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A POPULATION STUDY OF THE MEADOW MICE *(MICROTUS)* IN THREE SIERRA NEVADA MEADOWS*

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Introduction

The importance of information concerning the exact numbers of organisms in a natural organic community, and the factors influencing changes in such populations, have become more and more evident as ecological studies have progressed.

The present study is an investigation into the numbers of meadow mice (*Microtus*)† inhabiting three neighboring meadows in the Canadian Zone of the central Sierra Nevada of California, at an elevation of about 7,500 feet, during 1937, 1938, and 1939. This area was selected because the natural meadow habitat of *Microtus* was small in proportion to, and quite distinct in character from, the surrounding terrain, and it was hoped that the factors influencing the existence of the meadow mice could therefore be more easily recognized. The three meadows totaled nineteen acres and were in the proportion of about one acre of meadow to fifty acres of rocky surroundings.

Live trapping was employed and the individual mice were given distinctive marks by means of a system of toe clipping, were then released, and those recaptured provided the detailed data that are presented and analyzed in the following pages.

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† The two forms that are found in this area are: *Microtus montanus yosemite* and *Microtus longicaudus sierrae*. Throughout this report, these forms are referred to by the specific names only.

Consideration is given to total and relative numbers per unit area, methods of estimating these, extent of territory occupied by individuals, length of life, competition between species, and such other factors as seem to cause changes in the population. An examination is made as to the adequacy of the number of traps to determine accurately the number of mice and it is shown that except for the first year of this study, the number of traps was sufficient to indicate the total population with a fair degree of accuracy.

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DESCRIPTION OF THE AREA

GEOGRAPHY

The area studied is located about ten miles south of Lake Tahoe in Eldorado County, California, and is locally known as the Echo Summit area, and the meadows as the Benwood meadows. This area is on a bench of a thousand feet above and immediately west of the extreme southern end of Lake (Tahoe) Valley. Also the bench is a thousand feet below and immediately east of the crest of the Sierra Nevada at this point. A portion of this bench, including the three meadows under study, drains into Lake Tahoe and thence into the Great Basin, while another portion of the bench drains into one of the uppermost tributaries of the American River, and thence into the Pacific. U.S. Highway 50 passes over the divide immediately north of the three meadows.

GEOLOGY

The predominant rock is granitic and forms part of the great batholith of the Sierra Nevada. Due to uplift and consequent erosion, the former superincumbent sedimentary rocks have been largely stripped off, although not far distant, in the Glen Alpine Canyon, a portion of the old roofing is still in evidence in the form of highly metamorphosed slates. On the ridge south of the Echo Summit area, as well as in other places more distant, can be found remnants of volcanic outpourings that were extruded at different times during the Tertiary uplift. These extrusions, largely tuffs and breccias and some lavas, have been extensively worn away and now exist mainly as cappings on the higher ridges. They have been but little disturbed in attitude, and form nearly horizontal layers, tilted slightly to the west.

During the Pleistocene, glaciers occupied the high Sierra several times and left their unmistakable marks. The two lower Benwood meadows (1 and 2) are former morainal lakes, now in the last stages of filling, while Benwood 3 is a rock basin, also sediment filled, that was formerly scooped out by the glacier which descended from the cirque-like canyon on the south. The rock walls that rise steeply from all sides of this meadow except at the outlet serve to isolate it with a greater degree of sharpness than is found in any other meadow in this vicinity.

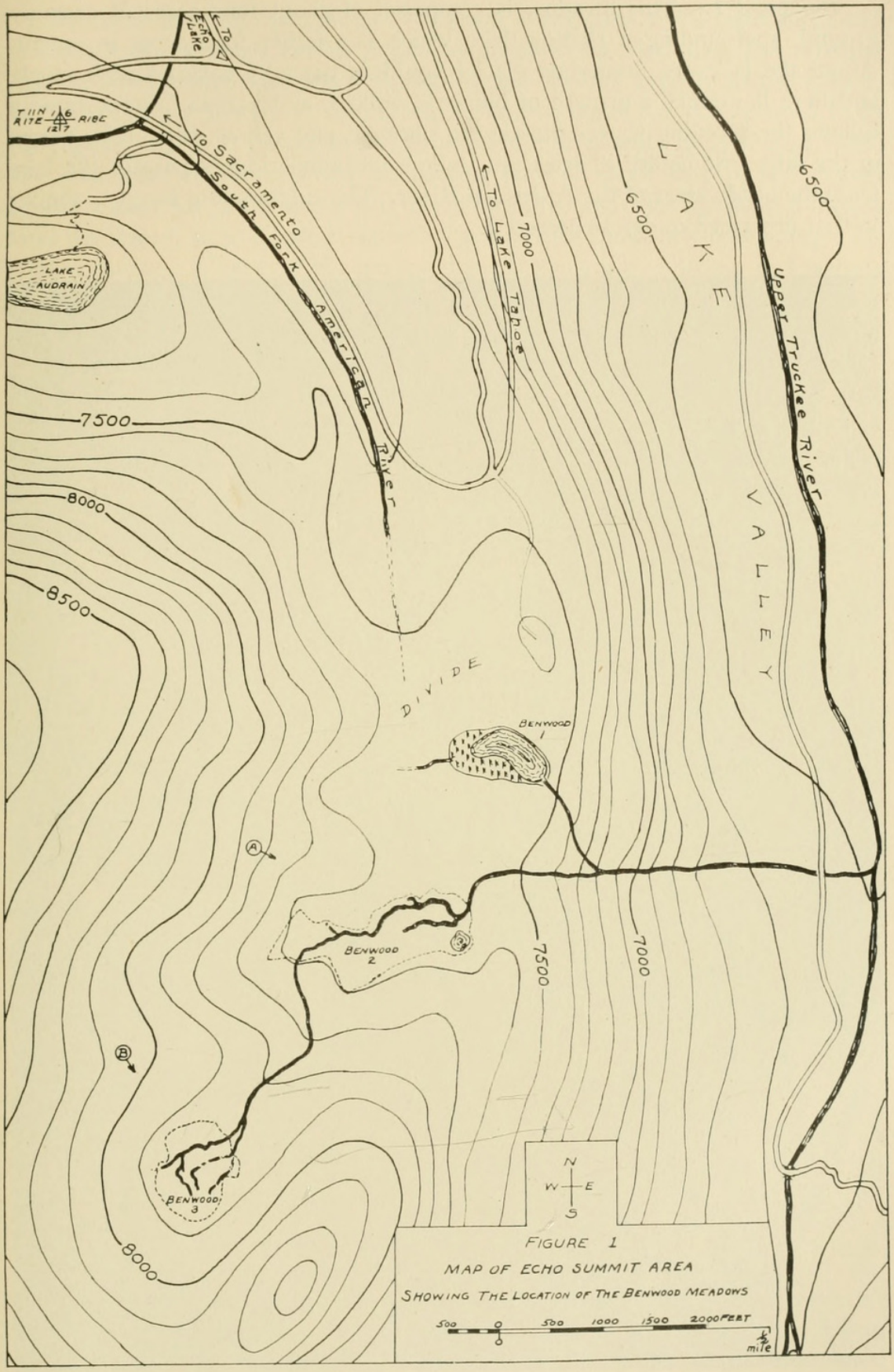

FIG. 1.—Map of Echo Summit area, showing the location of the Benwood meadows

Benwood 1.—This meadow is composed of about four acres of swampy ground, surrounding a shallow lake which is another four acres in extent. About the lake are numerous glacial boulders partially covered with muck, and here flourishes a growth of bilberry, willow, and kalmia. Carex rapidly follows the receding waters during the summer, and yellow water lilies bloom in the lake just before it dries up. A low morainal ridge separates the lake from the headwaters of the American River. The surrounding forest is similar to that described under Benwood 2.

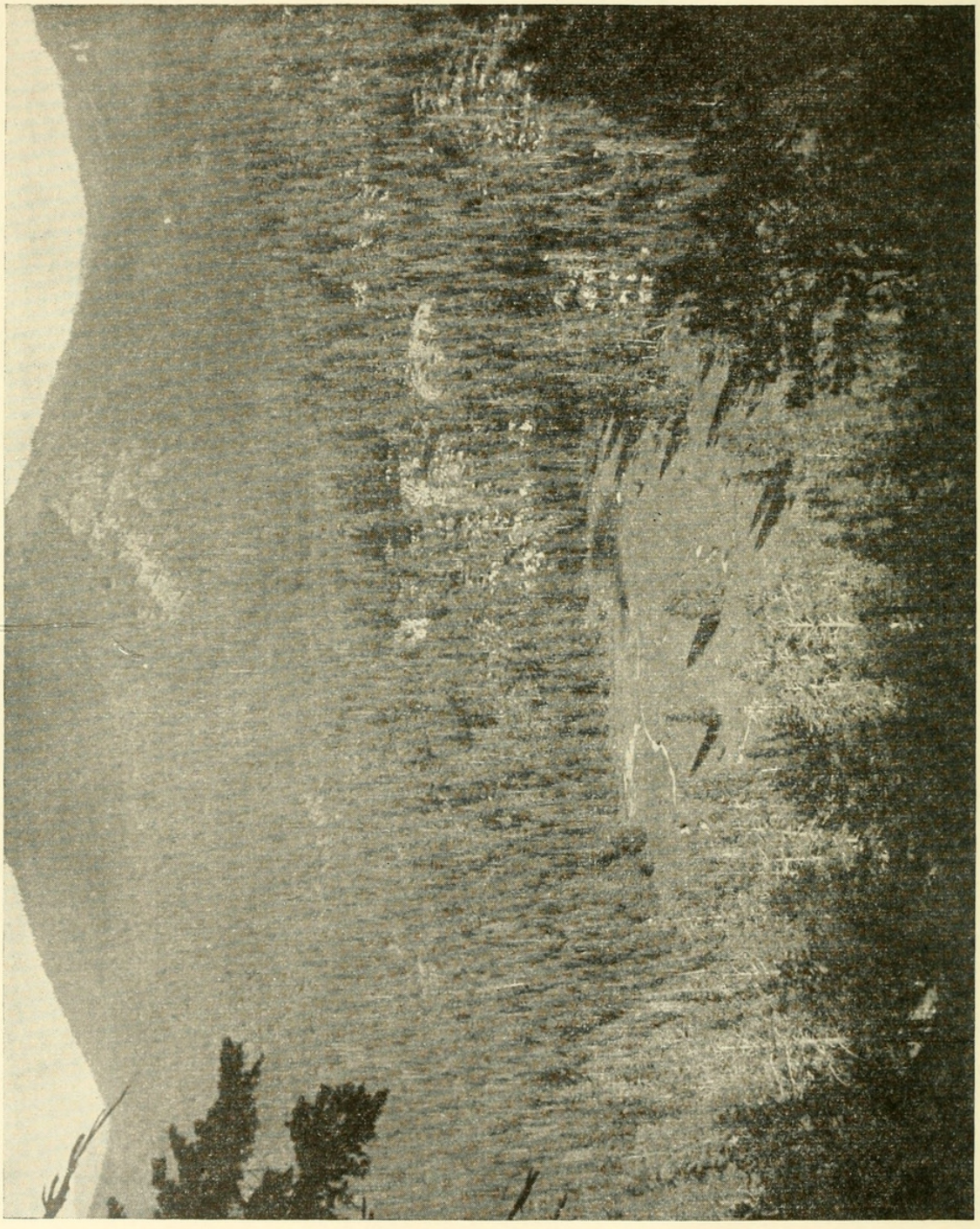

FIG. 2.—Benwood 2. Camera at location *A* on the map. August 22, 1937

Benwood 2.—The open part of Benwood 2 measures about eight acres and is quite level although cut in places by meandering streams. The streams assume flood proportions when the snows are melting rapidly in the spring, but stop flowing shortly after the last vestige of snow has disappeared from the higher ridges. This occurred in the middle of August in 1937 and 1938, and somewhat earlier in 1939. A shallow lake of about half an acre forms behind a sand bar at the lower end of the meadow and dries up about a month after the stream stops flowing. Meadow grasses are constantly competing with stream cutting. Whenever the stream changes its course, a strong turf fastens itself upon the old stream bed. Then when the stream comes back across a turfed area, cutting may start in some new spot, and a depression resembling a pot hole boils out and begins to cut headward. Reduction of flow gives the grass another chance to come in and reclaim the spot to turf. All over the meadow are depressions more or less grown over with grass. Some are completely covered by long bladed Carex growing luxuriantly, thanks to the added moisture in the depressions, while other depressions are clean-cut and filled with fine white sand left by the active stream.

As portions of the meadow become slightly better drained, lodgepole pine, the forest tree most tolerant of wet feet, invades the meadow. Willows and alders abound along the more permanent stream courses and at the edges of the meadow where incoming water seepage is held near the surface of the ground owing to the shallowness of the soil. Surrounding the meadow the predominant trees are lodgepole pine where the ground-water table is higher, then red fir, Jeffrey pine, and Western white pine. Juniper occupies the higher, drier rocky slopes, and, on the ridge eight hundred to a thousand feet above the meadow, alpine hemlock predominates. White fir is scattering and apparently has reached the limit of its altitudinal endurance.

Benwood 3.—This meadow contains seven acres and is about 300 feet higher in elevation than the other two meadows. It is more restricted in the sense that the meadow floor terminates abruptly as it reaches the rocky walls that surround it. Thermometer records showed, for the months of July and August 1938, lower maxima and minima than on Benwood 2, while for September the maxima were higher and the minima lower. The season appeared to be about two weeks later in Benwood 3 than in Benwood 2, judging from both relative temperatures and amount of ground moisture. The meadow bordered closer on the Hudsonian Zone than Benwood 2, as shown by a greater invasion of alpine hemlock. Otherwise the vegetation was about the same.

CLIMATE AND LIFE ZONES

The first snows in the autumn are sometimes followed by warm periods or rain, causing the snow to disappear quickly. Heavier storms may come in November, and the snow pack usually starts to form in December. From then on the pack increases, and a density equivalent to 30 or 40 percent

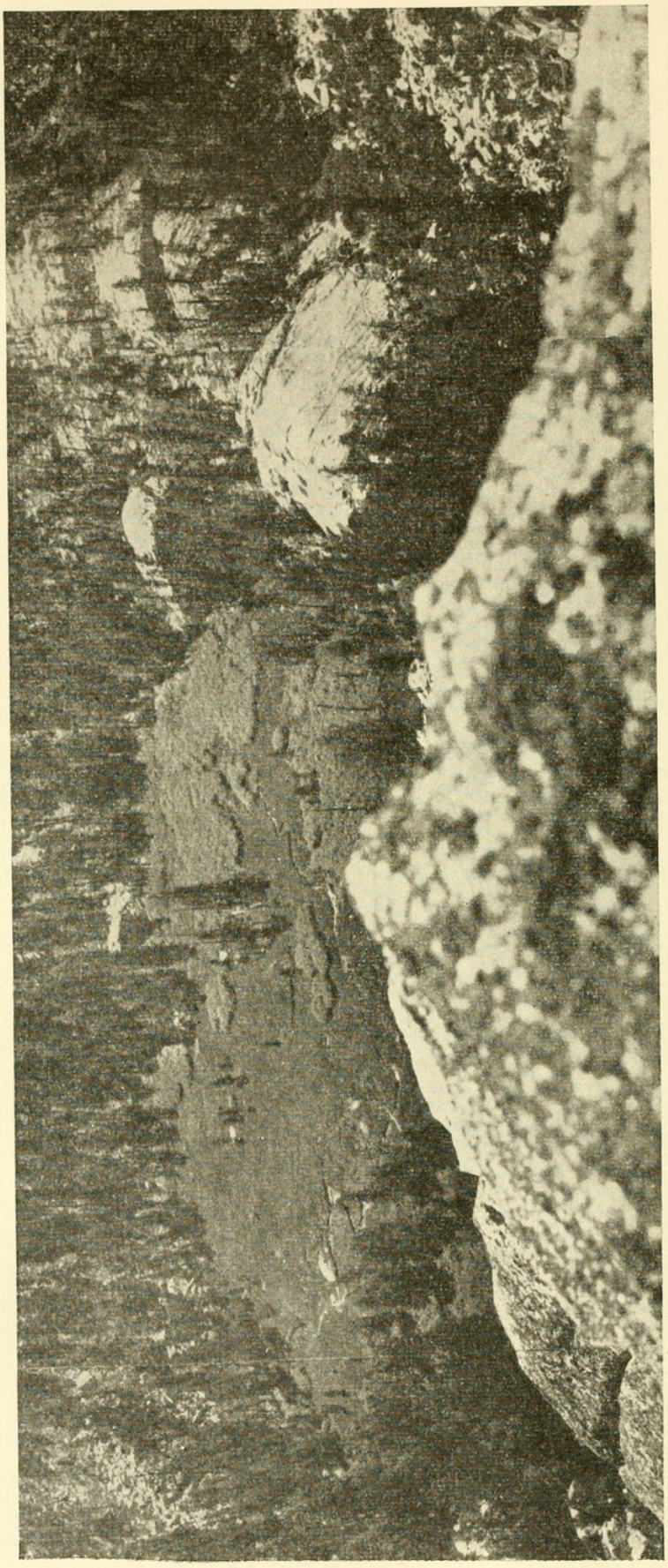

FIG. 3.—View of terrain, showing the restricted character of Benwood 3. Camera at location *B* on the map. August 5, 1938

of water may be reached. In April the snow may still be falling in considerable amounts, and by May or June it will start to melt and run off, owing to warmer weather and rainfall. By July usually the only snow remaining is that on the higher ridges, disappearing gradually through the summer. The following records from Twin Lakes, Alpine County, 7,970 feet, ten miles south of the Benwood area, are taken from the climatic summary of the United States Weather Bureau, 1930, Sec. 17, pp. 41 and 46.

Snowfall in Inches. 12-Year Average (1919–1931)

July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June	Seasonal
0	0	1.3	13.5	27.8	58.3	72.6	57.1	51.6	40.9	6.2	1.8	331.1

Total Precipitation in Inches. 11-Year Average (1919–1930)

July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June	Seasonal
.46	.24	.88	2.04	3.41	6.70	7.47	5.83	5.16	4.46	1.46	1.41	39.52

During the summer months (July, August, and September) the temperature is mild, ranging from about 70 and rarely 80 degrees F. in the middle of the day to 40 or 50 degrees at night. Occasionally the temperature drops at night to 32 degrees and a light frost may be seen on the meadows. At this time of year thunderstorms of short duration, and with little precipitation, may occur during the middle of the day but on the whole there is an abundance of sunshine.

The Benwood meadows are within the Canadian Zone as is indicated by the flora.

FAUNA

Only those vertebrates that seemed to have any ecological relation with *Microtus* are noted below and no attempt is made to present a complete list of all of the animals occupying the territory. Those which were observed are marked with an asterisk (*). The others listed are those which might be expected on these meadows.

Possible predators:

* *Accipiter gentilis.* Goshawk.
Accipiter striatus. Sharp-shinned hawk.
* *Buteo jamaicensis.* Red-tailed hawk.
Bubo virginianus. Horned owl.
Strix nebulosa. Great gray owl.
* *Cyanocitta stelleri.* Steller jay.
* *Canis latrans.* Coyote.
Vulpes fulva. Red fox.
* *Martes caurina.* Pine marten.
Mustela frenata. Long-tailed weasel.
* *Mustela erminea.* Short-tailed weasel. This diminutive predator no doubt takes a heavy toll on the mouse population of the meadows. In Benwood 2, three short-tailed weasels were collected, and another was captured, marked, and released. In Benwood 3 still another was collected.
Mustela vison. Mink.
Taxidea taxus. Badger.

Food competitors:

* *Peromyscus maniculatus.* White-footed mouse.
* *Thomomys monticola.* Pocket gopher.
* *Zapus pacificus.* Jumping mouse.
* *Citellus beecheyi.* Ground squirrel.
* *Citellus lateralis.* Golden-mantled ground squirrel.
* *Eutamias speciosus.* Tahoe chipmunk.
* *Odocoileus hemionus.* Mule deer.
* Domestic stock. Horses, cattle, and sheep.

METHODS OF WORK

General plan.—The field work for this study was carried on during the three summer seasons of 1937, 1938, and 1939. Occasional week-end visits were made to the area between the summers.

At first, forty-five live traps were made and tried out in Benwood 2. It was soon seen that these would be inadequate to give a true picture of the population of the meadow. One hundred additional traps were then constructed in camp and put into service as rapidly as possible.

During this same summer of 1937 a preliminary map was made of the area. This was followed up in the autumn of that year, and at times during the summer of 1938, with a more accurate survey. Transit and stadia rod were used to outline the meadows, locate the main features, and tie the meadows to one another and to the main highway. An observation was taken on Polaris to determine true North.

Within the meadows a plane table and telescopic alidade were used, setting up on stations previously determined by the transit and stadia rod. The trap locations in Benwood 1 and 3 were determined by this method, but in Benwood 2 hub stakes were set on corners of fifty-foot squares determined by stadia and engineer's tape. These hub stakes were further marked by lath which stood above the grass and made it easy to see location of traps as well as plant growth, stream cutting, gopher workings, etc.

Before starting field work in 1938, 300 live traps had been completed, which allowed the placing of 27 traps in Benwood 1, 176 in Benwood 2, and 80 in Benwood 3, and which also allowed a surplus to replace traps that got out of order.

Traps and trapping procedure.—The first traps used were patterned after that described by Moore (1936, p. 372, Fig. 1). A modification of this trap was adopted as shown in Figure 4. The advantages were: (1) longer can with more room, (2) square can to prevent rolling, (3) snap trap inside of can where ground moisture could not so readily affect the wooden base, (4) wire screen door for easier observation.

The traps were scattered over the meadows as evenly as possible. A greater number was placed in Benwood 2 than in Benwood 3 although the area of the two meadows was nearly the same. The results, however, seemed to indicate that the number in Benwood 2 was more than necessary, instead

of the number in Benwood 3 being inadequate. If the trap was in a position liable to receive the full force of the sun at some time during the day, it was covered with brush or with V-shaped board covers. Cotton was placed in the back of each trap to afford nesting material as a protection against cold. Rolled oats were used exclusively for bait. In 1937 the traps were visited three or four times a day, but in 1938 and 1939 once a day, in order to give time to cover a greater trapping area.

Mice taken from the traps were handled as follows: A wide-mouthed, Mason glass jar was held against the open door of the trap and the mouse was shaken down into the jar. It was then easy to transfer the mouse to a small cloth sack. By turning down the folds of the sack an examination of the parts of the mouse could be made without danger of escape or damage to the mouse or to the fingers of the observer. No anaesthetic was used. The procedure was first to weigh the mouse, measure the tail, determine sex, and then to examine for a previous mark, or, if the mouse were a new capture, to mark accordingly.

Marks were made by clipping the end of one or two toes at the last joint to represent numbers as indicated in Figure 5. This permitted the use of numbers up to 89. After that the numbers that had been given to mice that died were used over again without causing confusion. When these numbers became exhausted, combinations of two toes cut on front feet and none on the hind, or two on the hind and none on the front, served for identification and this was sufficient to care for all needs. Records were kept of date, time, trap

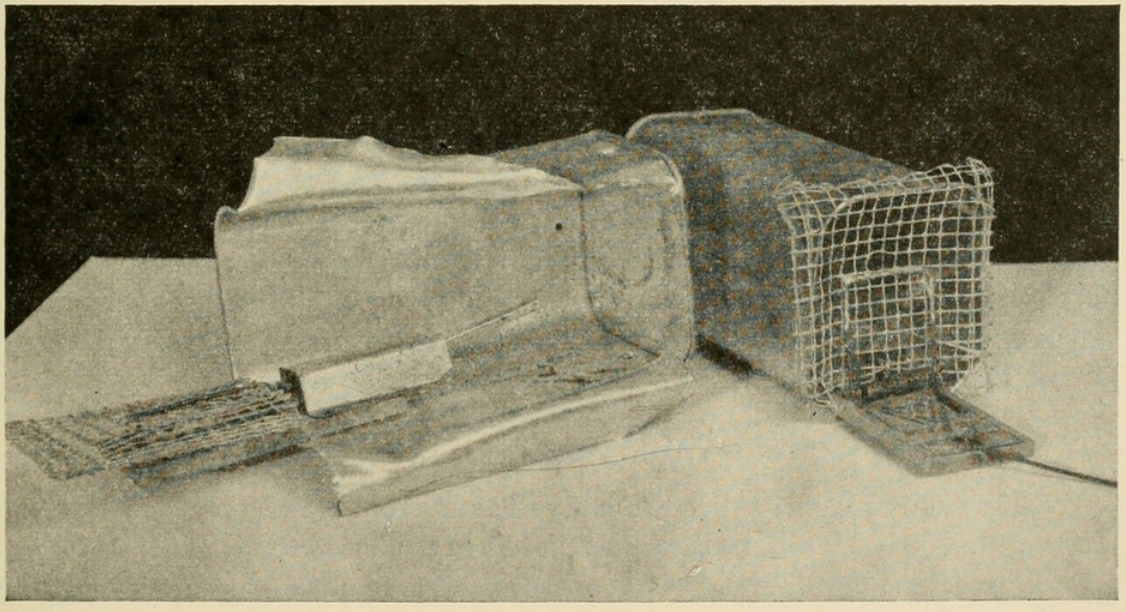

FIG. 4.—Live trap used in these operations, cut open to show: common snap trap fastened to inside of can; wire screen door soldered to loop on trap; extension treadle partially covered by guard to permit mouse to get well into can before springing. Can is 6¼ x 3½ x 3 inches and is known as an "asparagus can number 2½."

number, mouse number, sex, weight, and tail length. Separate pages were used for posting the records of each individual mouse. All records were carried in the field, and before a recaptured mouse was released the data were compared with past records as a check against the possibility of incorrect reading of the toe numbers.

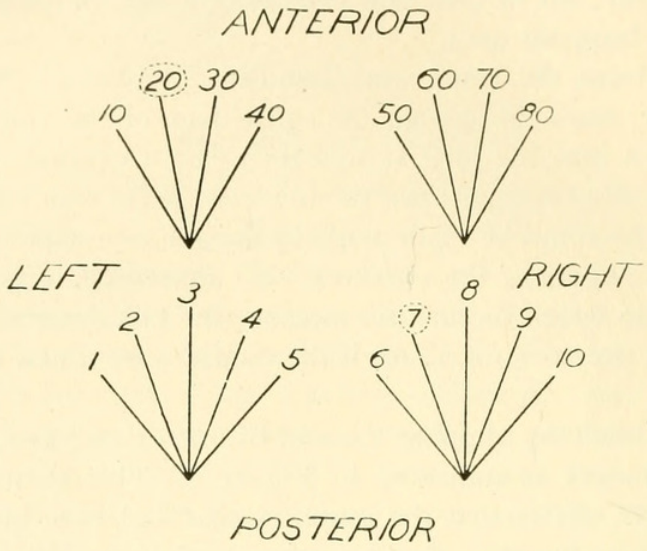

FIG. 5.—Diagram indicating the order of numbers assigned to toes. If those encircled by dotted lines were cut at the first joint that mouse would be recorded as No. 27.

Species identification.—Determination of weight and tail-length was necessary to differentiate *Microtus longicaudus* from *Microtus montanus*. Specific characteristics include a slight color difference, but this was difficult to be sure of when examining one mouse at a time, without a series for comparison, and especially out of doors under varying conditions of light and shade, and with a live, wriggling mouse. Tail length relative to body length is considered a good differentiating character by systematists. With a live specimen, tail length was easy to obtain by using the cloth sack as described, but body length could not be accurately determined without possible damage to the mouse. Therefore, weight was taken as a substitute for body length, and differentiation was easily made in every case. The relation between weight of mouse and length of tail for the two species is plotted graphically in Figure 6.

ANALYSIS OF DATA

Table I (p. 55) shows that 195 individual *Microtus* came under observation during this study. It will be seen that there were about twice as many *M. longicaudus* as *M. montanus* and one and one-third as many males as females. Within species limits, the *montanus* males outnumbered the *montanus* females by nearly two to one, while the *longicaudus* males were approximately one-fifth more numerous than the females. Other significant data are shown in this table, for later reference.

POPULATION DENSITY

In Figure 7 the total length of the bars indicates the cumulative first captures or, in other words, indicates the total number that had been marked, up to the date of record. After each first capture the mouse was marked and released and the methods of capturing, marking, and identification have already been described.

The length of the stippled portion of the bars denotes the cumulative number of mice that were found dead in the traps or that were purposely killed.

The difference between the cumulative first captures (total bar length) and cumulative known deaths (stippled portion of bar) would give the maximum possible number of marked individuals that could be at large on the meadow for any date indicated, and is represented on the chart by the distance

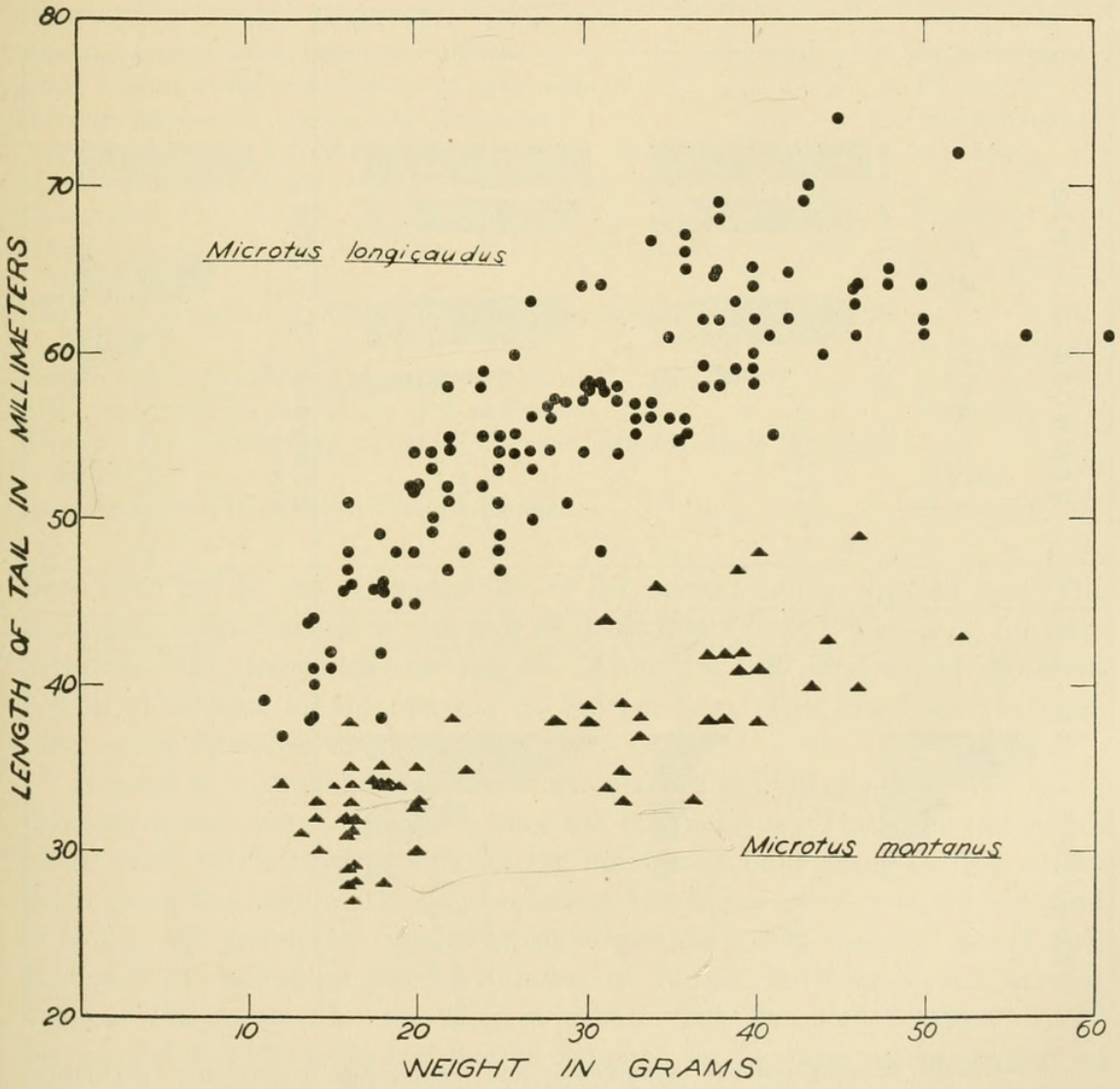

FIG. 6.—Graph showing relation between weight of mouse and length of tail for the two species.

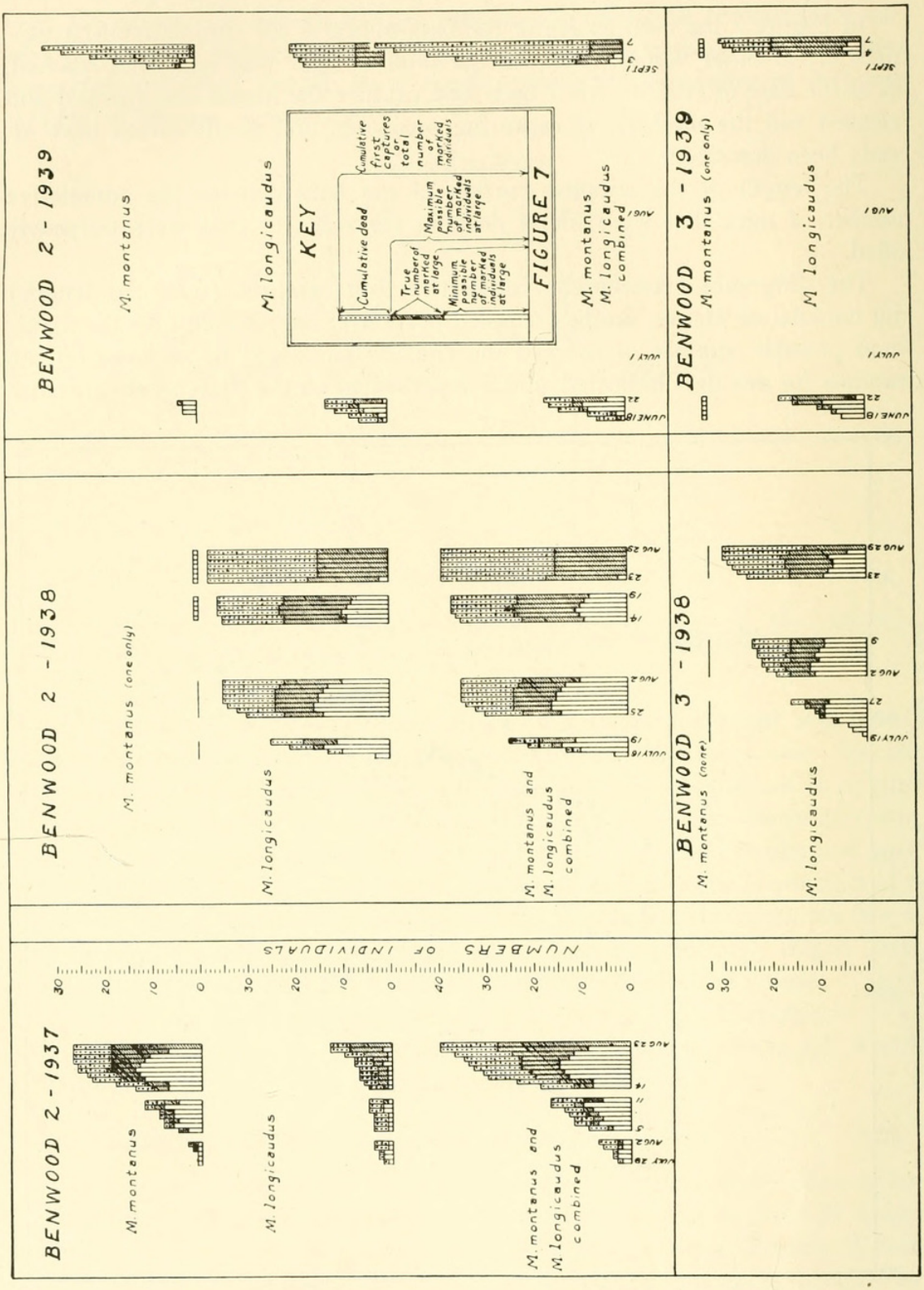

FIG. 7.—Graphs showing number of *montanus* and *longicaudus* trapped (i.e., population density) in Benwood 2 and 3 during 1937–1939

TABLE I

Number of *Microtus* captured:

	Males	Females	Total
M. montanus	41	21	62
M. longicaudus	73	60	133
Both species	114	81	195

Total number of acres trapped	19 acres
Maximum number of traps operated at any one time	283 traps
Average number of traps per acre	15 traps
Number of seasons (1937–1938–1939)	3 seasons
Total number of season-acres (1 x 4, 3 x 8, and 2 x 7)	42 season-acres
Total number of days of trapping	70 days
Maximum distance in a straight line between the outside edges of the three meadows	5,800 feet
Total number of trap-days (one trap-day equals one trap in operation 24 hours from noon to noon	10,839 trap-days
Total number of captures (including recaptures)	645 captures
Average number of trap-days per capture	16.8 trap-days
Total number of different individual mice captured	195 mice
Average number of trap-days per individual	55.6 trap-days
Average number of individual mice per acre per season in all meadows	4.55 mice
Maximum number of individuals per acre for any meadow (as found on Benwood 2)	6.5 mice
Minimum number of individuals per acre for any meadow (as found on Benwood 1)	2 mice
Number of times each individual was caught: minimum 1; maximum 15; average	3.3 times caught
Known dead (including those purposely killed)	113 mice
Same, expressed in percent of total individuals	58 percent
Known dead (found dead in traps and not including those purposely killed)	73 mice
Same, expressed in percent of total individuals	37 percent

from base line to top of shaded bar or the bottom of the stippled bar. The maximum point reached by the tops of shaded bars is at Benwood 2, for total *montanus* and *longicaudus* on August 22 and 23, 1937, and would represent a total of 28 mice for the meadow or 3.5 per acre. This is referred to hereafter as the "possible maximum."

It must be assumed that some of the marked individuals died after being released or that they might even have left the meadow. Therefore the length of the clear bar is used to indicate the number of individuals that up to the dates given had been marked and released, but which were certainly not dead or lost as was proved by capture at some later date. This number would then represent the minimum possible number of marked individuals that were at large on the meadow for the dates indicated. This number, of course, would be reduced to zero on the last day of trapping, for the obvious reason that no more subsequent recaptures were made, and therefore there could be no proof that the mice were still living.

The true number of marked mice at large on the meadow must then lie somewhere in the shaded bar between the top of the clear bar and the bottom of the stippled bar, for any date indicated, and lacking further evidence, one may make an arbitrary assumption that the true number of marked mice at large lies nearest to the mid-point within this shaded area. This mid-point reaches its peak of 20 mice on Benwood 2 on July 26 and 27, 1938, or 2.5 mice per acre. This figure may then be taken as the best estimate of the maximum number of marked mice that were at large at any one time on any meadow. This is referred to hereafter as the "probable maximum."

To recapitulate, we have the following figures for the three Benwood meadows for the summer seasons of 1937, 1938, and 1939:

Number of marked *Microtus* per acre at large at any one time on any meadow:

Possible maximum	3.5 mice per acre per season
Probable maximum	2.5 mice per acre per season

Number of *Microtus* per acre, cumulative for any entire season:

Average for all three meadows and three seasons	4.55 mice per acre per season
Maximum in Benwood 2, 1939	6.5 mice per acre per season
Minimum in Benwood 1, 1938	2.0 mice per acre per season

An examination will now be made of the adequacy of the number of the traps used, in giving a true picture of the total numbers in the Benwood area.

It will be noted upon referring to Figure 7 (total *montanus* and *longicaudus* combined, Benwood 2, 1937), that the curve representing cumulative total captures rose steadily during that season. This was the first year of trapping, and because some of the traps had to be manufactured in the field, they were only gradually placed in operation, starting with 45 or 5.6 per acre at the beginning of the season and increasing up to 140 or 17.5 per acre at the end of the season. Therefore the steady rise in captures was due in part to the increase in the number of traps.

The graph for Benwood 2, 1938, represents the effect of applying the full number of traps (176 total or 22 per acre) at the beginning of the 1938 season. Here will be noted a sharp rise in cumulative captures at first, and then a flattening off of the curve toward the end of the season. During the last week 103 additional traps were placed in the meadow, and all mice captured in any traps were purposely killed. This was done in order to test thoroughly for total population at this time, and in spite of the added trapping efforts, no new individuals were discovered. This seemed to indicate that the number marked very closely approached the total population. Another point of interest was that, during the first two days of this final week, only eight recaptures (of marked mice) were made. During the following five days of trapping with 279 traps operating on eight acres, there were no captures of *Microtus* at all. This would seem to indicate that only eight *Microtus* were at large on the meadow at the beginning of this final week. At the date August 23, 1938, the number eight will be seen to lie very close to the middle

of the shaded bars, the upper and lower limits of which indicate the estimated maximum possible and minimum possible number of marked mice that could be at large. This then would seem to substantiate the assumption that the mid-point of the shaded bars gives the best estimate of the true number of marked mice at large.

In Benwood 3, 1938, the number of traps was increased from 60 to 80 in the first two weeks, and here the curve of cumulative captures rose steadily, seeming to indicate the effect of the increased trapping effort. The curve finally flattened off but not so early in the season as with Benwood 2, 1938, and also at a slightly lower level. It was further noted in Benwood 3, 1938, that the total captures (including recaptures) per acre per day were exactly the same as for Benwood 2, 1938, while the total marked (or first captures) for the season, for Benwood 3, 1938, were but 88 percent of the total marked for Benwood 2, 1938. This would seem to indicate that the 80 traps on Benwood 3 (11.4 traps per acre) were enough to ascertain the true population, while the 176 traps on Benwood 2 (22 per acre) were not only enough but included a surplus that insured a fair record of the whole population.

To conclude, then, we can assume that by the end of the 1937 season and for the 1938 and 1939 seasons the number of traps was sufficient to indicate the total populations with a fair degree of accuracy, and the number of *Microtus* at all times was not over 6.5 mice per acre per season, or to express this in round numbers, was not more than 10 per acre per season.

This figure seems surprisingly low. Published records of the density of population of *Microtus* in other localities are given in Table II, page 58.

It is interesting to note in the records quoted, that the excessively high numbers, of over 1,000 per acre, were termed "plagues" by the authors. Numbers of over 100 per acre occurred during periods which the authors thought to be the peaks of population cycles. I suggest, then, on the basis of my figures for the two species dealt with in this paper, that less than 10 per acre may be taken as an indication of borderline living conditions continually threatening local extinction.

The factors in these borderline living conditions that restrict population increase in the Benwood meadows to this low number of less than 10 per acre are probably as follows, listed in the order of importance:

1. *Predator control.*—This is very likely the chief limiting factor for mouse populations here, although the evidence was not complete. The total area of the three meadows is nineteen acres and they are surrounded by a much larger extent of wooded, brushy, and rocky country, which is not adapted to the life of the meadow mice but which does form a natural habitat for several predators. The areal proportion of meadow to nonmeadow in this general region is 1 to 50 or more. One can imagine that the weasels, badgers, coyotes, or other predators of this region might regularly make the rounds of the meadows in order to pick up some small morsel of mouse flesh, so easily caught. Evidence of this is in the presence of the three weasels (*Mustela*

erminea) that were caught in Benwood 2 in 1937 and the one in Benwood 3 in 1939. Quantitative data regarding weasel populations and feeding habits are quite meager, yet the high potential mouse predator value is very obvious. It concerns an animal which is small enough to enter a mouse runway, and which was found in my experiments during a short period of captivity to consume more than one mouse per day. Coyotes and pine martens were seen at no great distance, and what were thought to be badger diggings were noted in the meadows. Other predators are known to inhabit the Sierra Nevada at this elevation and may have invaded this territory. In the light of this evidence, I assume the predators to be the chief controlling factor of increase in population.

2. *Climatic control.*—Climate is probably favorable most of the time but may occasionally act suddenly to the great disadvantage of the mice. Accumulated snow merely followed by a gradual melting in the spring is probably not very detrimental to the mice. Tunnels were found under the snow where food had been stored in the form of grass roots and other preserved plant materials. Slight differences in the ground level could afford sufficient escape from water saturation, and thus moderate rainfall and gradual melting of snow might work no hardship. However, climatic extremes will undoubt-

TABLE II

PUBLISHED RECORDS OF *Microtus* NUMBERS

Authority	Species	Country	Authors' figures converted to number per acre
Pidoplichka as reported by Vinogradov (1934)	*M. pelliceus*	U.S.S.R.	2½
Wooster (1939)	*M. haydeni*	Kansas	0 to 4
Seton (1909, p. 522)	*M.* [*pennsylvanicus*] *drummondi* plus *M. minor*	Manitoba	16
Merriam (1884, p. 274)	*M. pennsylvanicus*	Adirondacks	23
Hamilton (1937*b*, p. 789)	*M. pennsylvanicus*	Northeast United States	15 to 40 (low) 50 to 250 (high)
Townsend (1935, p. 96)	*M. pennsylvanicus*	Central New York	2 to 67
Elton, Davis and Findlay (1935, p. 279)	*M. agrestis*	England	50 to 250
Selle (1928)	*M. californicus*	Kern County, California	4,000
Piper (1908)	*M. montanus*	Humboldt Valley, Nevada	8,000 to 12,000
Hall (1927, p. 192)	*M. californicus*	Kern County, California	12,342

edly reduce populations, as for example, a sudden downpour of rain and resulting flood conditions such as are described later. Another condition that could cause particular hardship to the underground forms, although we have no actual record of such an occurrence in this area, would be a hard freeze following quickly after the meadows became water-saturated.

3. *Food control.*—As long as predators, plus any adverse climatic conditions, hold the number of mice to a low level, the food factor would not be operative. Apparently the food was very abundant in proportion to the numbers of mice observed, and no evidence was noted of a depleted supply. Only if and when the numbers of mice became greatly increased could food be a limiting factor.

4. *Disease* was not observed. The mice seemed in good physical condition when they had not been in the traps too long. No doubt scarcity of population makes infection less likely, while abundance of food and elimination of the weaker by predators and climate would make for selection of the healthier individuals.

Species Differences

Figure 7 not only shows the differences in total population density of *Microtus,* but also indicates certain significant differences in the numbers of the two species. In brief, *M. montanus* shows greater yearly differences in numbers, and apparently is more sensitive to environmental changes than is *M. longicaudus.*

On Benwood 2, in 1937, the numbers of *montanus* exceeded those of *longicaudus* two to one, and in 1938 *montanus* had disappeared until the end of the season, when a single female appeared and was caught seven times in nine days. No other *montanus* were taken that season, although *longicaudus* had increased in numbers. In seeking for an explanation it is noted that in December 1937 a sudden downpour of rain occurred in this region. Records from the United States Weather Bureau showed for Twin Lakes, ten miles south of Benwood 2, on December 10, 3.82 inches of rain in 24 hours, and on December 11, 3.58 inches. Locally the forest rangers and others reported excessive flooding in the meadows and streams. Check dams and trails where present were washed out and meadows were heavily flooded. An animal that was largely restricted to the meadow would be fairly caught and drowned out. Grinnell (1939) noted a marked depletion in the terrestrial mammal population of northeastern California following this same storm.* In 1938 the golden-mantled ground squirrels had completely disappeared from the Benwood area, while the tree-dwelling Tahoe Chipmunk showed no diminution in numbers. *M. montanus* has been found inhabiting burrows and making use

* Dr. Grinnell refers to this storm as occurring on "December 10" preceding "June 1937," therefore indicating the date of the storm as December 10, 1936. Mrs. Hilda W. Grinnell writes me as follows: " 'June 1937 . . . .' should have read 1938. It was a misprint which we ourselves overlooked when reading proof, but noted in the printed article."

of runways, while *M. longicaudus* was never found using burrows or runways. Also, as is shown farther on in this article, the range of *montanus* proved to be restricted to smaller areas than *longicaudus*. *M. montanus* was not found to leave the meadow, while at least three individual *longicaudus* were noted to have left one meadow and entered another during the time of the field observations. Grinnell and Storer (1924, p. 130) noted that *longicaudus* "lives chiefly along the banks of swift-moving mountain streams and in marshes, but also on dry hillsides at some distance from water." Thus the indication is that *montanus* was caught and nearly eliminated from Benwood 2 in the winter of 1937–38, while *longicaudus* was able to come back probably from the surrounding higher ground. It is interesting to note that one *montanus* female did come into this meadow late in the summer of 1938, thus showing the difficulty of a complete extinction of this type of animal.

At the end of the 1938 summer, all *Microtus* of both species that were taken on Benwood 2 during the last seven days of trapping were purposely killed in order to see what the effect would be upon the next year's population. There was no storm of sudden flood proportions during the winter between 1938 and 1939, and apparently, in spite of the artificial reduction in numbers in the late summer of 1938, enough mice escaped to bring the population back in 1939 to 6.5 per acre.

Just why Benwood 3 showed no *montanus* in 1938 and but a single specimen in 1939 is not clear. It is quite probable that if there were any *montanus* in that meadow in 1937, the storm of December 1937 destroyed them, just as it did in Benwood 2. It is possible that the restricted physical nature of Benwood 3 made the storm more effective in drowning out the meadow-dependent *montanus* and also in making it more difficult for them to migrate from other localities, while the wider-ranging *longicaudus* could more easily come in and fill the niche left by those destroyed.

BREEDING AND LENGTH OF LIFE

Most collectors of mammals are at work during the summer only, therefore their many published records concerning specimens containing embryos only tell us that breeding goes on in the summer, as we might well guess. However, the painstaking work of some recent investigators sheds light on this important phase of the life history.

In England, John R. Baker and R. M. Ranson (1933) collected *M. agrestis* each month for two years, and from 2,500 specimens taken, determined that this species has a well-marked breeding season from mid-March to late September (rarely February and October), with no evidence of breeding in the winter (November, December, and January).

In central New York, W. J. Hamilton, Jr., (1937*b*, p. 785) found *M. pennsylvanicus* commonly breeding from mid-March until mid-November. He noted further that although the mice do not customarily breed during the winter months (December to February), yet in a year of greatest mouse

abundance the animals continued to produce young throughout the winter. At the same time, however, there was a considerable decrease in litter size and frequency of breeding. These facts have considerable bearing on the problem of cycles of population and mouse plagues.

During the three seasons of investigation on the Benwood meadows and out of a total of 62 marked *M. montanus,* none was recaptured during a second season. Of 60 female and 73 male marked *M. longicaudus* only 3 male *longicaudus* were recaptured during a second season. This would seem to indicate that the *Microtus* seldom live more than a year, due very likely to their early attainment of sexual maturity, extreme prolificness, and high metabolic activity, as has been noted by several authors. I found pregnant females as late as September, and it is quite possible that breeding continued much later in the fall. The last litters which escaped marking were probably those that made up the breeding stock for the next year.

The Size and Character of Individual Ranges

Field observers have inferred that the home range of the meadow mouse was quite restricted. Seton (1909, p. 522) gave as his opinion that "the home range of the individual [*M. pennsylvanicus drummondi*] is probably less than 50 feet across. I have seen an isolated hollow of that size which was obviously the whole world of a dozen or more of these Mice."

Hamilton (1937*a*) arrived at very nearly this same figure after recapturing 100 of his 600 marked mice. He stated (p. 263) that "the home range of an individual vole seldom encompasses an area in excess of 1/15 of an acre [about 54 feet across] . . . . [Also on p. 261.] The results of this study point to a very limited home range, even in extensive areas of similar habitat. Males wander more widely than females, and are more likely to take up residence in new areas which have been previously unpopulated by the species. This is in keeping with the 'wandering tendency' theory proposed by Townsend (1935)."

My own records on the Benwood meadows showed that, with the exception of three individual mice, the average size range of all *Microtus* was an area with a diameter of 163 feet, increasing to a maximum diameter of 820 feet. The method of obtaining the field data has been described. Each catch was recorded by exact location and the position plotted on a large scale detailed map of the meadow. This gave for each individual mouse a series of points on the meadow where the mouse had at some time been found. Although it would never be possible to obtain a complete record of the area ranged over by any individual, it was desirable to obtain a measure of the range that would be reasonably comparable in indicating differences in size of ranges between sexes, species, etc.

To connect all of the points where an individual had been found would be to describe a geometrical figure with a measurable area. But since this area would become zero whenever all of the points happened to lie along a straight

line, comparison by this method would obviously be of little use. To measure the length of the broken line connecting all points would also be a poor measure, since an individual if caught often enough in a small area might show a longer total line than one that was caught but twice, even though the two captures were far enough apart to suggest a much greater width of range.

It was finally decided to use as the factor that would probably come nearest to expressing the comparative extent of ranges, the distance between the two points of capture that were most widely spaced, or in other words, the maximum diameter of the observed range. These distances were then scaled off on the large scale maps and recorded for each individual. A summary of these records is given in Table III, but with omission of all cases where but one capture was made, since in such cases there could be no opportunity to determine the size of the range. In cases where an individual mouse was each time captured in the same trap, the record was retained but the range was recorded as zero.

TABLE III

SIZE OF RANGES OF *Microtus*

Grouping	Number of Individuals	Length of Record in Days		Diameter of Range in Feet	
		Average	Extremes	Average	Extremes
Total *Microtus*	113	12.6	2 to 50	163	0 to 820
Total females	53	14.3	2 to 47	144	0 to 730
Total males	60	11.0	2 to 50	179	0 to 820
Total *montanus*	27	12.2	2 to 47	115	0 to 410
Total *longicaudus*	86	12.7	2 to 50	177	0 to 820
M. montanus females	11	12.5	4 to 47	82	0 to 360
M. montanus males	16	12.0	2 to 47	138	0 to 410
M. longicaudus females	42	14.8	2 to 46	161	0 to 730
M. longicaudus males	44	10.7	2 to 50	194*	0 to 820*

* These figures are for ranges within the meadow. Three individuals, all male *longicaudus*, were found to have left one meadow and to have appeared in another meadow. In two of these cases the distance covered (measured in a straight line from one meadow to the other) was 3,000 feet and in one case the distance was one mile.

From Table III it is seen that males have a wider range than females in both species, and that *M. longicaudus* has a wider range than *M. montanus* in both sexes, and even the *longicaudus* females have wider ranges than the *montanus* males.

To determine whether the ranges as given in Table III express the full size of the natural range of the species and sex groups of *Microtus,* Figures 8, 9, 10, and 11 may be examined. Here the diameter of range in feet for each individual is plotted on the y axis as against the time or length of record in days on the x axis for each of the following groups:

M. montanus females
M. montanus males
M. longicaudus females
M. longicaudus males

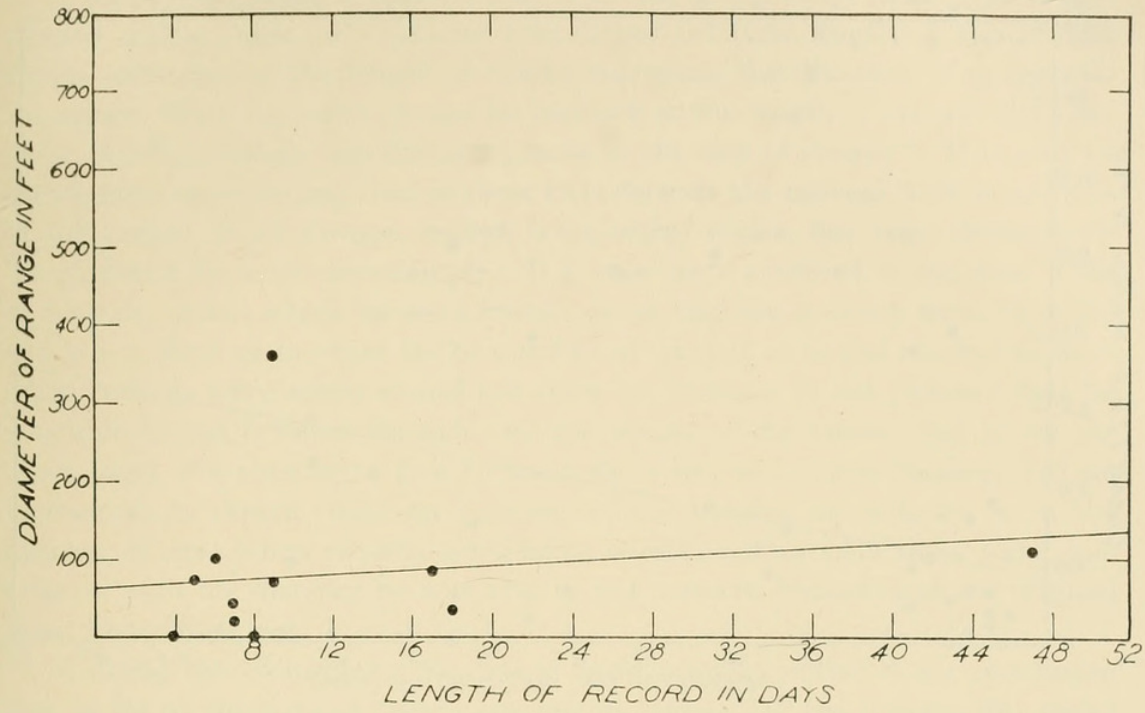

FIG. 8.—*Microtus montanus* (females)

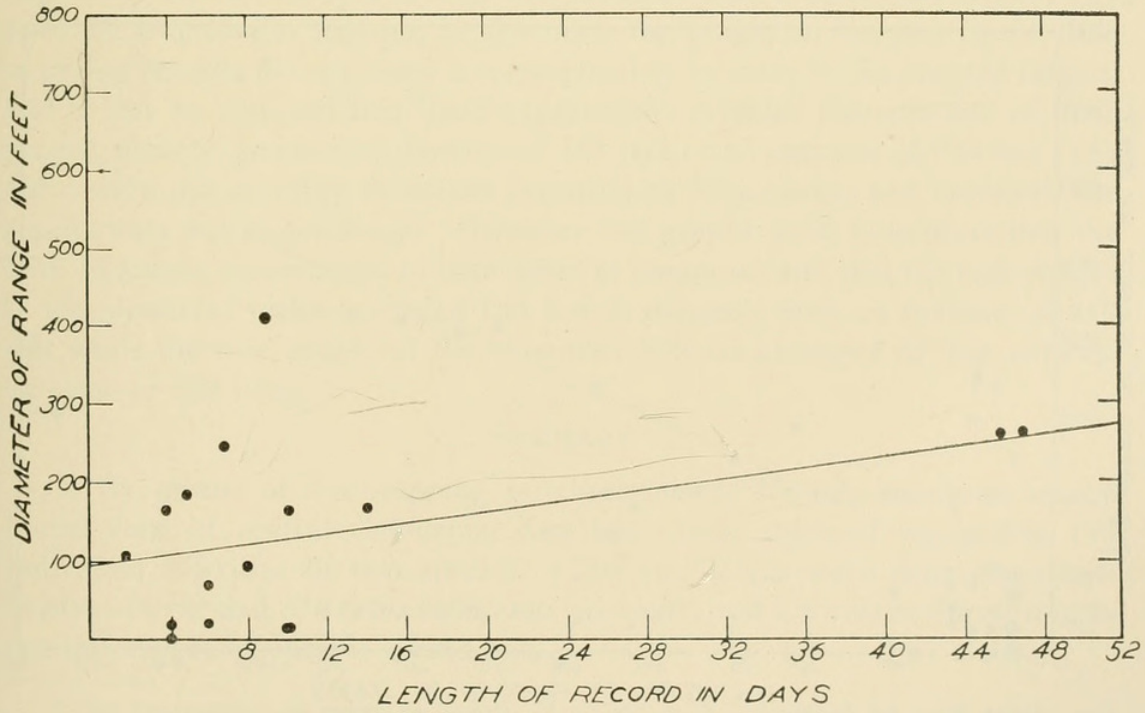

FIG. 9.—*Microtus montanus* (males)

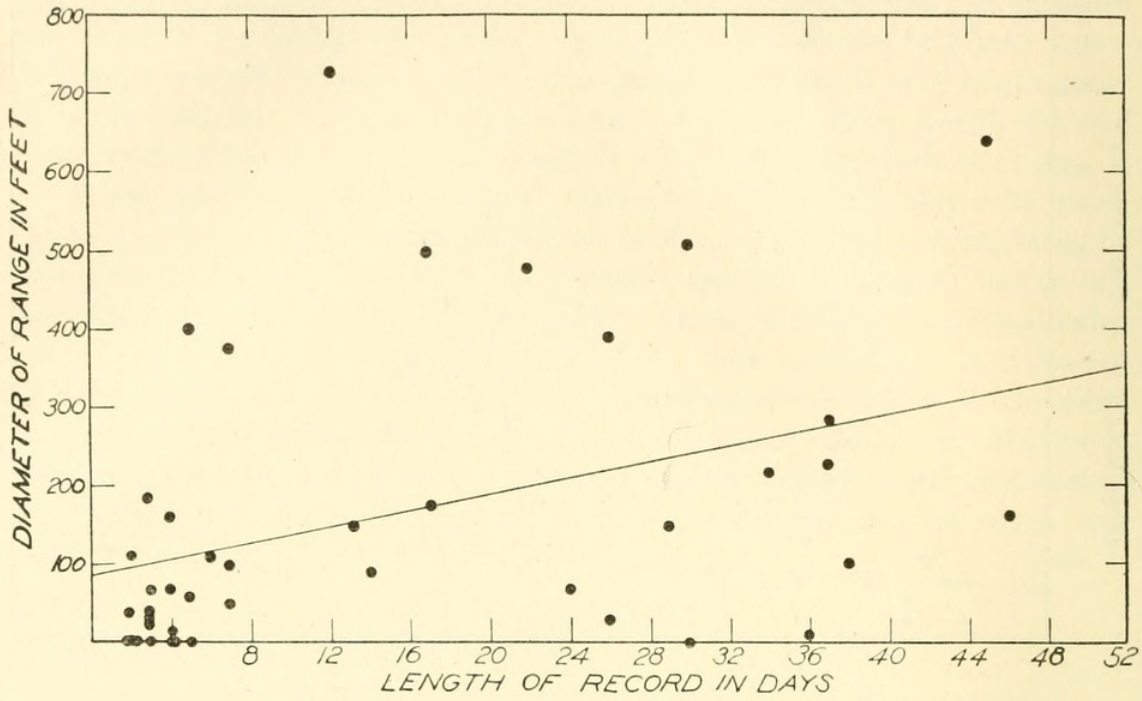

FIG. 10.—*Microtus longicaudus* (females)

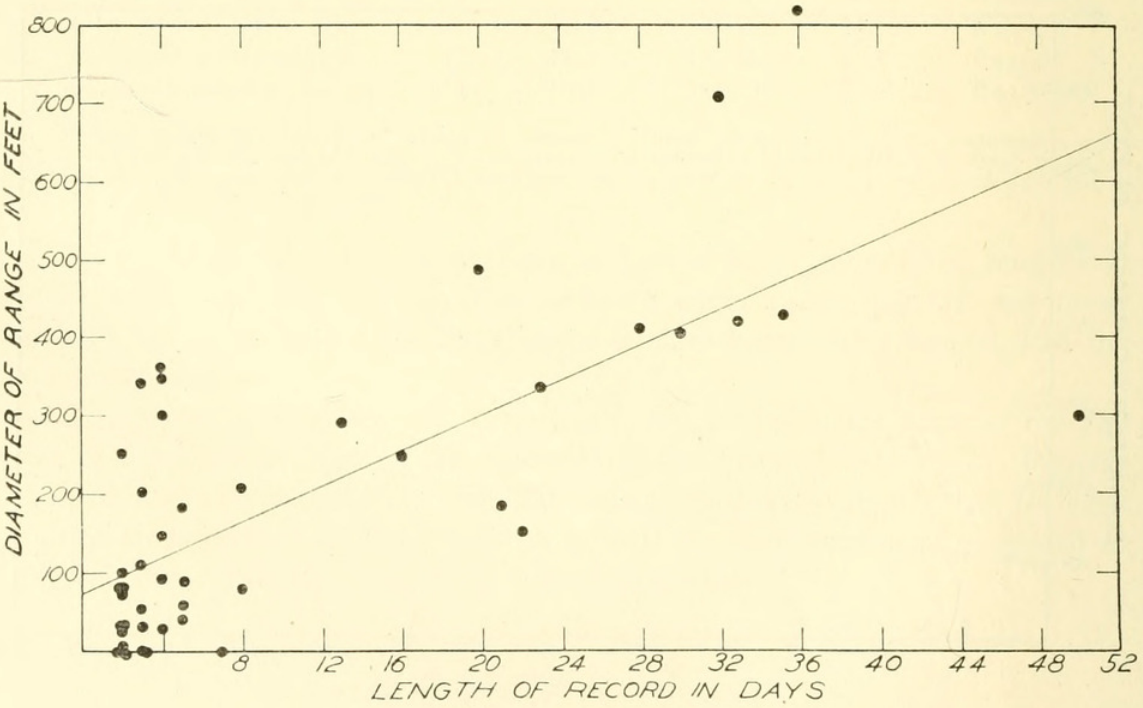

FIG. 11.—*Microtus longicaudus* (males)

From these graphs it appears that with one group only, namely the *longicaudus* males, there is a definite correlation between length of record and range, such that as the length of record increases, the diameter of range also increases. With the other groups an increase in the length of records does not show correspondingly significant increase in the size of ranges.* This may be interpreted as indicating that in these experiments the natural limit of the size of the ranges of all groups, except *longicaudus* males, has been determined. To elucidate by a simple example: If a man were confined to the four walls of a room, within which he were free to move, and his position were recorded every day, then an increase in the number of records or in the number of days when records were taken would not show an increase in the distance that he was able to put between himself and the center of the room. But if, on the other hand, the man were free to leave the room and, upon leaving, had no inclination to return, then an increase in the number of records or in the number of days when records were taken would continuously show some correlation with the distance he was able to put between himself and the original point of confinement.

Relating this example to the case in hand, we may arrive at the conclusion that as far as the data of these experiments show: (1) the *longicaudus* males are not limited in their ranges but continue to wander farther and farther from the initial point of capture, and that the previously noted "average diameter of range" of 194 feet and the "extreme" of 820 feet within the meadows and the "extreme" of one mile from one meadow to another, were merely the average and the extremes as obtained during these experiments, and did not express a true measure of the natural ranges of the *longicaudus* males; (2) with the *longicaudus* females, as shown on the graph, an increase in the time of taking records did not show a corresponding increase in the sizes of ranges, and it may be assumed that these experiments revealed the true size of their ranges, namely, an average distance of 161 feet or an extreme of 730 feet; (3) there were not as many *montanus* captured as *longicaudus* and therefore the results were not as conclusive. However, the graphs seem to indicate that the limit of ranges was reached in both sexes of *montanus* and that the true ranges of the *montanus* males averaged 138 feet in diameter with an extreme of 410 feet while the true ranges of the *montanus* females averaged 82 feet with an extreme of 360 feet.

SUMMARY

1. By means of live-trapping on three Sierra Nevada meadows in the boreal zone of central California, data have been obtained concerning 195 individual *Microtus* of two species. (The two forms were *Microtus longicaudus sierrae* and *Microtus montanus yosemite*, and are referred to throughout this report by specific names only.)

* The regressions of range on length of record were calculated for each group, and the regression coefficient was found to differ significantly from zero only in the case of the *longicaudus* males.

2. The population density of *Microtus* as indicated by the method of trapping used, in the three meadows totaling 19 acres, during the summer seasons of 1937, 1938, and 1939, averaged 4.55 mice per acre per season, with a possible maximum of 6.5 mice per acre per season, and a probable maximum of 2.5 mice per acre at any one time. Therefore, by allowing a margin of safety in the estimate, it is reasonably certain that the population, if expressed in round numbers, was never more than 10 per acre for any season.

3. It is suggested that a population density of over 1,000 per acre may be taken to represent so-called "plague" conditions, over 100 per acre to represent normal peaks in population cycles, and less than 10 per acre to indicate the presence of borderline conditions of existence threatening local extinction. The factors producing such borderline conditions are thought to be as follows: (*a*) *predation,* first in importance and of continuous application; (*b*) *climate or weather,* second in importance and of only intermittently controlling influence; (*c*) *food* and (*d*) *disease,* both of which do not become controlling factors as long as *a* and *b* impose severe restrictions on populations. In other words, when populations are low, due to predation or adverse weather conditions, then food is entirely sufficient and disease is not readily transmitted.

4. Differences in the population behavior of *Microtus montanus* and *Microtus longicaudus* are noted as follows: *M. montanus* was seen to fluctuate more in numbers, even disappearing entirely for a time, while *M. longicaudus* maintained a more nearly uniform, though low, population density. The difference is thought to be due to the greater dependence of *M. montanus* upon meadow conditions, while *M. longicaudus* could survive outside of the meadow and was therefore able more readily to reinvade the meadow.

5. The length of life of *Microtus* seemed to be, with but few exceptions, less than a year. Very likely the breeding stock of each season was recruited principally from litters last born in the preceding season.

6. Individual ranges were measured for purposes of comparison by taking the greatest distance between any two points of capture for each individual *Microtus* and the following conclusions are reached: (*a*) Males of both species have wider ranges than females. (*b*) Individuals of *M. longicaudus* have wider ranges than those of *M. montanus* in both sexes. (*c*) The determined ranges are shown to be as follows:

	Number of Individuals	Average Diameter of Range	Extreme Diameter of Range
Total *Microtus*	195	163 feet	820 feet
M. montanus females	21	82	360
M. montanus males	41	138	410
M. longicaudus females	60	161	730
M. longicaudus males	73	194	820 feet within meadow up to 1 mile out of meadow

The natural limits of the ranges of the first three groups above were apparently reached in these experiments, whereas with the last group, namely

the *M. longicaudus* males, the limit of the range was still increasing at the close of the experiments, thus indicating that the *M. longicaudus* males were not restricted as to range but continued to wander during the season.

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