier National Park, Montana, two forms of *Peromyscus maniculatus* occur. Here the range of *Peromyscus maniculatus osgoodi,* a prairie form, meets the range of *Peromyscus maniculatus artemisiae,* a forest form. Osgood (1909), in his classical revision of the genus, after an examination of 26 specimens from St. Mary, states that the two forms are apparently free from hybridization in this

[1] A condensation of a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the University of Michigan.

locality. They are called subspecies, however, because it is assumed that they intergrade indirectly through *borealis* to the north and *sonoriensis* to the south.

In the summer of 1927, from June 18 to September 13, while employed as a park ranger at St. Mary, I was able to secure some information on the ecological and genetical relationships of *osgoodi* and *artemisiae* in the region. The material was studied at the Museum of Zoology, University of Michigan.

I am indebted to President Alexander G. Ruthven, then Director of the Museum of Zoology, for his support and encouragement, to Dr. Lee R. Dice for valuable advice and criticism, and to Dr. C. V. Green and Dr. H. D. Bruce for helpful suggestions relating respectively to statistics and colorimetry.

Physiography

St. Mary lies on the eastern border of Glacier National Park in a valley about 20 miles long, extending from the continental divide to the open prairies. Glaciers have carved out 2 deep lakes, each approximately 10 miles long and having a maximum width of about a mile. St. Mary Lake lies near the head of the valley and Lower St. Mary Lake in the lower part. A small stream less than a mile long joins the 2 lakes.

At the head of St. Mary Lake the mountains rise abruptly from an elevation at their base of 4472 feet to an elevation of over 9000 feet. Farther down, the mountains rise more gradually and the valley widens out. At its mouth it is bordered by low wooded hills.

A narrow tongue of sagebrush prairie extends along both shores of Lower St. Mary Lake and continues along the west shore of St. Mary Lake for 5 miles before the forest replaces it. This tongue of prairie is perhaps nowhere more than a mile wide. The forests bordering it are composed mainly of Douglas fir, alpine fir, spruce, lodgepole pine, cottonwood, and aspen. At the upper end of the prairie where I did most of my trapping, the transition to forest is rather abrupt in most places (Fig. 1).

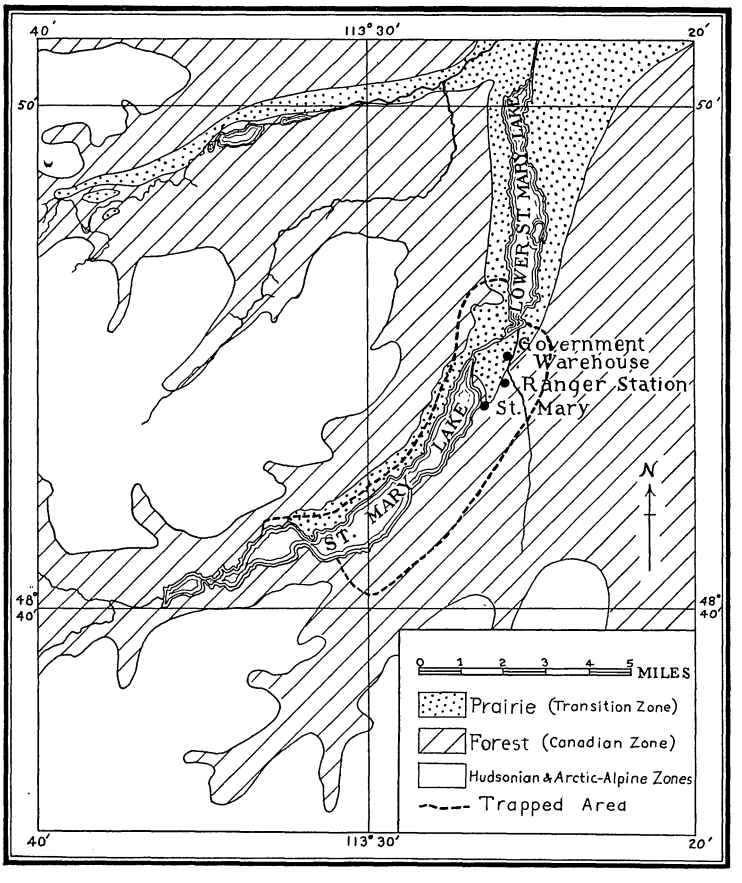

FIG. 1. Map of the St. Mary region (after Bailey, 1918) showing extent of the prairie and the approximate area trapped.

MATERIAL

Trapping was carried on chiefly at the north end of St. Mary Lake, for my duties as park ranger prevented me from spreading my operations. Intensive trapping was done where the prairie and forest meet, and in the adjacent prairie and forest, to determine how closely each subspecies is confined to its own habitat, and whether hybrids occur. Much

trapping was done in the buildings at the edge of the forest which harbored both subspecies.

The mice were all taken in live-traps of the "Delusion" brand, which proved very serviceable, for as many as 5 mice were sometimes taken at a time. The inner compartment of the trap was provided with a nest of cotton to keep the mice warm, but in spite of this precaution the mice were often found unconscious from exposure during the cold mountain nights. If not too nearly dead, mice in this condition often were revived by warming them in the hands.

A total of 551 *Peromyscus* were trapped alive in the St. Mary region. Of these, 112 are *artemisiae,* and 326 are *osgoodi.* The identification of 113 mice which escaped or died en route to the Museum was not recorded. The sexes are divided as follows: *artemisiae,* 42 females, 70 males; *osgoodi,* 150 females, 176 males; lost en route, 58 females, 55 males.

All of the adult mice, 26 *artemisiae* and 70 *osgoodi,* and a few of the immature mice, 35 *artemisiae* and 51 *osgoodi,* were killed and prepared as specimens on the day of capture. Of the immature mice kept alive, 137 *osgoodi* were killed the following May when a little less than 1 year old, and all of the *artemisiae* were killed a year later when nearly 2 years old. The *artemisiae* were kept alive 2 years in a futile effort to breed them.

The mice in the laboratory were fed a standard ration and kept under the conditions as described by Dice (1929).

Habitat Restriction

P. m. osgoodi and *artemisiae* were found to be closely confined to their respective habitats, that is, *osgoodi* to the prairie and *artemisiae* to the forest. This habitat restriction prevailed even on the west side of St. Mary Lake where one might expect some overlapping because of the narrowness of the strip of prairie bordering this side of the lake. In no instance was *osgoodi* taken in the forest and in but one was *artemisiae* captured in the prairie. This individual was taken in some road cribbing about a quarter of a mile from a lodge-

pole pine forest, the intervening distance, however, being somewhat shrubby.

P. m. osgoodi was exceptionally numerous in rock piles, cut banks along the road, in the cliffs, and under bridges. *P. m. artemisiae* was abundant at the borders of forest meadows, and along the lake shore where numerous retreats in the cliffs were available to them.

In buildings at the edge of the forest the 2 subspecies were found together. Both forms were found in the government warehouse, in the ranger station, and in the hotel buildings. At the hotel the 2 subspecies were at times taken in the same trap, but usually those found together in a trap were of the same subspecies. Generally those taken together were immature animals of about the same size and probably belonging to the same litter.

The position of the buildings in relation to forest and prairie seemed to determine the relative numbers of each subspecies in them. At the government warehouse, 6 *artemisiae* and 34 *osgoodi* were taken, at the hotel 50 *artemisiae* and 47 *osgoodi,* and at the ranger station 5 *artemisiae* and 7 *osgoodi.* A scraggly growth of trees 50 yards long extends from the forest proper to the warehouse. The relatively few *artemisiae* (6) taken at the warehouse is probably correlated with its partial isolation from its forest habitat, and the large number of *osgoodi* trapped is in accord with the greater availability of the building to the prairie mouse. The hotel and ranger station, both at the edge of the forest, appear to be about equally accessible, so it was rather to be expected that approximately the same number of mice of each subspecies should be taken at both places.

Why these 2 subspecies should be so closely confined to their respective habitats is difficult to say. Any one or more of a great many factors may be involved. Antagonism between species, which has been suggested as a limiting factor for some animals, does not seem to be an important factor at St. Mary, for in captivity the 2 subspecies live together peaceably, and in the field both inhabit and reproduce in the same buildings.

The almost complete infertility of *artemisiae* in captivity, in contrast to the high fecundity of *osgoodi,* suggests that the 2 subspecies differ in their physiological requirements for reproduction. These differences may have some bearing on the habitat distribution of the 2 forms but would not explain directly why individual mice so rarely wander out of their habitat. Before much headway can be made in the determination of causes of habitat restriction and its effect on geographical distribution, thorough ecological studies of the forms concerned must be made. Such studies may bring to light important factors which now are not even considered in relation to the problem.

Variability

In computing the averages, given in Tables 1, 2, and 3, the specimens of each subspecies are divided into two groups, "wild" and "captive." The group designated as "captive" consists of the mice which were trapped as immature animals during the summer of 1927 and kept in captivity a year or more. The mice designated as "wild" were trapped as adults in the field between June 18 and September 13, 1927, and prepared as specimens on the day of capture. The sexes are dealt with separately in all the computations except in the color analyses of "wild" *artemisiae.*

To insure all of the mice being in the same state of relaxation when measured, external measurements were taken a few moments after etherization. Foot length, ear length, and incisive foramen length were taken with a vernier caliper reading to .1 mm. All of the skeletal measurements, except incisive foramen length, were made with a micrometer reading to 0.01 mm. Most of the measurements used are described by Dice (1932: 6) and need not be repeated here. The following measurements were not used by Dice. *Incisive foramen length* is the greatest length. *Interorbital width* is the shortest distance across the orbital constriction. *Humerus length* is the greatest length, from the head of the humerus to the tip of the trochlea.

For the determination of color differences in the pelage the Ives Tint Photometer was used. By means of this apparatus it is possible to compare the brightness of the light of any particular color reflected from the pelage with the brightness of the light of that color reflected from a magnesium carbonate block. The magnesium carbonate block is used as a standard, for it has been found to reflect incident light almost non-selectively. Thus a reading of 10 for the red filter means that the pelage reflects only 10 per cent of the amount of red light reflected from the magnesium carbonate block. In order to facilitate making the color readings, the skins were put up flat by means of a stretching board (Sumner, 1927: Fig. 6) and degreased by a series of baths in cleaner's naphtha. The area of the pelage analyzed is approximately a semicircle 8 mm. by 17 mm. in the middle of the dorsal stripe beginning about 60 mm. from the tip of the nose. Readings were taken through the following color screens: red, yellow, green, peacock blue, and blue-violet. Further details concerning the operation of the Tint Photometer may be obtained from Sumner (1927) and Dice (1932). My methods differed somewhat from those of Sumner but were about the same as those used by Dice.

Effects of Captivity

The captive mice averaged slightly greater in foot length than the wild mice. The difference between the captive and wild *osgoodi* is .17 mm. in the females, .32 mm. in the males, respectively about 2 and 3 times their probable errors. The differences between captive and wild *artemisiae* is .69 mm. for the females and .20 mm. for the males, and the differences are approximately 3 and 1 times their probable errors. Although the differences are barely significant in only 2 cases, the fact that the captive mice average slightly more than the wild mice in each case indicates that there is a real difference present. Part of this difference in foot length is probably due to a difference in the amount of wear on the claws. It was noted that the wild mice had more wear on their claws than the captive mice, which had no opportunity to use their claws for digging.

TABLE I

AVERAGE BODY MEASUREMENTS OF *Peromyscus maniculatus osgoodi* AND *Peromyscus maniculatus artemisiae*, ST. MARY, GLACIER PARK, MONTANA

Stock	No.	Measurements in mm.				Weight gm.
		Body length	Tail length	Foot length	Ear length	
osgoodi	♀ 40	90.53 ± .31	77.47 ± .45	19.15 ± .08	17.22 ± .09	22.38 ± .38
(wild)	♂ 30	87.94 ± .45	77.46 ± .67	19.33 ± .08	16.84 ± .08	21.30 ± .26
osgoodi	♀ 51	85.36 ± .41	75.98 ± .45	19.32 ± .06	17.12 ± .07	21.28 ± .39
(captive)	♂ 89	86.71 ± .25	78.70 ± .30	19.65 ± .05	17.25 ± .05	24.12 ± .32
artemisiae	♀ 9	93.06 ± .91	101.39 ± 1.21	20.33 ± .22	19.23 ± .36	22.50 ± 1.20
(wild)	♂ 15	88.70 ± .50	101.50 ± .98	20.94 ± .13	19.18 ± .13	20.97 ± .28
artemisiae	♀ 14	90.21 ± .57	100.00 ± .83	21.02 ± .10	19.54 ± .09	19.50 ± .33
(captive)	♂ 21	91.42 ± .41	103.43 ± .53	21.14 ± .07	19.88 ± .10	23.04 ± .43

TABLE II

AVERAGE MEASUREMENTS OF SKULL, FEMUR, AND HUMERUS

Peromyscus maniculatus osgoodi AND *Peromyscus maniculatus artemisiae*

ST. MARY, GLACIER PARK, MONTANA

Measurements in mm.

Stock	No.	Skull length	Condyle-zygoma	Incisive foramen	Interorbital width	Femur	Humerus
osgoodi	♀ 35	24.30 ± .07	17.48 ± .04	5.24 ± .03	4.09 ± .02	16.75 ± .07	12.64 ± .06
(wild)	♂ 28	24.49 ± .09	17.56 ± .07	5.27 ± .03	4.02 ± .01	16.49 ± .09	12.95 ± .06
osgoodi	♀ 46	24.14 ± .07	17.27 ± .05	5.02 ± .02	4.11 ± .01	15.70 ± .08	12.18 ± .05
(captive)	♂ 85	24.38 ± .04	17.41 ± .03	5.11 ± .02	4.12 ± .01	15.88 ± .05	12.50 ± .04
artemisiae	♀ 9	25.55 ± .18	17.86 ± .13	5.83 ± .05	4.22 ± .04	17.49 ± .17	13.20 ± .09
(wild)	♂ 15	25.50 ± .10	17.63 ± .05	5.75 ± .05	4.39 ± .02	17.12 ± .16	13.08 ± .10
artemisiae	♀ 14	25.63 ± .10	17.61 ± .06	5.66 ± .04	4.22 ± .03	16.76 ± .16	12.93 ± .07
(captive)	♂ 21	25.78 ± .08	17.70 ± .06	5.81 ± .04	4.22 ± .01	17.32 ± .07	13.31 ± .06

TABLE III

AVERAGE COLOR OF DORSAL STRIPE

Peromyscus maniculatus osgoodi AND *Peromyscus maniculatus artemisiae*

ST. MARY, GLACIER PARK, MONTANA

Tint Photometer Readings

Stock	No.	Red	Yellow	Green	Peacock blue	Blue-violet
osgoodi	♀ 35	8.24 ± .18	6.83 ± .16	5.58 ± .13	4.88 ± .11	4.50 ± .11
(wild)	♂ 28	9.70 ± .27	7.79 ± .22	6.16 ± .20	5.27 ± .16	4.88 ± .15
osgoodi	♀ 47	10.44 ± .22	8.90 ± .19	7.40 ± .16	6.47 ± .13	5.70 ± .11
(captive)	♂ 87	9.93 ± .11	8.43 ± .11	6.85 ± .08	6.00 ± .07	5.44 ± .07
artemisiae (wild)	♀ + ♂ 26	7.20 ± .22	5.84 ± .11	4.68 ± .14	4.14 ± .11	3.68 ± .10
artemisiae	♀ 15	7.10 ± .30	6.13 ± .21	5.30 ± .11	5.13 ± .12	4.76 ± .13
(captive)	♂ 22	7.45 ± .15	6.88 ± .12	5.70 ± .14	5.45 ± .11	4.79 ± .12

The captive mice, in general, become more fat than do the wild mice. This is especially true for the males, some of which become exceedingly fat, so that some individuals may weigh practically twice as much as the average mouse. One extremely fat animal weighed 43 grams.

The pelage of the captive series averages lighter than that of the wild mice, but this may be a seasonal difference since the 2 series were killed at different seasons. The wild mice were in various stages of molt while the captive mice were nearly all in good pelage.

Apparently there was no stunting of the captive mice. The *artemisiae* kept 2 years average about the same as adult *artemisiae* taken in the field. The captive *osgoodi* average a little less than wild *osgoodi* in a few measurements, but this may in part be due to an average age difference between the 2 series, for the wild mice probably were older than the captive mice.

Differences between Males and Females

In foot length the males exceed the females consistently even in those series in which the females average more in body length. In the captive *osgoodi* series the males average .33 mm. more than the females, a difference 4 times its probable error. In the other three series the difference is not quite significant. Sumner (1924) and Dice (1932) have found this same sexual difference in other forms of *Peromyscus*.

In skull length there appears to be a tendency for the males to exceed the females.

In brightness of pelage there are sexual differences, but they are not consistent. In the captive *osgoodi* the females average brighter, but in the captive *artemisiae* and wild *osgoodi* series the males average brighter.

The innominate of the two sexes differs in shape, so strikingly, that the sex of a specimen can be definitely determined by a glance at this bone. The infero-posterior portion of the ischium is drawn out to a sharp angle in the females while in

the males this part of the ischium is rounded as shown in Figure 2. Because of this the females tend to average more than the males in innominate length.

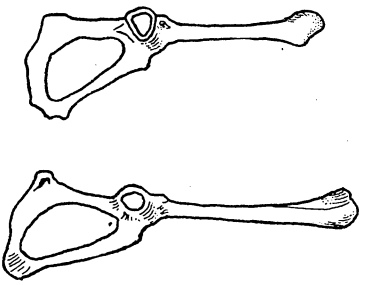

FIG. 2. Innominate bones of *Peromyscus maniculatus artemisiae*. The upper figure is of the male, the lower figure of the female.

DIFFERENCES BETWEEN *OSGOODI* AND *ARTEMISIAE*

As shown in Table I, *artemisiae* averages significantly greater than *osgoodi* in the external measurements of tail length, ear length, and foot length, so much so that these three measurements are diagnostic field characters. Comparing the wild *osgoodi* series with the wild *artemisiae* series, the average difference in tail length is about 24 mm. in both sexes, about 20 times its probable error in each sex; the average difference in foot length in the female is 1.18 mm., about 5 times its probable error, in the males 1.61 mm., about 10 times its probable error; the average difference in ear length in the female is 2.01 mm., about 5 times its probable error, in the males 2.34 mm., about 15 times its probable error. These differences are present in about the same degrees in the captive series.

In the skeletal measurements of skull length, incisive foramen length, interorbital width, and femur length there is a significant statistical difference in the wild series, averages of *artemisiae* being greater in each case. Again comparing the wild series, the average difference in skull length in the females is 1.25 mm., about 6 times its probable error, in the males 1.01 mm., almost 8 times its probable error; the average difference in incisive foramen length in the females is .59 mm.,

about 9 times its probable error, in the males .48 mm., about 8 times its probable error; the average difference in the interorbital width in the female is .13 mm., about 3 times its probable error, in the males .37 mm., about 18 times its probable error; the average difference in femur length in the females is .74 mm., about 4 times its probable error, in the males .63 mm., about 3 times its probable error. In humerus length *artemisiae* average more than *osgoodi,* but the differences are not significant throughout, although a real difference probably exists. If the captive *artemisiae* were compared with the wild *osgoodi* the differences would be about the same as in the above comparisons, for the averages of the two *artemisiae* series are very close except in femur length, in which measurement the captive females average smaller than the wild females.

P. m. artemisiae averages considerable darker in color than *osgoodi.* For each of the 5 color filters used in making the tint photometer readings, the darkest wild *osgoodi* series (females) averages brighter than the wild *artemisiae* series (sexes combined), the difference ranging from 1.04 units in the red to .74 units in the peacock blue, and being at least 3 times its probable error for each color filter. The differences would be considerably greater if the wild *artemisiae* were compared with the wild *osgoodi* males. Also in the captive series, the *artemisiae* average considerably darker than the *osgoodi.* In comparing the brightest *artemisiae* series (the males), with the darkest *osgoodi* series (the males), the two captive series which approach each other nearest in brightness, the differences range from 2.48 units for the red filter to .55 units for the peacock blue filter, these differences ranging from 13 times its probable error in the red to 4 times its probable error in the peacock blue and blue-violet.

In fertility under our laboratory conditions, *osgoodi* and *artemisiae* differed strikingly. Although *osgoodi* bred readily, only 2 of 16 pairs of *artemisiae,* mated for about a year and a half, produced any young. These 2 pairs each had a litter.

INTERGRADATION

In crossing 2 subspecies of *Peromyscus,* Sumner (1923 and 1925) found that F_1 and F_2 generations are more or less intermediate between the two parents in all characters by which the parents differ, so that if crossbreeding between *osgoodi* and *artemisiae* occurred at St. Mary one would expect a certain proportion of the mice to be of an intermediate character. In considering characters of two forms in which there is some overlapping but an average difference, a bimodal histogram would indicate the presence of two distinct populations while a trimodal histogram would indicate two distinct populations with a considerable third population of intergrades. If there is any character in which there is practically no overlapping of variability curves, it is almost certain that there has been no crossbreeding.

The plotting of measurements of the characters in which *osgoodi* and *artemisiae* differ, results in bimodal histograms. When the average difference is small there is much overlapping, and the bimodal character of the histogram is not as pronounced as it is where differences are larger.

Lack of intergradation is best shown in tail length where there is practically no overlapping. In the *osgoodi* series, wild and captive mice combined, tail length varies from 67 mm. to 91 mm., with the mean at about 77 mm.; in the *artemisiae* series, wild and captive mice combined, tail length varies from 90 mm. to 112 mm., with the mean at about 101 mm. The curves do not deviate far from a normal variability curve. In only two instances does an *osgoodi* have as long a tail as the shortest tail length found in the *artemisiae* series. These two long-tailed variants in the *osgoodi* series together with the two short-tailed *artemisiae,* with tail lengths of 90 mm., might be suspected of being intergrades. These mice were, however, in all other characters typical of the form to which they are allocated.

From inspection of individual specimens and plotting of the measurements in which *osgoodi* and *artemisiae* at St. Mary differ from each other, it seems quite certain that crossbreed-

ing in the area does not occur, or at most is of extremely rare occurrence.

An effort was made to cross *osgoodi* and *artemisiae* in the laboratory but without success. Forty-one reciprocal matings between the 2 subspecies produced no offspring during a period of over a year and a half. Since *artemisiae* scarcely bred in the laboratory *inter se,* offspring from crosses could not be expected.

In nature, it appears that the 2 subspecies of *Peromyscus* as they are found at St. Mary simply differ too much to interbreed. Although the forms have different habitats and thus are somewhat isolated, individuals of each subspecies have now much opportunity to intermingle and breed if they are so inclined. I refer particularly to the presence of the buildings at St. Mary where both forms occur together. Even before these buildings were erected, individuals from each subspecies no doubt often came in contact at the edge of the ranges. Lack of intergradation in the field may be due to psychological factors. Possibly each subspecies has a characteristic odor or some other trait which may be attractive to individuals within the one subspecies but repugnant to individuals of the other subspecies.

The relationships between *artemisiae* and *osgoodi* at other localities where their ranges meet is unknown. Perhaps they intergrade in some localities and remain distinct elsewhere. *P. m. artemisiae* varies much geographically, having a much longer tail at St. Mary than in most parts of its range. In tail length some specimens from Idaho which I examined averaged about 85 mm., from Grande Ronde, Washington, about 80 mm., from Okanagan, British Columbia, 80 mm., and from Ashcroft, British Columbia, 75 mm. Possibly *artemisiae* differs more widely from *osgoodi* at St. Mary than it does in other localities where the ranges meet. In such other hypothetical localities where differences between the 2 subspecies are less than those found at St. Mary, intergradation might occur. At St. Mary *osgoodi* and *artemisiae* are sufficiently distinct to be called species, either on the criterion of amount

of difference or lack of intergradation. Should intergrading forms presumably existing elsewhere be exterminated, these forms would have to be considered full species. Further critical studies at other points along the line of contact of the 2 subspecies are needed for a complete understanding of their relationships.

Summary

By means of live-traps 551 specimens of *Peromyscus maniculatus osgoodi* and *Peromyscus maniculatus artemisiae* were secured in the vicinity of St. Mary, in Glacier National Park, Montana.

It was found that in nature *osgoodi* is here closely restricted to a prairie habitat and that *artemisiae* is as closely restricted to a forest habitat.

An examination of individual specimens and a statistical summary of a number of measurements indicate that no crossbreeding occurs in the area.

Literature Cited

Bailey, Vernon, and Florence Merriam Bailey

1918 Wild animals of Glacier National Park. U. S. Department of the Interior, National Park Service, 21 pp., 37 pl., 1 folded map, 94 figs.

Dice, Lee R.

1929 A new laboratory cage for small mammals, with notes on methods of rearing *Peromyscus*. Jour. Mamm., 10, No. 2: 116–124.

1932 Variation in a geographic race of the deer-mouse, *Peromyscus maniculatus bairdii*. Occ. Pap. Mus. Zool., Univ. Mich., No. 239: 1–26.

Osgood, Wilfred H.

1909 Revision of the mice of the American genus *Peromyscus*. U. S. Dept. Agric. No. Amer. Fauna, 28: 3–285, 8 pl.

Sumner, F. B.

1923 Results of experiments in hybridizing subspecies of *Peromyscus*. Jour. of Experimental Zool., 38, No. 2: 245–292.

1924 The stability of subspecific characters under changed conditions of environment. Amer. Nat., 58: 481–505.

SUMNER, F. B. and R. R. HUESTIS
1925 Studies of coat-color and foot pigmentation in subspecific hybrids of *Peromyscus eremicus*. Biol. Bull., 48, No. 1: 37–55.

SUMNER, F. B.
1927 Linear and colorimetric measurements of small mammals. Jour. Mamm. 8, No. 3: 177–206.