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MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 45

TERRITORIAL BEHAVIOR AND POPULATIONS OF SOME SMALL MAMMALS IN SOUTHERN MICHIGAN

BY
WILLIAM HENRY BURT

ANN ARBOR
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FREDERICK M. GAIGE
Director of the Museum of Zoology

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TERRITORIAL BEHAVIOR AND POPULATIONS OF SOME SMALL MAMMALS IN SOUTHERN MICHIGAN*

INTRODUCTION

THE present study, initiated in the spring of 1935, is the result of an attempt to secure information about the breeding seasons and populations of certain small mammals in southern Michigan. It seemed desirable, for a study of this nature, to concentrate on one species. The wood mouse (*Peromyscus leucopus noveboracensis*) was selected because it commonly occurs throughout wooded areas and readily comes to traps.

The study was carried out almost entirely within the boundaries of the Edwin S. George Reserve of the University of Michigan, located near Pinckney, Livingston County, Michigan. This 1200-acre area is game-fenced. Formerly, parts of it were farmed, but now it is reverting to a wild state. It contains a number of wood lots varying in area from less than an acre to more than fifty acres (Map 2).

Two wood lots isolated from each other were selected as study plots. One of these, designated as Plot 1, is bordered on the north, west, and south by grassland, and on the east by an extensive swamp. It contains 3.72 acres. The other wood lot, Plot 2, is surrounded on all sides by grassland and is located, for the most part, on a steep north-facing slope (Map 1). It contains 1.8 acres. Plots 1 and 2 (Map 2) are connected by an old fence row with a few trees. A fence row leads eastward from Plot 2 and connects with another wood lot.

In 1935 these areas were trapped intermittently May 5–October 20, when severe weather prevented further work. On June 10, 1936, the work was resumed, and traps were set at least once or twice a month until September 10, 1937. In addition to these two study plots, thirteen other wood lots were trapped for periods ranging from a week to three months. Roland Abegg assisted me on the George Reserve June 25–September 18, 1936. In the early spring of 1936 he had trapped around Ann Arbor to determine the beginning of the breeding season of the wood mouse. For three weeks in July, 1937, W. Frank Blair trapped some of the wood lots surrounding the principal study plots.

The method of study was developed primarily for the wood mouse. Other species often were caught in the same traps, however, and it soon became evident that much data on these other species might be obtained with little extra effort. In this study the wood mouse is treated in considerable detail, the other species less extensively.

There were 1722 animals marked and released on the George Reserve.

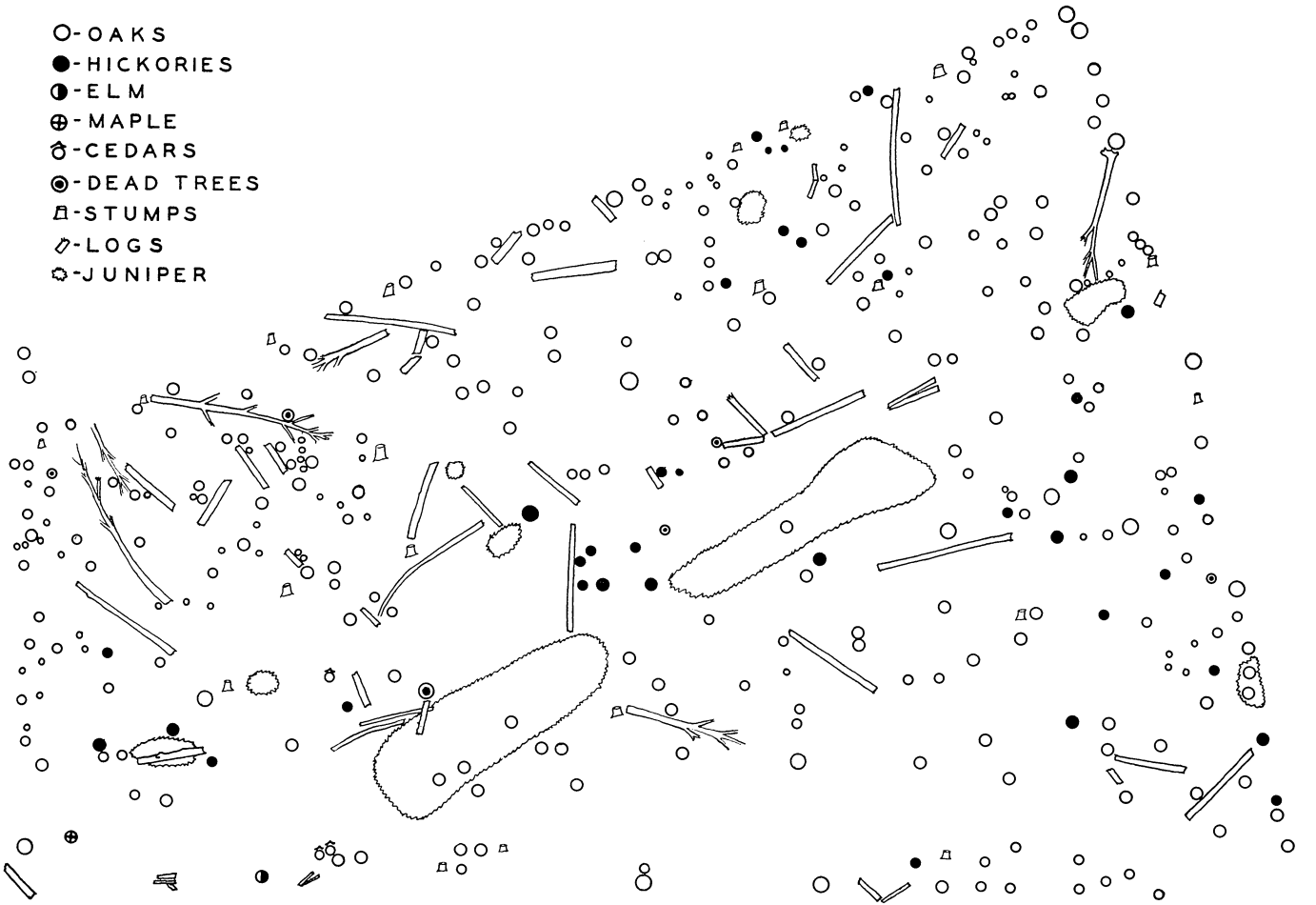
* A contribution from the Edwin S. George Reserve.

These represent ten different species, as follows: *Blarina brevicauda talpoides,* 61; *Citellus tridecemlineatus tridecemlineatus,* 7; *Tamias striatus lysteri,* 109; *Glaucomys volans volans,* 46; *Peromyscus maniculatus bairdii,* 10; *Peromyscus leucopus noveboracensis,* 1382; *Synaptomys cooperi cooperi,* 47; *Microtus pennsylvanicus pennsylvanicus,* 30; *Pitymys pinetorum scalopsoides,* 28; *Zapus hudsonius hudsonius,* 2. Six of these species are treated in the present discussion; too few data were gathered to provide the basis for an adequate treatment of *Citellus, Peromyscus maniculatus, Microtus,* and *Zapus.*

ACKNOWLEDGMENTS

I am especially grateful to Lee R. Dice and Frederick M. Gaige for their enthusiastic support and unselfish counsel at all times. Colonel Edwin S. George enhanced the efficiency of the work and rendered it enjoyable by extending his hospitality in the manner of comfortable living quarters to Mrs. Burt and myself during the three summers. My thanks are due Lawrence Camburn, Custodian, for many favors, and Roland Abegg and W. Frank Blair for the energetic manner in which they performed their respective duties.

Financial support from the Faculty Research Fund of the University of Michigan and from the Museum of Zoology made possible the employment of an assistant in 1936. The Laboratory of Vertebrate Genetics contributed the services of W. Frank Blair during July, 1937.



MAP 1. Plot 2 (1.8 acres). The distribution of trees, logs, and juniper clumps over the area. The different sizes of the circles, representing standing trees, indicate relative sizes of trees present. The largest trees are about two feet in diameter.

MATERIALS AND METHODS

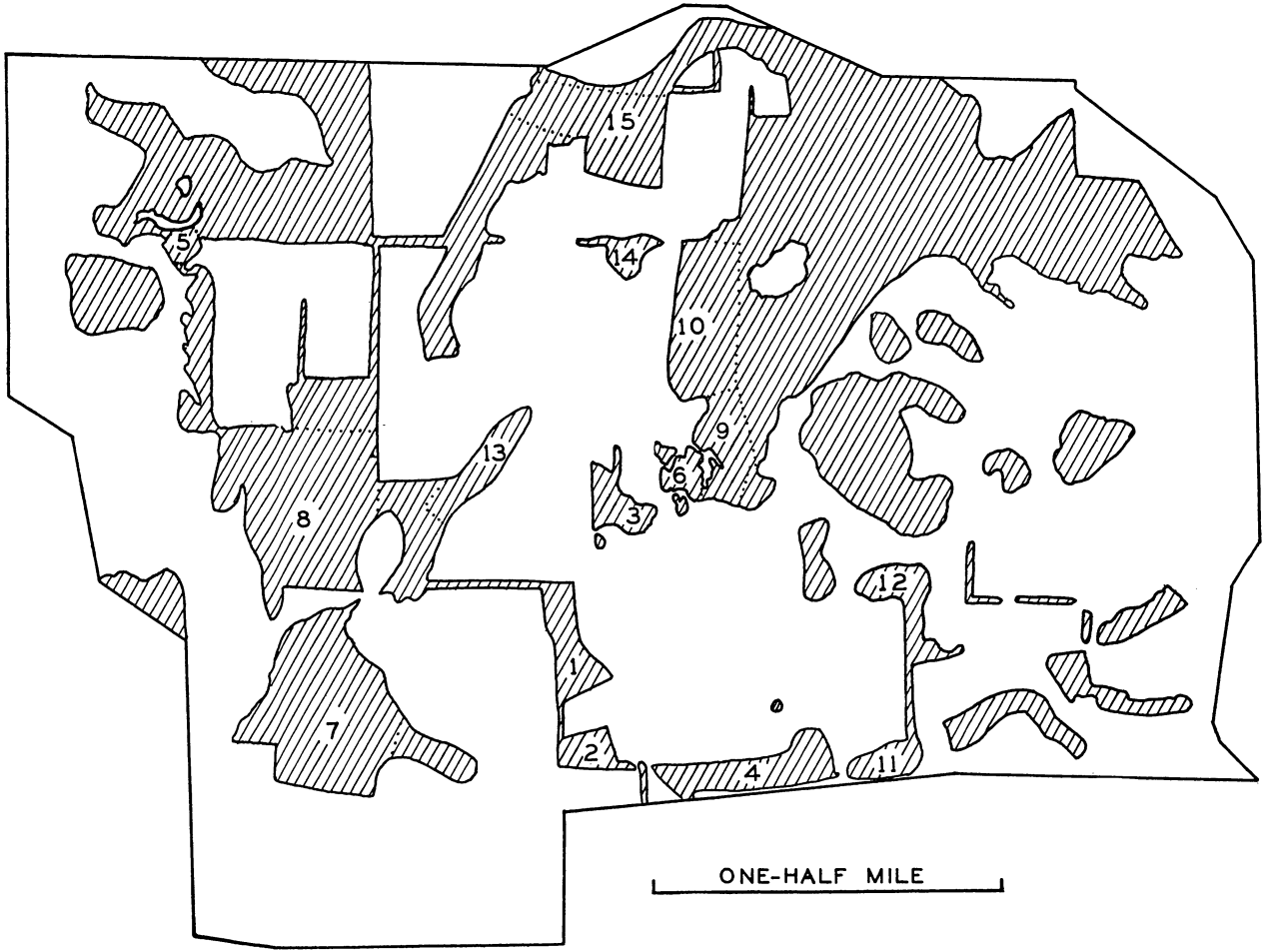
Description of Traps

During the 1935 season a metal trap with internal dimensions of six by two by two and one-fourth inches was used. The trap, designed by L. C. Fisher at the University of Michigan, holds mammals up to the size of chipmunks and has a door which closes from the outside. Although efficient in catching small mammals, this trap was not entirely satisfactory because many of the animals caught in it died. Death resulted from overheating in the summer months, from cold during the winter, and from exhaustion, when animals squeezed under the slightly elevated treadle.

In the new trap, made of half-inch boards except for the front (Pl. I, Fig. 1), the mortality was appreciably reduced. The trap is similar to that figured by Stoddard (1931: Pl. 58, Fig. 1). Its inside dimensions are six by two by two inches. A door of wood forms the back; a small metal well, with a free-swinging trap door hinged at the top, is placed in a lower corner in front. The opening is one inch square, and the trap door slopes backward into the box at an angle of 45 degrees. The remainder of the front is covered with screen. The mouse pushes his way in by lifting the free-swinging door. When he is inside, the door falls back into place and closes the entrance. The door fits so that when the animal tries to escape it sees no open spaces there and attempts to go through the screen front. The one-inch opening was designed as a selective mechanism to prevent the entrance of chipmunks; however, they, too, readily entered it. The type of trap constructed for ground squirrels, chipmunks, and flying squirrels is larger and has a door swung across the entire front, about one-half inch below the top. These traps are, in cross section, of the same inside dimensions as the one just described, but are twelve inches long. A narrow strip of screen covers the space above the door. The screen front allows sufficient ventilation to reduce the possibility of death from overheating. If cotton and food are placed in the trap, an imprisoned animal can endure extreme cold. A further advantage is that more than one animal at a time may be caught. This may be a disadvantage, for sometimes two animals enter and one kills the other—the only serious cause of mortality in the multiple-catch trap. I have found this type of trap satisfactory in the present study, especially for *Blarina, Peromyscus, Citellus, Tamias,* and *Glaucomys.* I suggest, however, that before it is used extensively for other species it be given a trial in order to ascertain whether or not it works well.

Bait

A mixture of hempseed, wheat, millet, and rolled oats proved to be a satisfactory bait, but during the summer months, when rains were frequent, rolled oats was eliminated because it formed a sticky mass when wet.



MAP 2. The Edwin S. George Reserve. The oak-hickory wood lots are shaded areas. The wood lots numbered were trapped. Dotted lines indicate the parts of the wood lots which were trapped.

Arrangement of Traps

Traps were numbered and set in a grid pattern to facilitate plotting their positions on the map of the area. At the beginning of the study they were spaced ten, fifteen, and twenty yards apart, respectively, in different areas. For *Peromyscus,* the distance of fifteen yards between traps is most satisfactory, and for *Blarina,* ten yards. *Citellus, Tamias,* and *Glaucomys* all have considerably larger home ranges than does *Peromyscus.* For these wider-ranging species I found the most satisfactory spacing between the traps to be twenty yards. It is obvious that the most desirable spacing of the traps depends on the habits and normal home ranges of the animals to be caught. Different methods of arranging traps have been employed by

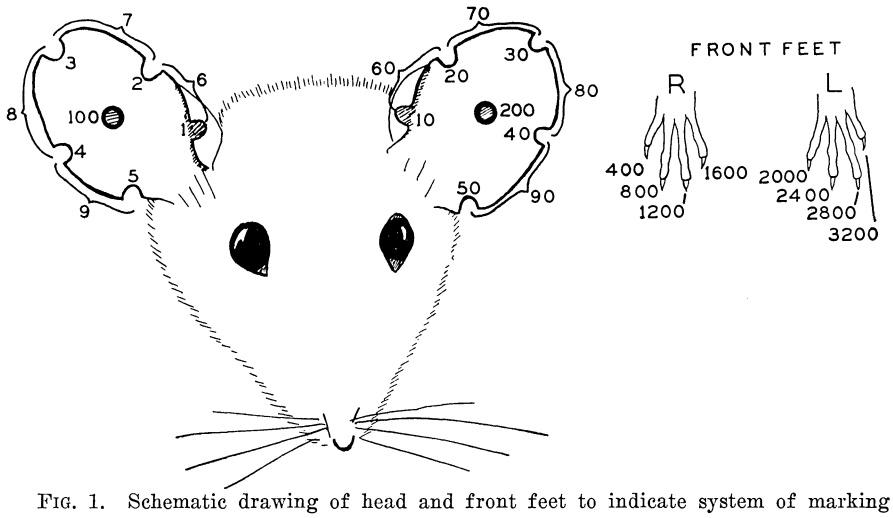


Fig. 1. Schematic drawing of head and front feet to indicate system of marking animals.

other workers and will be discussed later in the section on populations. Instead of designating quadrats within a wooded area, I set the traps throughout each of several more or less isolated wood lots. I trapped the entire wood lot in order to reduce the error in estimating populations and home ranges of species more or less restricted to these areas.

Method of Marking Animals

The animals were marked by notches punched in the ears and by clipped toes (Fig. 1). With this system, various combinations may be used and the possible numbers may be run up into thousands without repetition. With somewhat different combinations, the system has been used successfully at the Laboratory of Vertebrate Genetics of the University of Michigan. Shrews (*Blarina*) were marked entirely by toe-clipping, chipmunks and flying squirrels by ear-notching. With *Peromyscus,* both ear-notching and toe-clipping

were employed. All animals were marked in the field at the place of capture. Animals were not etherized, since ether might have weakened them, especially in cold weather. The marking was done so quickly that they registered little or no pain when an ear was notched or a toe clipped. A poultry punch was used to notch the ears and a pair of small scissors to clip the toes. Injured parts usually healed within forty-eight hours. No signs of infection were observed, and I have no reason to believe that any mortality resulted. Chitty (1937) employed a "ringing technique" in marking small mammals: a metal ring or band, carrying a number, was placed around the leg of the animal.

Method of Keeping Records

All traps were numbered and their positions plotted on outline maps of the areas trapped. Each area was given a number and indicated on a large outline map of the entire George Reserve. When an animal was caught for the first time it was marked, and in a field notebook were recorded the number of the area, the date, the species, the number of the animal, age, sex, trap number, and any information on breeding condition, pelage, and apparent disease. These data were recorded also whenever an animal was retaken. All records and data were kept according to species in a loose-leaf notebook.

Efficiency of Trapping Methods Employed

I do not believe that I caught all of the individuals of some species living within the area trapped. I do believe that the methods used were nearly 100 per cent efficient for *Peromyscus, Glaucomys,* and *Tamias.* Of course, there may have been a few wary individuals that never entered a trap, but my experience with these mammals indicates that they will go to no end of trouble to reach any food that is available. The same individuals were recaptured many times throughout the year and did not become trap shy.

The efficiency of trapping *Peromyscus leucopus noveboracensis* is indicated in Table I. Eighty traps were set in a part of a wood lot during the four

TABLE I

Efficiency of Trapping *Peromyscus leucopus* for the First Time in an Area, July 20–23, 1937

Trapping Night	Unmarked	Previously Marked
First	23	.....
Second	8	17
Third	4	19
Fourth	1	23

nights July 20–23, 1937, inclusive, and spaced fifteen to twenty paces (forty-five to sixty feet) apart. This was the first time the area had been trapped.

The number of new mice taken on successive nights decreased rapidly, whereas the number of mice previously taken increased. When traps were spaced as indicated above, about all of the mice in the area were caught in four nights of trapping.

These results compare favorably with those obtained from an area where the mice had been trapped for some time previously and the population was known. In one of the study areas (3.72 acres) there were eighty-nine traps. Set during the period June 10–14, these traps took twenty mice; set June 24–28 they took nineteen mice; July 7–11, twenty mice; and July 21–26, eighteen mice. During this last period, all of the mice taken had been captured previously in the same area. In Table II the catch on each of the

TABLE II

EFFICIENCY OF TRAPPING *PEROMYSCUS LEUCOPUS* IN AN AREA WHERE ALL MICE HAD BEEN PREVIOUSLY MARKED, JULY 21–26, 1937

Trapping Night	Number Taken	Number Not Taken Previously in This Trapping Period
First	11	11
Second	15	4
Third	6	1
Fourth	16	.....
Fifth	15	1
Sixth	12	1

six nights July 21–26, inclusive, is summarized. All but one of these mice were caught during the next trapping period, August 4–9, and all had been taken and marked during previous trapping.

In trapping the selected areas where I had records of the animals, I found that if an animal previously taken there was not caught in six nights of trapping, I rarely took that animal again in that area. I interpret this to mean that the animal either had moved to another area or had been captured by a predator. I have records of several animals that were recaptured after they had moved, but the majority never again were taken.

EFFECT OF PROLONGED TRAPPING

In his recent paper, Chitty (1937) stated, rightly, that the effects of trapping were difficult to evaluate. He stated further that if natural conditions were to be maintained individuals should be caught "as infrequently as possible." A somewhat more lucid statement, I believe, would be that it is desirable to catch them "as infrequently as practicable" for the end in view. The type of study one is making should govern the desired frequency of capture of an individual. Animals will come back to the same trap night after night if that trap is kept set. Obviously, if one is studying movements he must avoid this repetition.

Chitty raised a number of questions concerning the effects of trapping; some of these I shall attempt to answer here. For example: what would be the consequences of liberating nocturnal animals in the daytime? Inasmuch as *Glaucomys* and *Peromyscus* are the only truly nocturnal mammals considered in this study, my remarks pertain to these two forms. These animals, when released, almost without exception go directly to a retreat; whether it be their nesting site I do not know, but I suspect that frequently it is. They are under cover before any predator has a chance to take them. I cannot see how releasing the animals in the daytime should affect the animals seriously, although it is possible that such a disturbance might alter their normal activity. Also, if a mother should not return to her young until evening they might be endangered. I believe that unless she is absent too long there is little danger that the young will die in the nest, although repeated long absences of the mother might lower the vitality of the young and expose them to enemies. I have one record of newly born *Peromyscus* which lived sixty hours without parental care of any kind. More serious than this, I believe, is a possible systemic reaction due to exhaustion from fighting the trap while attempting to escape. I have observed no evidence of disease caused by the repeated use of trap and nesting materials, and see little danger of infection if traps are kept clean and if the nesting material is frequently changed. I had a sufficient number of traps so that no one trap was set more than five days in every fourteen.

The chances of an individual's meeting a mate are probably less if a single-catch trap is used, but on several occasions I have caught male and female *Peromyscus* together in this type of trap. In the multiple-catch trap this difficulty is removed, and it is the usual thing to catch male and female in the same trap. I have evidence to show that, at least at times, wood mice travel in pairs. Townsend (1935: 81) also found evidence of this in New York.

SPECIES ACCOUNTS

Peromyscus leucopus noveboracensis

HABITAT PREFERENCES

This species is found chiefly, but not exclusively, in areas which are wooded or covered with heavy brush. Unsettled individuals, especially young ones, often appear in open grassland several hundred yards from the woods, but I doubt that they long remain in this type of habitat. On the George Reserve the wood lots are chiefly of oak and hickory with an undergrowth of grass or sassafras, black cherry, witch hazel, and black huckleberry. Practically all of the work was done in these wood lots.

Within the oak-hickory woodland are the habitats preferred by these mice. The character of the ground cover seems to be important to them. In those parts of the woods which are fairly open there is a thick cover of grass; in the more densely wooded sections the undergrowth is chiefly of other herbaceous plants. The latter sections harbor the greater number of these mice (Pl. II, Fig. 1).

BREEDING

During the spring of 1935, females were live-trapped near Ann Arbor and brought into the laboratory each week from March 2 to April 22. Here they were retained until they gave birth to young or until sufficient time had elapsed to make it certain that they were not pregnant when captured. In all, thirty-one females were thus trapped. Nine of these, taken on or before March 11, were not pregnant and, therefore, apparently had not bred before capture. Fifteen females were captured at intervals between March 11 and March 31. Six of these were pregnant at the time of capture; nine apparently had not bred. Seven females brought in after March 31 were all pregnant. Young were born in the laboratory to ten of the field-caught females, on March 31, April 1, 2, 9 (2 ♀), 10, 16, 17, 18, and 21. Three of the pregnant females died in the traps. The above data apparently indicate that in this region, in the spring of 1935, a few old females started breeding about March 10, and that by April 1 most, or perhaps all, of them had mated.

In order that the findings of the 1935 season might be checked, an assistant was employed to live-trap field animals in the spring of 1936. Trapping was commenced on March 8 and was continued through May. Fifty-four adult females were trapped during this time. The results were similar to those just given for 1935, except that the first litter was born on March 23, about a week earlier than the first litter in 1935.

In the first season, 1935, an external examination was made of the testes of all males taken. Of the seven males trapped March 2, all had the testes abdominal, but in practically all males taken after March 11 the testes had

descended to a scrotal position. Thus, the time that the males came into breeding condition, as determined by external examinations, was coincident with the breeding of the first females.

The above data, although based on relatively few records, are sufficient, I believe, to give a fairly accurate notion of the beginning of the breeding season of the wood mice in this area.

The technique employed at the George Reserve in following the breeding condition of females through the remainder of the season was less positive, but, nevertheless, fairly reliable. The mice were live-trapped, marked, and released at the point of capture. The condition of females always was noted. By recapturing a female on the average of ten times a month, one can record her breeding activities fairly accurately. It is not difficult to determine externally whether or not an old female is about to give birth to young or is lactating. In 1935, only three old females were observed throughout the entire period May–September at intervals of a week or less; observations of one were continued until October. The records of these three old females, additional data on twenty other females that were observed over shorter periods in 1935, and the data on forty-two old females in 1936, indicate that most old females raise two litters in the spring, but some raise three. The litters follow one another in fairly rapid succession from early April until early June. The last spring litters are weaned in late June or early July. The next litter usually does not appear until about the middle of August, although a few litters arrive as early as the first of August. Normally, two litters are raised in the fall by each old female, the last appearing in September or early October. Each old female that lives throughout the breeding season has four, or possibly five, litters.

Among the mice caught in any month of the period April–October, inclusive, there may be females with embryos, and hence one might reasonably conclude that they breed throughout the season. If, however, the history of one female is traced, a rest period of a month or more is discovered. It occurs in July or August, depending upon the time when she starts breeding in the spring. This rest period accounts for the scarcity of breeding females in midsummer as recorded in Table III and shown on the graph, Figure 2 *C*. The likelihood of reaching a wrong conclusion in this case is strong evidence of the importance of conducting life-history studies on living, rather than on dead, animals. Paradoxically, many life histories are based largely on data gathered from *dead* animals.

Young females of the year begin to breed at the age of two and one-half or three months; they give birth to their first litters when they are about fourteen weeks old. For only one female do I have both the date of her own birth and the date when her first offspring were born. This mouse was born on June 1, 1936, and had her first litter on September 12 of the same year,

TABLE III

BREEDING ACTIVITY OF ADULT FEMALES OF *PEROMYSCUS LEUCOPUS*

Month and Year		Total Number	Number Breeding	Number Not Breeding	Percentage Breeding
1935					
March	First half	9	.....	9	.....
	Second half	15	6	9	40.0
April	First half	7	7	.....	100.0
May	First half	9	6	3	66.6
	Second half	12	10	2	83.0
June	First half	7	6	1	85.7
	Second half	8	6	2	75.0
July	First half	6	.....	6	.....
	Second half	8	4	4	50.0
August	Second half	3	2	1	66.6
September	First half	3	2	1	66.6
	Second half	1	1	.....	100.0
October	Second half	1	1	.....	100.0
November	First half	1	.....	1	.....
1936					
March	First half	4	1	3	25.0
	Second half	17	2	15	11.8
April	First half	3	2	1	66.6
	Second half	6	3	3	50.0
May	First half	20	7	13	35.0
	Second half	9	6	3	66.6
June	First half	6	6	.....	100.0
	Second half	3	3	.....	100.0
July	First half	41	10	31	24.4
	Second half	43	2	41	4.6
August	First half	25	5	20	20.0
	Second half	39	7	32	18.0
September	First half	30	13	17	43.3
	Second half	19	11	8	58.0
October	First half	10	8	2	80.0
	Second half	10	7	3	70.0
November	First half	7	.....	7	.....
	Second half	4	.....	4	.....
December	Second half	6	.....	6	.....
1937					
February	Second half	20	.....	20	.....
March	First half	21	.....	21	.....
May	Second half	13	12	1	92.3
June	Second half	10	5	5	50.0
July	First half	18	3	15	16.6
	Second half	73	5	68	6.8
August	First half	17	1	16	6.0
	Second half	16	8	8	50.0
September	First half	16	6	10	37.5

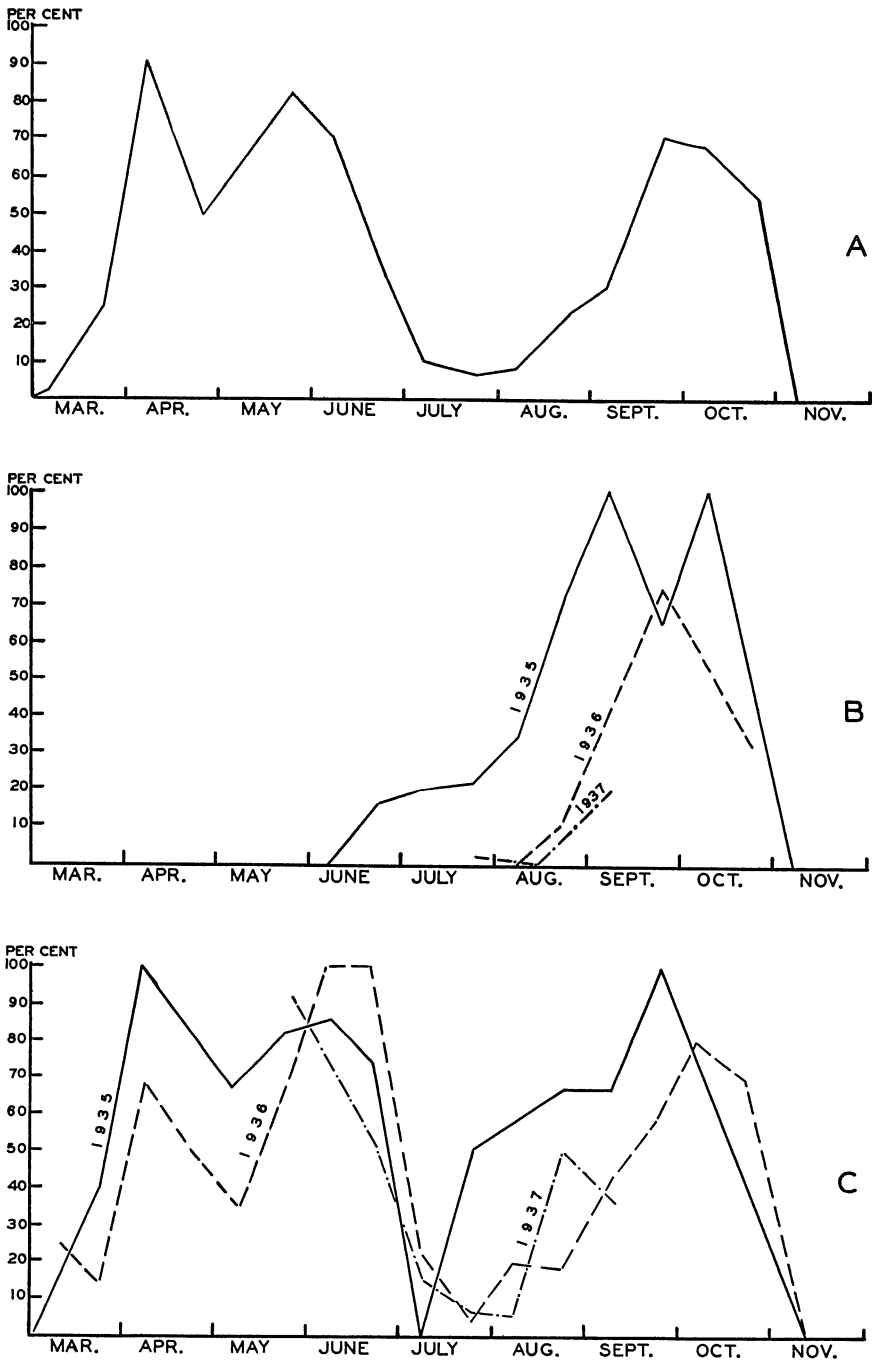


FIG. 2. The percentage of females of *Peromyscus leucopus noveboracensis* in breeding condition throughout the season from March to November: *A*, all breeding females for the three seasons 1935–37; *B*, young spring-born females, plotted separately for the three seasons; *C*, adult females, plotted separately for the three seasons.

at the age of nearly fourteen weeks. Additional records, covering periods of from six to nine months, on fourteen females that were between twenty-five and thirty days old at the time they were first captured, indicate that none of them bred before she had reached an age estimated as two and one-half months. Most of them had their first litters at the age of thirteen or fourteen weeks. As far as I know, none of the autumn young—those born after August 1—breed until the following spring. My records indicate that most of the spring-born females breed in the fall, when each raises one or two litters. A few of the young females of the first spring litter may be expected to start breeding the latter part of June, but it is not until late August or early September that the majority of them are in breeding condition (Table IV and Fig. 2 *B*).

Occasionally a barren female is found. I have records of an old female for seven consecutive weeks, during which time she showed no signs of breeding, although other females were breeding actively. From external appearance, she was a healthy individual. Females probably do not breed while in a weakened condition from disease. I have records of one such female over the period June 3–September 10, 1935. When first captured she was lactating and appeared normal in every respect. On June 18 she was still lactating slightly, and the hair on her forehead had started to fall out as the result of an infection of an ectoparasite. By the first of July she had become nearly naked, her tail was badly swollen, and she appeared to be weak and near death. By July 15 she had shown slight improvement, and by August 25 she had completely recovered. She showed no signs of breeding up to September 10, the last date on which she was captured.

Records were made of the number of young per litter for the litters of thirty-nine females. The extremes are two and six, and the average is 4.26 per litter. Svihla (1932) found the mean number of young for fifty-three litters to be 4.36; Townsend, in New York (1935: 83), found that embryos ranged from three to seven with an average of 4.7 per litter; and Coventry (1937), in Ontario, found the mean number to be 5.04.

By knowing the average number of litters per year and the average number of young per litter one can calculate the average number of offspring of a single pair of mice in one season, provided the sexes are evenly divided, there are no mortalities, and all individuals breed normally. An old female in the wild state will raise at least eight young in the spring, four females and four males. She also will raise the same number in the fall, a total of sixteen. In addition, the four females born in the spring each will raise four, and possibly eight, young in the fall, a grand total of at least thirty-two offspring, and thirty-four mice, including the original pair. This probably rarely, if ever, happens where predators are present to eliminate a certain percentage of both the young and the adults. If, however, there

TABLE IV

BREEDING ACTIVITY OF YOUNG SPRING-BORN FEMALES OF *PEROMYSCUS LEUCOPUS*

Month and Year	Total Number	Number Breeding	Number Not Breeding	Percentage Breeding
1935				
May — First half	4	.....	4	.....
May — Second half	13	.....	13	.....
June — First half	15	.....	15	.....
June — Second half	12	2	10	16.6
July — First half	10	2	8	20.0
July — Second half	27	6	21	22.2
August — First half	12	4	8	33.3
August — Second half	11	8	3	72.7
September — First half	3	3	.....	100.0
September — Second half	3	2	1	66.6
October — Second half	2	2	.....	100.0
November — First half	2	.....	2	.....
1936				
June — First half	11	.....	11	.....
June — Second half	10	.....	10	.....
July — First half	49	.....	49	.....
July — Second half	36	.....	36	.....
August — First half	47	.....	47	.....
August — Second half	41	4	37	9.8
September — First half	34	3	31	8.8
September — Second half	29	22	7	75.8
October — First half	12	7	5	58.3
October — Second half	10	3	7	33.3
November — First half	13	.....	13	.....
November — Second half	25	.....	25	.....
1937				
May — Second half	1	.....	1	.....
June — Second half	5	.....	5	.....
July — First half	19	.....	19	.....
July — Second half	30	1	29	3.3
August — First half	13	.....	13	.....
August — Second half	14	.....	14	.....
September — First half	10	2	8	20.0

were no predators, no defense of territorial rights, and if there were sufficient food and shelter and all the young lived and bred, at the end of the second season there would be at least 578 individuals from the single pair. I cite these figures to indicate the rapidity with which a population might be built up, under favorable conditions, and the difficulty of trying to control certain prolific rodents by artificial means. Unless all of the animals were exterminated in an area, in one or two seasons the population would

return to normal, if limiting factors remained relatively constant. Predators are the natural checks for these rodents and play an important role in eliminating the surplus.

SEX RATIO

Table V gives the number of individuals caught for the first time during each of the three seasons, as well as the number of each sex and the per-

TABLE V

SEX RATIOS FOR *PEROMYSCUS LEUCOPUS*

Year	Number Trapped	Number of Males	Percentage Male	Number of Females	Percentage Female
1935	317	156	49.21	161	50.79
1936	856	459	53.62	397	46.38
1937	378	212	56.08	166	43.92
1935–37 ...	1551	827	53.32	724	46.68

centages of the whole. Individuals marked and retaken later were not counted after the first capture. During the 1935 season the sexes were nearly equal in number. The males exceeded the females in 1936 and again in 1937, when 56.08 per cent were males, and 43.92 per cent were females. In the three seasons combined, 53.32 per cent were males and 46.68 per cent were females. The above percentages are based on a total of 1551 individuals.

The excess of the number of males over the number of females may be apparent rather than real. A greater tendency of the males to wander might account for a higher proportion of males to females trapped than obtains in nature. At any rate, the departures from the hypothetical "fifty-fifty" ratio are not considered significant. Townsend (1935: 42, Table 12) found that of 291 mice, 194 (66.6 per cent) were males. He attributed part of the excess of males over females to the greater wandering tendency in the males.

HOME SITES

Wood mice select diverse sites for homes. Nests have been observed by Audubon and Bachman (1852: 302–5) in deserted squirrel nests, in bird nests, in hollows in trees, in buildings, under stone heaps and old logs, and in the ground. Evermann and Clark (1911: 17), reporting upon the habitat of this animal in Indiana, state:

> Any old pile of wood, boards, logs or brush, stack of straw or hay, or shock of fodder is almost sure to contain at least one family of these beautiful and interesting little animals. They may also be found in almost any old dead tree, whether in open woods or dense forest, in which there are natural hollows or deserted woodpecker holes.

These are but a few of many statements with regard to the variety of con-

ditions under which the wood mice nest. I have found them in old stumps, in squirrel nests, in the hollows in trees, and in almost every conceivable place around buildings that afforded shelter. At the living quarters on the George Reserve, I found nests of these mice in a lime sack (mother and two young), in kegs and boxes of various kinds, in a metal toolbox on a mowing machine (old male), on top of the battery in my frequently used automobile, and in one of my hip boots, where a female built a nest sometime in the early evening and gave birth to four young before 10:00 o'clock that night! The boots had been in use during the day. Practically any soft materials available are used in building the nest. The instance just cited, of the female that built her nest in my boot and gave birth to young within a period of three hours, indicates that a female may build a nest to hold each new litter of young. This affords more sanitary conditions than would be provided were she to raise them in an old nest, possibly infested with ectoparasites. Probably more than one nest is used by the same mouse, as was suggested by Seton (1920: 138). It would be a distinct advantage for a mouse to have several nests: if disturbed in one place, it could retreat to another immediately and lessen the danger of death from exposure or predation. Adequate nesting sites and retreats are necessary for the welfare of any animal, be it predator or prey.

FOOD STORAGE

Hubbard (1887: 329), describing a nest of the wood mouse, noted that "just over the nest was found two quarts of peeled acorns, with a large quantity of beach-nuts and seeds." I had an unusual opportunity on the George Reserve to observe the storing habit of these mice. A sack of mixed seeds was always on hand for bait. My first knowledge that the supply was being raided by these mice came when I discovered a small handful of seeds in one of my boots. Soon afterward, small stores of seeds were found on shelves, in wastepaper boxes, and at various other places. The storing habit of wood mice is displayed not in any one season alone, but whenever an abundance of food is available—in nature, when the seeds and nuts which help make up their food supply are ripening. I often have taken mice from traps in the evening to find that they had stuffed their cheek pouches so full of seeds that they bulged like two balls, one on either side of the face. I also have watched them, in captivity, busy themselves carrying the food from the container and caching it in various parts of the cage. In captive animals this habit is displayed to a greater degree by some individuals than by others. Whether or not the same is true in nature I do not know. Of the captive mice that I kept in a few cages for a short time there was one mouse in particular, a tireless worker, that would not stop until he had cached every bit of food placed in the container.

SOCIABILITY

It is difficult to study the social habits of a nocturnal animal such as *Peromyscus leucopus*. I have, however, a few data on this phase of their conduct, gained by casual observations and trapping records. I have reason to believe that during the breeding season old females are antagonistic toward one another. During this time they maintain definite territories which apparently they protect from others of their sex (Figs. 3 and 4). This will be discussed later. In only one instance during the last two seasons, when I used multiple-catch traps, did I find two adult females together in the same trap. This occurred in December when they were not breeding. In two instances I took adult females in the same traps with young males, and in eight instances with young females. When the young are first out of the nest they evidently run with the parent for a short time. This friendship between parent and young is probably short-lived, except in the case of the last litter in the fall. In one case, on June 15, 1936, I was so fortunate as to witness an old female chasing a young female. From all appearances it was not a friendly chase. It was evident that the old female was attempting to drive the young one, possibly her own offspring, out of the home territory.

Old males are apparently more tolerant of both young and adults of the same sex than are old females. Indications of intolerance were shown in but two of the nine instances when old males were found together in the same traps. In each of these two instances one of the males was dispatched by the other. These occurred on August 25 and 26, 1936, during the breeding season. Old males were taken with young females five times and with young males but once. The most frequent combination, however, when two mice are found in the same trap, is that of an adult male and an adult female. This combination occurred thirty-seven times in the total of seventy instances when two or more mice were so recorded. I have one record of a male and female taken in the same trap on the night previous to parturition.

The mice are more likely to be taken in groups during autumn and winter and singly during spring and summer. That males and females occasionally nest together and travel together is evident from the following records: On June 11, 1936, I took an adult male and female together in a single-catch trap, which necessarily had to be entered by both at about the same time. The female, No. 48, appeared to be in breeding condition. On February 13, 1937, adult male No. 328 and adult female No. 332 were found occupying the same nest. They were left in their nest and disturbed as little as possible. Traps were set that evening, and the next morning these two mice were together in a trap about sixty feet distant from the nest. I have no way of knowing that the two animals traveled together, but I do know that they left the same place in the evening and reached the same trap. There were three other traps, all of which were closer to the nest than the one

entered, so it would seem that had they not traveled together they would have been likely to encounter different traps.

The data, though meager, indicate that *Peromyscus leucopus,* is not, strictly speaking, a social animal. This is especially true during the breeding season, when territorial behavior is displayed. In late fall and winter, after breeding activities have ceased, wood mice seem to be more sociable and individuals of the same or different sexes are found together.

ACTIVITY

These mice, unless disturbed, usually spend the daytime in their nests and come out to forage at the approach of dusk. Trapping records indicate that they are most active, at least in their search for food, during the early part of the night. Males wander farther than do females, and in this respect are more active. They are good climbers and do not confine their activities to the ground. I often caught these mice in traps attached, about five feet above the ground, to the trunks of trees. I have no direct evidence that they are more active in certain types of weather than they are in other types of weather, but my general impression is that one is likely to have a better catch on a dark, rainy night than on a clear, moonlight night. Whether the mice are more active or whether they can detect the bait more readily on a damp night I do not know. They remain active throughout the winter.

HOME RANGE

The home range of an animal, as here defined, is that area about its established home which is traversed by the animal in its normal activities of food-gathering, mating, and caring for young. It excludes those areas traversed by vagrants or other individuals in search of home sites. In *Peromyscus leucopus,* and probably in many other species of mammals, the home ranges of the two sexes differ appreciably. By trapping only, it is difficult to determine accurately the extent of the home range of an individual, because it is not certain that the animal has been caught in all parts of its range. Furthermore, because of the irregular shapes of the ranges, it is not easy to calculate the areas covered. Then, too, the range may shift from time to time so that the area covered by an animal in one period may not be the same as that covered by the same animal two or three months later. Therefore, my figures representing home ranges are subject to considerable error. They may serve, nevertheless, to indicate the size of each home range.

In order to eliminate some of the error that might occur in instances of shifting ranges, I have grouped the records of each individual by periods of one month. The calculated area covered by an individual within a period of a month may be explained by the following example: If traps are set ten yards apart in a grid pattern, each trap represents a unit one hundred

square yards in area. If, during the trapping period, a mouse is caught at points throughout an area covered by ten traps, then this area, one thousand square yards, is considered to be the home range. The great variation in size of home ranges indicated by my figures is probably exaggerated; undoubtedly there is considerable variation in size of areas covered by different mice and in the size of the area covered by the same mouse at different times. The smaller figures probably indicate insufficient trapping records rather than extremely small home ranges. The ranges of a few individuals, the records of which are fairly complete, are given in Table VI. It should be noted that some individuals—No. 403 (female), for instance—maintain a fairly large range throughout an entire season, but that the ranges of others fluctuate in size from month to month. For adult females, in sixty-five monthly periods the ranges averaged 1012 square yards (0.208 acres), with 300 square yards (0.062 acres) as a minimum and 1800 square yards (0.372 acres) as a maximum. In fifty-eight periods for adult males, the average range was 1312 square yards (0.27 acres), with a minimum of 800 square yards (0.165 acres) and a maximum of 2600 square yards 0.54 acres). I suspect that in this species the size of the home range is about the same as the size of the territory, the protected part of the home range.

TABLE VI

SIZES OF HOME RANGES OF *PEROMYSCUS LEUCOPUS*, 1936

Mouse Number	June		July		August		September	
	Times Caught	Square Yards	Times Caught	Square Yards	Times Caught	Square Yards	Times Caught	Square Yards
217 ♂ *	8	1600	9	1800	10	2400	7	2400
220 ♂	7	1600	7	1400	.....	.....	.....	.....
409 ♂	8	1800	12	1600	.....	.....	.....	.....
402 ♂	8	1400	11	2000	6	1400	6	800
404 ♂	10	1400	12	1400	7	1600	6	1400
408 ♂	8	1400	8	1000	7	1200	7	1600
415 ♂	7	800	6	800	4	1000	9	1400
416 ♂	5	1000	10	1000	8	1400	9	1400
400 ♀	8	1200	11	1000	6	800	.....	.....
403 ♀	8	1600	10	1600	8	1800	9	1200
406 ♀	9	1200	10	1000	4	400	5	1000
407 ♀	7	1200	9	800	12	1000	10	1000
410 ♀	4	600	9	1000	7	1000	11	1200
414 ♀	5	800	8	1200	4	800	8	1000

* All of the mice were adult except those listed in the June column below the first three.

TERRITORIAL BEHAVIOR

Territoriality can exist only when there is a defense of all or of part of the home range of an animal. This defense is directed primarily against members of the same species. I found it impossible to study the territorial

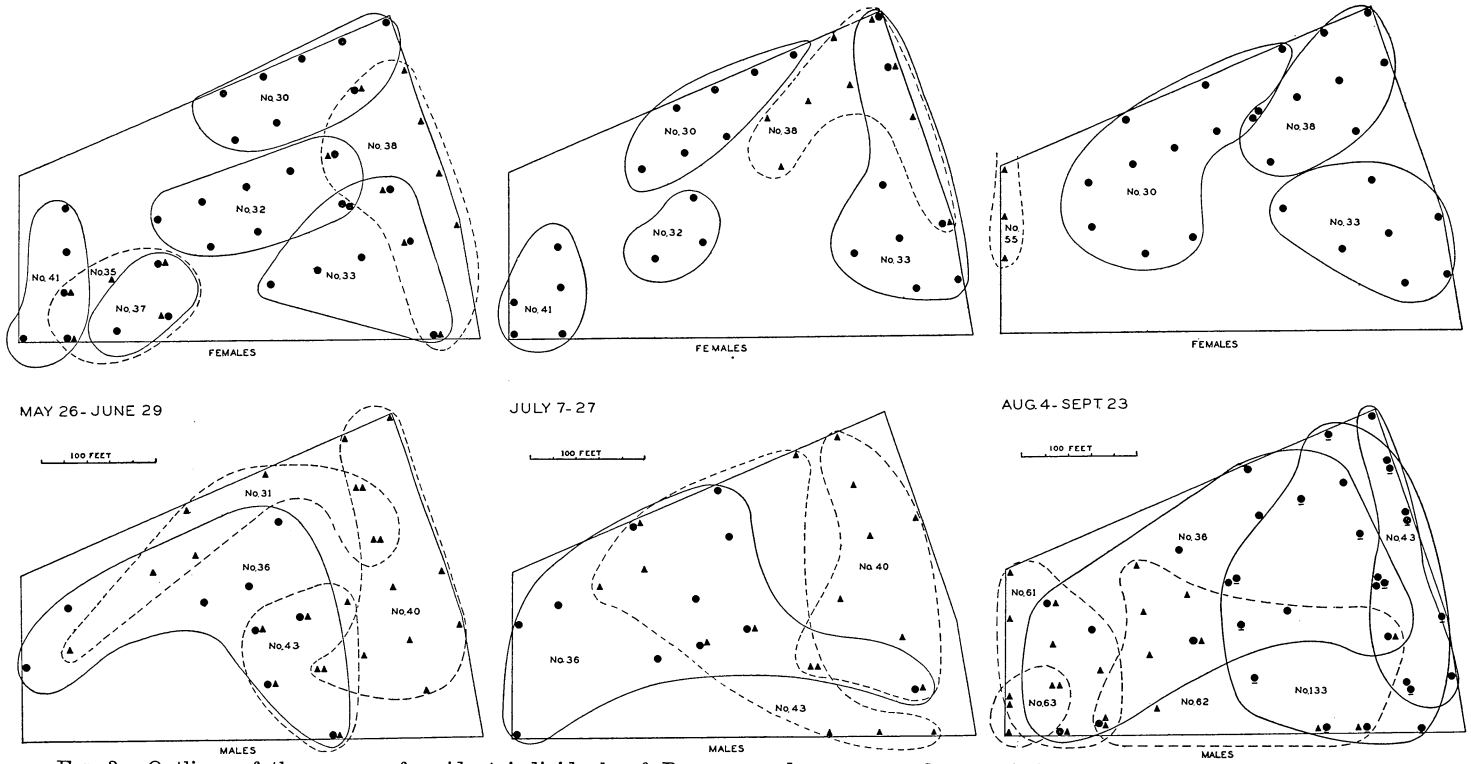


FIG. 3. Outlines of the ranges of resident individuals of *Peromyscus leucopus noveboracensis* in Plot 2 during the season May 26–September 23, 1935. Closed circles represent places of capture of adults, and triangles those of young animals. Approximate areas covered by different animals are outlined in solid lines (adults) and broken lines (young animals).

behavior of such nocturnal animals as *Peromyscus* by direct observation. It was necessary, therefore, to rely upon data gathered by live-trapping and marking the animals. By plotting the positions of capture of the different individuals on the map of an area, I find that the area of each of the breeding females is separate—that although areas sometimes adjoin one another, they seldom overlap. I interpret this to mean that there is a defense of territory, that trespass is not tolerated. Whether or not members of this species defend their territories against invasion by other species is not known.

The finding of the territory is probably a matter of chance. Available evidence indicates that a young animal that is forced away from the territory where it was born wanders more or less at random—sometimes leaving its preferred habitat—until it finds an unoccupied area where it can establish a permanent home. Some animals find places near by; others are forced to travel relatively long distances before they find vacancies. Once a mouse settles down and establishes a territory, it usually, but not always, remains there for life. A breeding female ordinarily remains at least until the end of the breeding season. Territories of females may shift slightly from season to season, but rarely do they shift any great distance. When an old female shifts her territory, a young female will usually take up her old abode. During my studies there was no time when all of the available habitat under consideration was occupied by adult breeding females (Figs. 3 and 4).

A mouse apparently is familiar with every part of its territory. Although it may not form runways, it apparently has definite trails which it follows fairly closely. I always watched each animal after it had been released; in nearly every instance the animal seemed to know where it was going, if it were released in its home territory. One female, caught several times, often took a rather roundabout way, but always went to the same retreat. She climbed up into a small shrub, crossed by way of its branches to a fallen tree, went down its trunk to the base, and thence into a hole. Most animals, however, took a more direct course. In many instances they disappeared into holes not visible from the point of release. When a mouse is carried to a place beyond the limits of its territory and is released, it often wanders for some time before it finds a retreat in which it can seek protection. It is important for a mouse to know its territory if it is to escape its enemies. Unless an animal is aware of all the retreats and of ways of reaching one in short order, it stands little chance of escaping the more alert predators.

The size of the territory maintained by individuals of a species is a significant factor in limiting the population of the species.

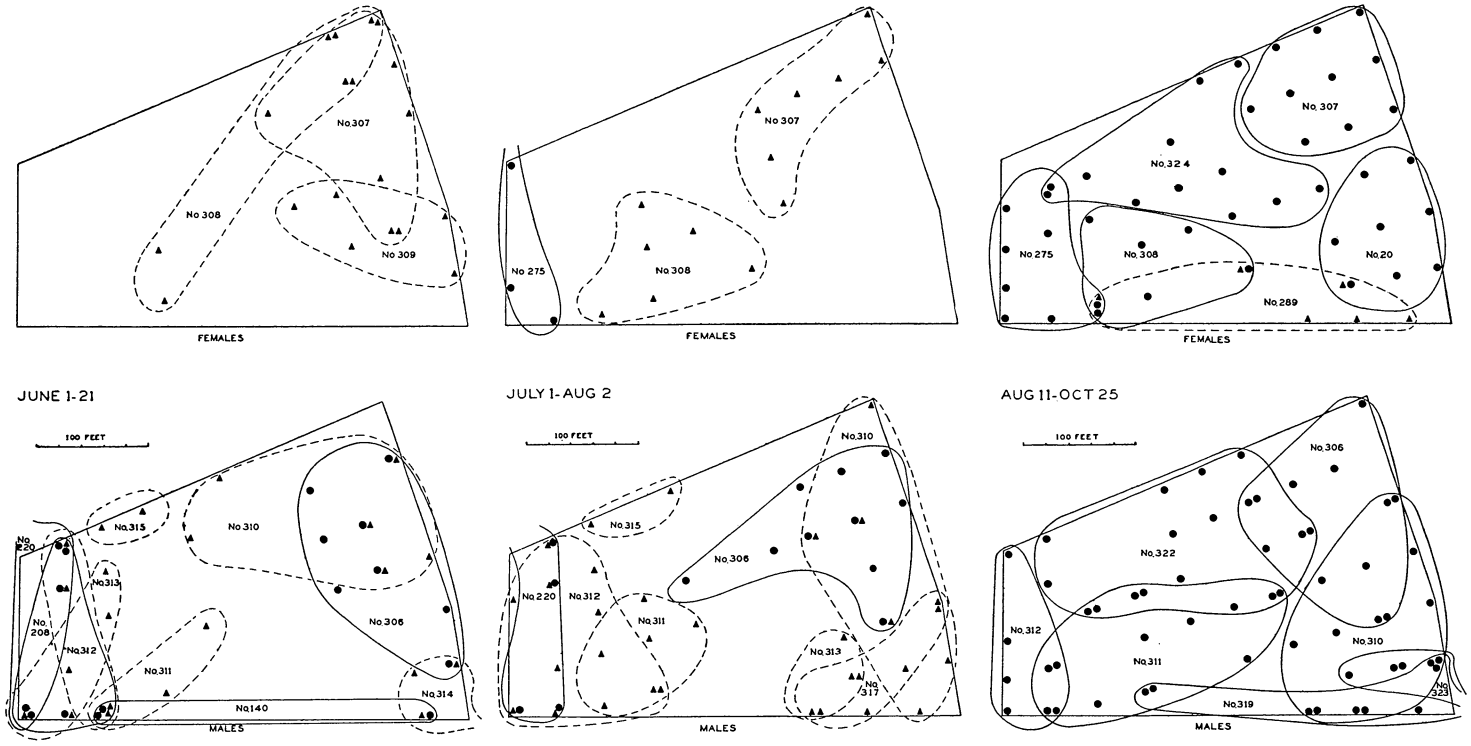


FIG. 4. Outlines of the ranges of resident individuals of *Peromyscus leucopus noveboracensis* in Plot 2 during the season June 1–October 25, 1936. Closed circles represent places of capture of adults, and triangles those of young animals. Approximate areas covered by different animals are outlined in solid lines (adults) and broken lines (young animals).

HOMING INSTINCT

There have been few attempts to determine whether or not these mice possess a "homing instinct." Johnson (1926) marked and carried three mice (*Peromyscus leucopus noveboracensis*) for distances up to 200 yards from the place of capture. Two of them returned, one from 150 yards and one from 200 yards. The third mouse, carried about 100 yards away, remained where it was released. Townsend (1935: 82), working with the same species of mice, found that "several of these, released at a distance of 100 yards, returned to practically the same locality where they were first taken." According to Hamilton (1937: 262), they return distances that vary from one-fourth of a mile to one mile. Murie and Murie (1931 and 1932), working with 176 marked *Peromyscus maniculatus,* a different species, found that one of them returned a distance of two miles.

Chitty (1937: 37) commented on the above experiments in the following words:

> (a) It is likely that returns from the shorter distances may be explained by the mice having a bigger home range than expected. (b) As an alternative hypothesis to that of "homing instinct" the following explanation might bear examination: that chance wandering combined with a high activity serves to bring the animal into an area of fairly large size with which it is familiar.

The Muries have some evidence that the dispersion from place of release is chiefly in one direction—homeward.

An experiment to determine whether or not *Peromyscus leucopus* possesses a homing instinct was carried out in the following manner: A quadrat 300 yards long and eighty yards wide was selected along one side of an extensive wood lot. Live traps were set in a grid pattern, about sixteen yards apart, throughout the area. All traps remained set for four nights, August 5–8, 1937, and each of the mice caught on the first three nights, as soon as it was first discovered in a trap, was carried to the center of the plot and released (Fig. 5). When they were taken from the traps they were marked and placed in a metal bucket with a tight lid, and could not see where they were being carried. Many of them were transported across the length of the quadrat several times before they eventually were released. The distances from the points of capture to the point of release ranged from ten to 155 yards. Inasmuch as the average normal range of an individual is rarely more than seventy-five yards in greatest diameter, the mice from areas more than three trap lines away from the center may be considered as having been carried out of their territories. The possibility of any one animal's knowing the entire area may be ruled out, I believe, because apparently the wood mouse rarely goes any great distance once it has established a home. Young animals in their search for a home constitute an exception. If there were no homing sense—no directing force—we should expect the mice to disperse equally in all directions from the point of release.

The experiment may be summarized as follows: Thirty-seven mice from throughout the area were released in the center of the quadrat. These were made up of the following categories: old males, thirteen; old females, nine; young mature males of the year, ten; young mature females of the year, four; young immature female, one. All of these mice except one young female were old enough to have established their homes, although, as will be pointed out later, some of them probably were still wandering in search of homes. If the mouse were recaptured not more than two traps distant from the point where it was originally taken, I considered it to have returned home; otherwise, it was considered to be lost or wandering. Twenty-eight individuals, or 76 per cent of the mice, returned home. Thirteen of these were recaptured in the same traps in which they were taken originally (Fig. 5 *A*). Two went in a direction almost exactly opposite to the direction of home. One of these (No. 556) came back nearly to the point of release on the second night. Another (No. 565) on the way to its home, which was 150 yards from the point of release, was stopped by a trap when it had gone but half that distance. One (No. 575) was taken near the point of release and was in its home territory. One (No. 576) entered a trap near the point of release, and another (No. 2123) went in the homeward direction, but beyond the place of initial capture, and then, on the second night, returned about 160 yards and was caught slightly beyond the point of release and in the direction opposite from the point where it was first taken. Since this mouse, a young adult male, had been marked in another wood lot less than two weeks prior to being captured here, it was probably a wanderer which had no established home to which to return. This explanation may account for the action of some of the others that did not return to the place of capture. Three of the animals (Nos. 561, 582, and 583) were not retaken (Fig. 5 *B*). The distances traveled by those that returned home are given in Table VII. Of these, nineteen returned the first night after release, five were taken on the second night, and four on the third.

TABLE VII

DISTANCES TRAVELED BY MICE ON THEIR RETURN HOME, FIRST EXPERIMENT

Yards returned	10	25	40	45	70	75	80	85	90	120	125	135	140	150	155
Number of males	1	1	2	1	2	2	1	1	.....	1	1	1	1	3	2
Number of females	.....	1	2	1	.....	.....	1	.....	1	2	.....	.....	.....	.....	.....

In Figure 5 *A*, I have attempted to show graphically the results of the experiment. The traps are represented by the small rectangles, the places of first capture by solid circles, and the points of recapture by open circles. The position of recapture of a mouse in the same trap is represented by a solid circle surrounded by an open circle. Arrows indicate the point of first capture (solid circle) and of recapture (open circle) of each individual. In

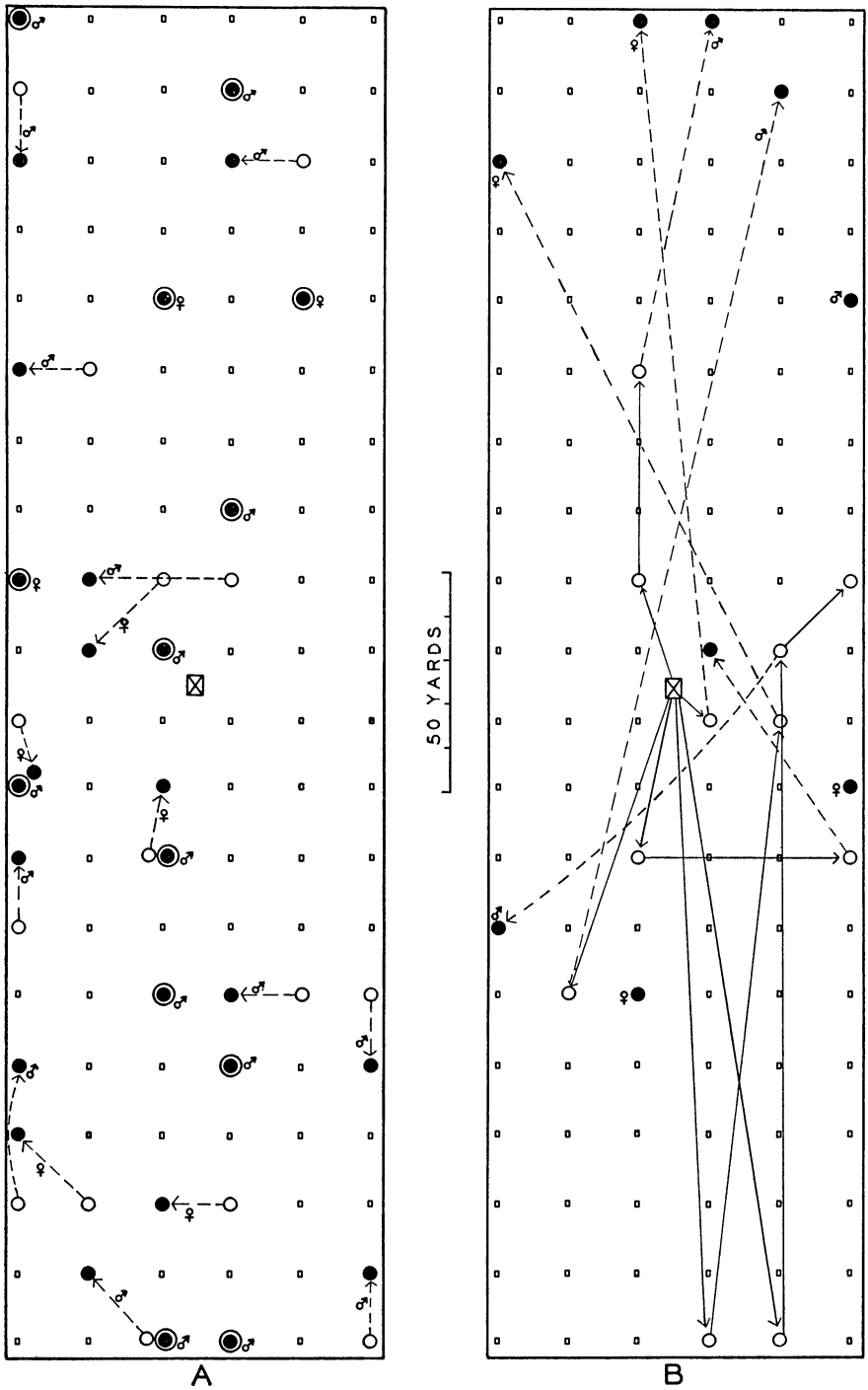


FIG. 5. First homing-instinct experiment with *Peromyscus leucopus noveboracensis*. *A*, positions of capture of mice that went home; *B*, positions of capture of mice that did not return home. For detailed explanation see pages 31 and 33.

Figure 5 *B*, I have included the recaptures on successive nights to show the wanderings of those that did not return home. The line from the center points to the place of recapture after the mice had been released. Solid lines represent their travels, and broken lines indicate where they should have gone to reach home.

A week after this experiment I trapped the same quadrat again for two nights, August 16–17, 1937. All of the mice that had returned to their homes, represented in Figure 5 *A*, were caught again, and all but one were still in the same territories. This one, a young adult male, had moved 145 yards toward the southeast corner of the quadrat. Of those represented in Figure 5 *B*, only one (No. 575) was taken. This mouse, as has been pointed out (p. 31), originally had been caught near the center of the quadrat, and the point of release was, no doubt, within his territory.

As a further check on the homing instinct hypothesis, another area was selected and the experiment was repeated. In this experiment, however, many of the animals were carried considerably farther from their homes. Otherwise, the details of the experiment were the same as those outlined for the first area. The second area, somewhat irregular in outline, was 350 yards in greatest length. Throughout slightly more than half its length it was 125 yards wide, the remainder being but forty yards in width (Fig. 6). This wood lot is surrounded by open fields, except at the narrow end, which continues as a strip of woods. All animals caught in the narrow strip (west end) were carried to the southeast corner and released (Fig. 6 *A*); those caught in the broader east section of the area were carried to the west end and released (Fig. 6 *B*). The greatest distance that an animal was moved in a straight line was 365 yards, and the shortest distance, 160 yards. Thus, the shortest distance that mice were moved was about three times the diameter of the normal range of an individual. Traps were set August 20–23 and against August 31—September 3, 1937.

Fifty-one mice, all but four being adults, were involved in this experiment. Thirty-two were carried from the east section and released at the west end; nineteen were carried from the west section of the plot and released at the southeast corner. Six of the nineteen released at the southeast corner returned home; the distances which they covered in returning were 270, 300, 300, 335, 360, and 365 yards, respectively. Eight started in the general direction of home and reached distances from the point of release of 40 to 110 yards. Five were not recaught. Of those released at the west end, thirty-two in all, eleven returned home from distances of 175, 175, 175, 185, 200, 210, 215, 240, 255, 300, and 355 yards, respectively. Nine started in the general direction of home and reached distances of ninety yards or less. One remained at the point of release, and eleven were not retaken.

The experiment in this plot may be summarized as follows: Fifty-one mice

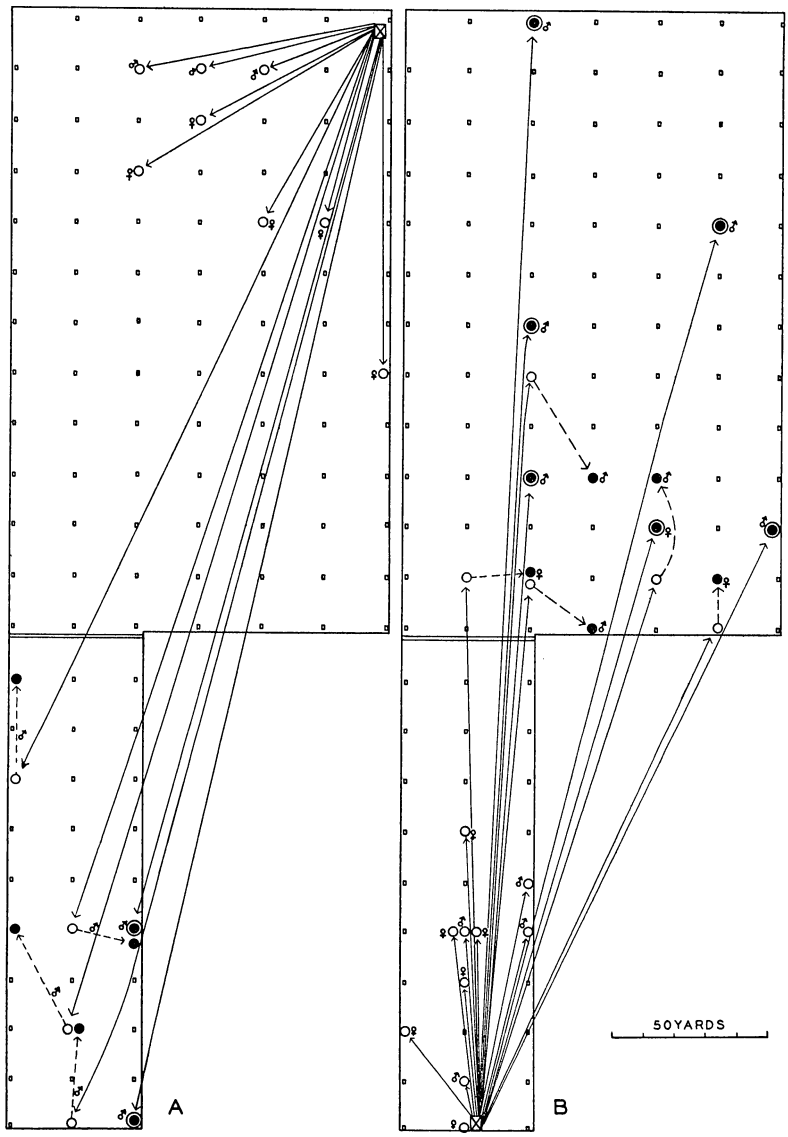


FIG. 6. Results of second homing-instinct experiment with *Peromyscus leucopus noveboracensis*. *A*, mice caught in lower section, below double line, were carried to upper right corner and released. *B*, those taken in upper section, above double line, were carried to lower edge and released. Solid line points to place of recapture—solid circle within open circle if mouse returned to same trap; otherwise, open circle. Broken lines point to place of original capture of mice that returned home, but not to same trap.

were moved distances of 160 to 365 yards. Seventeen mice, 33⅓ per cent of those moved, returned to their homes over distances of 175 to 365 yards (Table VIII). Seventeen, 33⅓ per cent, started in the proper direction and traveled 110 yards or less, but did not reach home. One, 2 per cent, stayed at the point of release, and sixteen, 31⅓ per cent, were not taken again.

TABLE VIII

DISTANCES TRAVELED BY MICE ON THEIR RETURN HOME, SECOND EXPERIMENT

Yards returned	175	185	200	210	215	240	255	270	300	335	355	360	365
Number of males	1	1	.....	1	1	1	1	1	3	1	1	1	1
Number of females	2	.....	1	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....

Mice released at the southeast corner were forced to start in the direction of home if they remained in the wooded area, as this corner was bordered by grassland. Those released at the west end had continuous woods in every direction. This may account for the higher percentage of directional movement towards home among mice released at the southeast corner than among those released at the west end (73.7 per cent as against 62.5 per cent). The grassland, however, is not a barrier to these mice.

It will be noted that in the first experiment, in which mice were carried ten to 155 yards and released (Fig. 5), 76 per cent returned to their homes, but that in the second experiment, in which they were carried 160 to 365 yards (Fig. 6), 33⅓ per cent returned to their homes. The smaller percentage of returns seems to be correlated with the greater distances that the mice were moved.

This, it seems to me, indicates that members of this species possess a homing sense of some nature. Random wandering would not account for the return of such a large proportion of the animals to the place of first capture, nor for the return of many to the same trap.

DISPERSAL

Dispersal of individuals in this species occurs chiefly while the animals are young and before they have established their homes. Once an animal selects a home site it rarely leaves, but usually remains there for the rest of its life. I have records of 287 animals that were taken between two weeks and a year after their initial capture. The distances between the points of initial capture and the points of subsequent captures are shown in Table IX. If animals remained within 100 yards of the place of original capture (nearly twice the radius of an average home range) they were considered not to have dispersed. It will be noted that of fifty-six old females only three moved appreciable distances from the points of initial capture, two moved between 200 and 300 yards, and one between 700 and 800 yards. Old males move greater distances than do old females but young males and females

TABLE IX

DISTANCES BETWEEN POINTS OF INITIAL CAPTURE AND POINTS OF LAST CAPTURE, AFTER AN INTERVAL OF TWO WEEKS OR MORE, OF *PEROMYSCUS LEUCOPUS*
The first column is within the normal range of the individual.

Yards	0–100	101–200	201–300	301–400	401–500	501–600	601–700	701–800	801–900
Old females	53	.....	2	.....	.....	.....	.....	1	.....
Old males	56	17	3	.....	.....	.....	.....	1	.....
Young females	60	10	3	1	1	.....	.....	.....	1
Young males	43	13	13	4	1	1	1	.....	2
Total	212	40	21	5	2	1	1	2	3

move farther than do old males. The animals that moved farthest (800 to 900 yards) were young. It is quite probable that a number of these animals had moved some distance before they were caught the first time, and some undoubtedly continued to move after the last capture. My records, therefore, do not necessarily indicate maximum distances traveled. They do, however, give some indication of the distances dispersed. The records show (Table IX) that about one-third of the young (fifty-one of the 154 recorded) moved distances of 100 to 900 yards from the place of initial capture, and that two-thirds remained fairly close to (within 100 yards of) the place where first taken. The average distance moved by the fifty-one young animals is 266 yards.

POPULATIONS[1]

In an attempt to determine populations of *Peromyscus* in central New York, Townsend (1935: Pl. I) used a stationary line of traps about one hundred feet long, and, "several yards away," a moving quadrat consisting of three lines of traps, the lines being a rod apart and each line thirty-three feet long. After each night of trapping, the line nearest the starting base was picked up and moved a rod ahead of the foremost line; thus the lines were advanced through the quadrat. The traps were set and changed in this fashion for fourteen days, after which time all were moved to another area. The moving quadrat and stationary line covered seventeen-eightieths of an acre. In the stationary line, only the catch of the first three nights was counted in his population estimates. Because his quadrat was only thirty-three feet wide by 264 feet long, and because an individual mouse normally ranges over an area of 150 to 300 feet in diameter, it is apparent that Townsend was using his traps not only for animals which ranged wholly within the quadrat but also for those which ranged in part outside the quadrat.

In calculating the population per acre, as I understand his experiment,

[1] An important paper by B. P. Bole (1939) was published after this had gone to press. He has discussed a number of problems regarding population studies; some of these I also treat here.

Townsend considered the area covered by his traps, plus a strip one-half rod wide at each end—a total area of about seventeen-eightieths of an acre. He should have included a strip no less than 125 feet wide (about one-half the diameter of a home range) all around his quadrat, provided the quadrat was well inside the habitat and not on one of its borders. Calculating his area in this way one would expect him to trap out two to three acres instead of seventeen-eightieths of an acre. His population estimates, are, therefore, possibly from ten to fifteen times greater than the actual population. It is impossible from the data Townsend presents to calculate the number of mice per acre. He does not give the distance between the stationary line and the moving quadrat, nor does he state whether his traps were near the border of the woods or well within it. Furthermore, it is essential to know the exact dates, because of the fluctuation in numbers from month to month. Suffice it to state that his estimates certainly were too high and were subject to a rather large error.

Williams (1936) used a still smaller quadrat (ten meters square) than did Townsend, and his error in estimating populations is, therefore, still greater. He, however, realized his error before the end of his studies, and stated that his estimates were undoubtedly too high. Inasmuch as his quadrat and his total catch were both so small, the resultant error is great enough so that his data cannot be considered of any significance for a proper estimate of the actual numbers of animals. If his table of total catches is studied (Williams, 1936: 362) one finds that in Quadrat A, for instance, he caught eight mice in 1932, one in 1933, none in 1934, and three in 1935. One may account for these differences in numbers in the following manner: Suppose, in 1932, that his quadrat were over a home where a litter of young mice were ready to leave the nest. If he caught this family and also one or two individuals that wandered in from the outside he would have his maximum population. His low catch in 1933 and 1934 may be explained: (1) by depletion of the population by a predator, and (2) by trapping in an unoccupied area. Williams (1936: 363) estimated that in the autumn of 1932 there were 218.52 wood mice (*Peromyscus leucopus*) per acre. This would be one mouse for every area fourteen feet square. His total of all mammals per acre, which he estimates at 529.25, is one animal for each area seven feet square—a veritable plague!

In order to determine the population of unit areas for a given species, it is essential first to select an area larger than the normal range of an individual of that species. The larger the area, the less will be the error. Townsend's quadrats covered, in length, a strip that would be covered by one animal, but in width they were much less. The quadrats used by Williams were about one-sixth the area covered by a single animal.

Another source of error in the findings of both these men is the use of snap

traps. When a mouse is removed from an area, its territory is made vacant and becomes available to another animal. In my population studies live traps were used; the only animals taken off the areas were those that died in the traps. Many were lost in this way at the beginning of the first season, but during the last two seasons, after the trapping technique had been improved, very few mice died in the traps.

The technique which I employed is not perfect, but I believe it gives a fairly reliable index to the population of *Peromyscus* per unit area. Three fairly isolated wood lots were selected on the George Reserve, covering 1.8, 3.72, and 24 acres respectively. Live traps were set in grid pattern every ten paces (about thirty feet) apart in the plot of 1.8 acres; in the plot of 3.72 acres, the traps were set twenty paces apart with the lines ten paces apart; and in the twenty-four-acre plot the traps were placed twenty paces apart in lines, which also were twenty paces apart. All traps were numbered and left in the same positions throughout the trapping period. The positions of the traps were plotted on a map of the area. Every animal caught was marked and was released at the point of capture as soon as its number, age, and sex, and other information concerning it, as well as the number of the trap and the date, had been recorded. Recaptured animals were recorded and released after external examination. The method of live-trapping and marking animals to determine populations was first suggested by Dice in 1931. If it be assumed that all the animals in the area were caught (except young animals not yet out of the nest) this method should give a fairly accurate count of the population at any given period of a week.

The results from the three areas, with traps spaced differently in each area, were about the same. The only advantage in placing the traps close to one another is that all the animals in an area may be caught in a shorter time. I believe the most practical distance between traps for the areas studied is about forty-five feet. Traps so spaced should catch the animals in the area in five nights.

In order to determine the population in a large tract in which it is impossible to trap all the animals of the species, I suggest that one select a quadrat of two to five acres and set traps in this for at least five nights. If the habitat is uniform beyond the outside line of traps, the area from which the animals come will be not only that in which the traps are set, but will include an additional strip about 125 feet wide along the borders. This is about one-half the mean width of the home ranges of males and females combined. The area thus computed should be that covered by the traps plus 125 feet of border to include marginal animals the ranges of which are partly within and partly outside the trapped area (Dice, 1938: 127). Individual mice range over an area 150 feet to 300 feet in diameter, depending on whether they are females or males.

During the three seasons in which the populations of *Peromyscus* have been followed (1935–37), there has been little fluctuation in numbers from year to year. There is, however, a considerable difference in the population from month to month within any one year. It should be stressed here that in making any population count it is important that the season in which the count is made be considered. In Plots 1 and 2 combined, from June, 1936, to June, 1937, the population varied from 10.87 per acre in November to 3.08 per acre in May (Table X and Fig. 7). In Plot 1 alone, the population was 12.6 per acre in November, 1936. The population curve throughout the year reflects the breeding activities of the animals. It is lowest in May before the first young are abroad. When the first young appear the curve goes up rapidly until about the latter part of June or early July. It then slowly descends, but not to the low point of the month of May. Again in August young come out of the nest, and the curve rises to a point higher than it reached in June. There is then a slight decline in September, but when the young of the spring females also appear, it goes up rapidly to the highest peak of the year in October and November. With the breeding season ended, the curve descends gradually until the lowest point of the year is again reached the following May. My figures, it will be noted, are much lower than those given either by Townsend or Williams.

TABLE X

POPULATION OF *PEROMYSCUS LEUCOPUS* IN PLOTS 1 AND 2 COMBINED, 5.52 ACRES, FROM JUNE, 1936, THROUGH JUNE, 1937

1936	June		July		August		September		October		November		December
	1–14	16–28	1–11	14–26	1–9	11–23	5–13	19–27	2–12	23–26	6–8	21–22	27
Total	28	32	30	28	29	39	39	38	43	57	58	60	45
Number per acre	5.07	5.8	5.43	5.07	5.25	7.07	7.07	6.88	7.79	10.32	10.5	10.87	8.15

1937	January	February	March	April	May		June
	.....	14	7	7	16	27–31	29–30
Total	.....	40	33	27	17	20	28
Number per acre	.....	7.25	6.0	4.9	3.08	3.62	5.07

The population in any area is never static. Old residents are disappearing and new ones are coming on the scene continually (Table XI). During the twelve months, June, 1936, through May, 1937, eighty-seven animals were trapped on an area of 3.72 acres. The greatest number taken at any one time was forty-seven (12.6 per acre) in November, 1936, and the smallest was thirteen (3.5 per acre) in May, 1937. The grand total of eighty-seven probably does not represent the actual number of animals that passed through the area, as some transients undoubtedly went through during peri-

ods when the traps were not set. A few of the animals that disappear from an area may be captured later in other near-by areas, but most of them never are seen again. Predators are undoubtedly responsible for the majority that disappear. The records just cited support the conclusion that of every eight animals which appear in a given area within a year's time, one will survive to propagate the race. As has been pointed out, one pair will produce, on

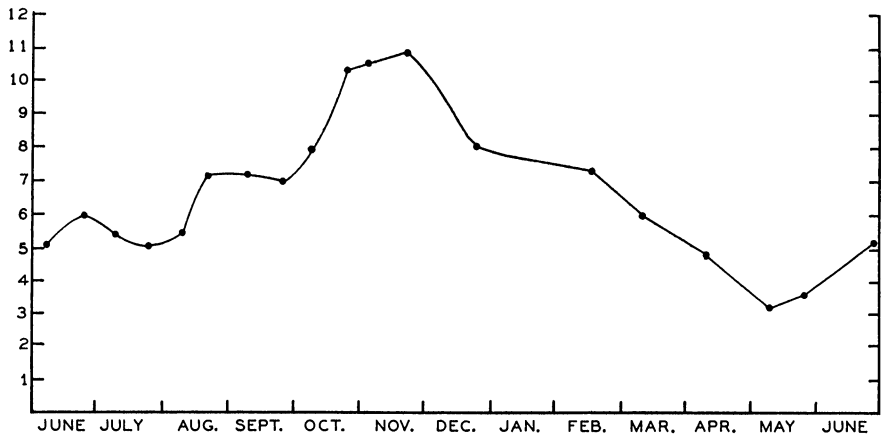


FIG. 7. Population curve for *Peromyscus leucopus noveboracensis*, from June, 1936, through June, 1937, with number of animals per acre (ordinate) during various months of the year (abscissa). Based on mice trapped in Plots 1 and 2, both isolated wood lots.

the average, about sixteen young during the breeding season. To maintain a population, then, the survival of one in eight at the end of a year is all that is necessary, and this seems to be what actually happens if my trapping data are reliable.

LONGEVITY IN THE WILD

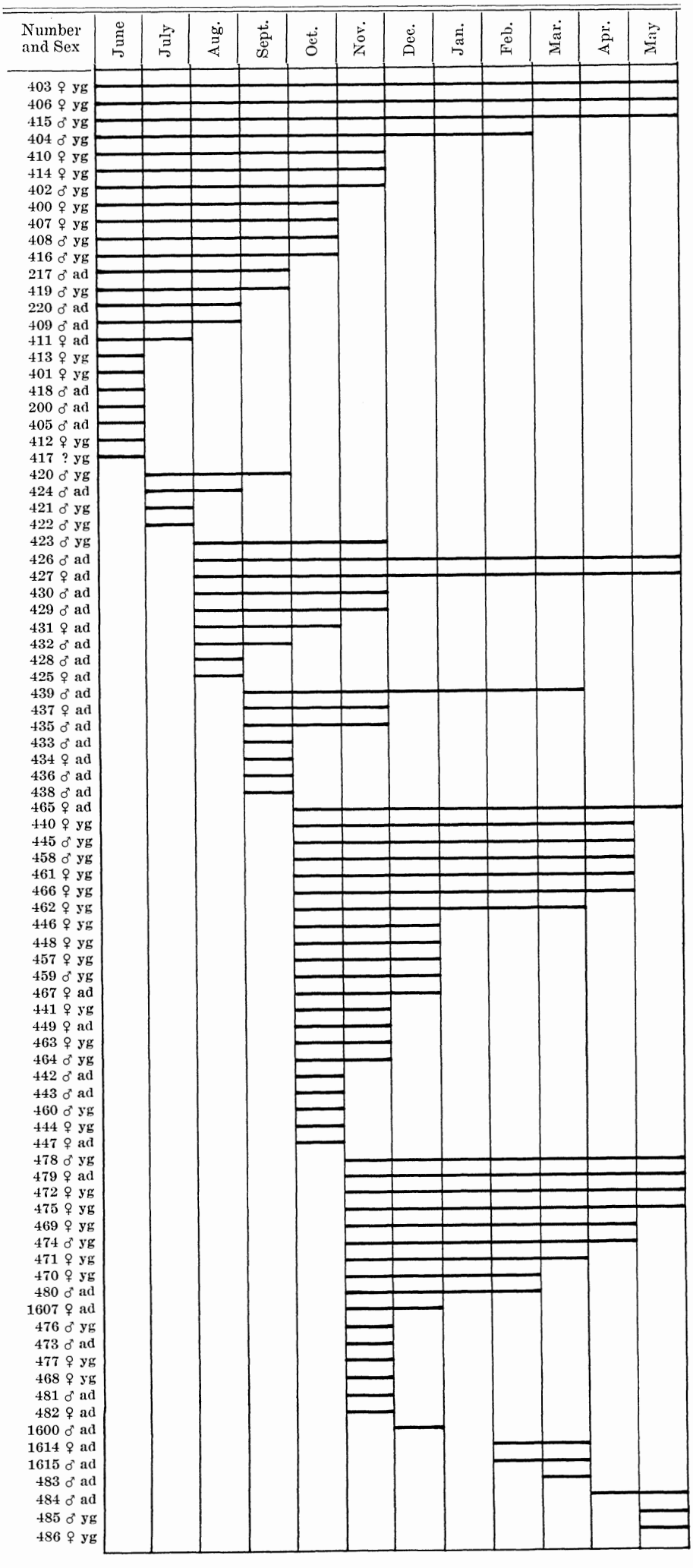
Most mice of this species probably are eliminated by predators or die from some other cause before they reach the age of one year. A few continue to live for a year, and an occasional individual may reach the ripe old age of two years or more. The oldest mouse of which I have a record was nearly two years old in July, 1937. She was taken first on November 9, 1935, at which time she was about a month old. Since then she has remained in the same locality. A nearly complete replacement of animals from year to year indicates that relatively few reach the age of one year. In August, 1936, twenty-six animals were marked in one wood lot. A year later, August, 1937, when the same area was trapped, only one mouse (a male) that had been there the previous year remained.

MORTALITY

It is likely that few, if any, of these mice ever die of old age. In three

TABLE XI

Peromyscus leucopus in Plot 1 (3.72 Acres), June, 1936, through May, 1937
Solid Line Indicates Presence of Animal in Plot



instances, two in the winter and one in June, I found carcasses of these mice. Neither of the two found in winter showed evidence of injury from another animal; however, they had been dead for some time, and it is possible that evidence of injuries sustained previous to death would not have been apparent by the time they were found. Both were less than one year old and surely could not have died of senility. The third, a young female, was found dead June 17, 1935. Her ears and mouth had been chewed by some animal. Another individual (No. 48), when taken November 7, 1936, had a broken right hind leg. She was found dead November 21, 1936. Death in this case could be attributed to the injury previously received. She was slightly more than one year old. Seton (1920: 134–38) cites a record of a nest in which he found dead a mother and three young; the mother apparently had died during parturition of the last young.

If animals as small as these die from causes other than predation, the probability of finding the bodies is remote. One never can hope, therefore, to obtain statistical data on their natural mortality. The statement above, that they rarely, if ever, die of old age, is based on indirect evidence. The fact that there is a nearly complete replacement of animals from year to year, and furthermore, the fact that animals in the laboratory will live five years or longer, is strongly indicative of a high mortality through predation. It is known, from stomach analysis, that nearly every predator of importance takes its toll of these mice. The greatest losses are undoubtedly among young animals. Some of the more important predators on the George Reserve are weasels, foxes, owls, and snakes.

PARASITES

During the three seasons that this study was being made, I noticed no evidence of any serious disease that would contribute materially to the death of these animals. No examinations were made for internal parasites.

There are two fairly common types of parasites which attack the mice in this area. One is a scab mite (*Scarcoptes scabei*), which produces swollen, scabby ears and tail and causes the hair to fall out, especially on the dorsal region of the head and body. The other is the botfly (*Cuterebra*), the larvae of which develop beneath the skin. All animals that became infected by one or the other of these parasites while under observation in the study areas recovered. I have no data on the death rate, if death does result, from these infections.

My records show that the scab is most common during the summer months. The earliest occurrence of the disease I have recorded is June 18, and the latest, August 26. I have not noticed it on any winter-taken specimens. Botfly infections occur somewhat later in the summer and in early autumn. I have records of infections from July 22 to October 5. Usually

one bot is all that is found in each animal, but two in an animal are not uncommon. They are most often located near the anal region. From the time the botfly larvae are first apparent, as discerned by external examination of the mouse, until they emerge is about two weeks.

I have one rather complete case history of a mouse infected with the scab parasite which I believe is worth giving in detail. Adult female No. 26 was captured first on June 3, 1935, at which time she was nursing young. On June 18 she showed the first evidence of the infection: hair began to fall out from her forehead. On June 21 the hair had been lost as far back as the base of the neck, and by June 30 she had lost the hair over most of her back. A scab was forming on her forehead. On July 5 her tail was swollen and she appeared to be in bad condition. By July 15 her tail had lost much of the swelling, but the scab was still apparent on her forehead. On July 28 she was noticeably better, and by August 12 the hair on her back had been mostly replaced, although her forehead was still bare and her tail slightly swollen. Less than two weeks later, August 25, she had recovered completely and again had the appearance of a normal mouse. The disease ran its course in slightly more than two months.

The percentages of animals infected with the scab parasite for the three seasons were: 1935, 1.6 per cent; 1936, 1.4 per cent; 1937, 0.54 per cent. No botfly infections were observed in 1935. In 1936, I recorded 0.7 per cent of the animals as being infected, and in 1937, 3.4 per cent.

Tamias striatus lysteri

HABITAT PREFERENCES

Chipmunks in this area rarely are seen at any distance from wooded or brush-covered areas (Pl. II, Fig. 1). They always seem to desire a protective cover and certainly are not at home in the open. It is not known why some species are so closely restricted to one type of habitat while other nearly related species may be found in another type of habitat. Each of two species, as far as we are able to discern, may appear fitted to live in both habitats, yet each remains in its own. I suspect that if we ever learn what operates in habitat selection among mammal species, the factors will be concerned to some extent with the mental processes of the animals of each species—that they live where they do partly because they feel more secure there than elsewhere.

BREEDING

I have but few data on the breeding of the chipmunks, but they are sufficient to indicate that breeding starts about April 1 in this region. The first young are born about May 1 and appear outside the nest about June 1, when nearly two-thirds grown. Old females breed again during the last week in July or early in August, and young females also breed at this time.

Hence, old females raise two litters a year, and young females, born in the spring, may raise one litter each in the fall. The gestation period, as determined from one young female, is thirty-one days. This female was two and one-half or three months old when, on the morning of July 24, 1937, an old male was observed copulating with her. She gave birth to young on August 24, thirty-one days later. The male and female both were numbered and regularly came to a feeding table just outside a window. I was thereby able to identify each accurately and to watch the progress of the female day by day without trapping or otherwise disturbing her. I do not know how long the young remain in the nest, but I believe a month is a fair estimate. This female had not brought her young out of the nest by September 20, at which time I left the George Reserve. A week later, however, when I returned, I saw a young chipmunk near her nest site. It may well have been a young of the female under observation; a month had elapsed since the date of birth of her litter.

I have one record of the number of embryos per litter. An old female found dead in a trap August 12, 1937, contained three large embryos. Dice and Sherman (1922) report, from the Cisco Lake region of Michigan, a female with eight large embryos. Probably eight is nearly the maximum number of young per litter.

SEX RATIO

During the three seasons, 106 chipmunks were marked on the George Reserve. Of these, sixty-four (60.38 per cent) were males and forty-two (39.62 per cent) were females. I doubt that the numbers are sufficiently large to give the true sex ratio, but a preponderance of males over females is indicated.

HOME SITES

Most authorities agree that these chipmunks live in burrows near the roots of trees, in old stumps and dead logs, and along banks. They also take advantage of man-made structures, if convenient to their habitat, making their homes under buildings and piles of stone or wood. On the George Reserve their burrows are to be found in the woods, usually near old stumps or logs. One old female had her home beneath one of the buildings in the center of the George Reserve.

FOOD STORAGE

The generic name *Tamias* was bestowed upon the chipmunk in 1811 by Illiger. It means "steward," and was given to the animal because even then its food-storing propensities were known. Few animals perhaps are more tireless workers when they discover a supply of food. They fill their cheek pouches to capacity and scurry off to deposit their loot in some underground granary, then return to repeat the process until all available food

is carried away and deposited in places probably known only to themselves. Whether or not they consume all of the food they store I do not know; in years of abundance they possibly store more than they can use.

SOCIABILITY

Chipmunks, as judged from my experience with them, are not sociable animals. The female, of course, will tolerate the young for about two weeks after they come out of the nest. During this time the young seem to associate with one another fairly well. Males and females are sociable for a short period preceding the time of mating, but after mating they almost immediately become antagonistic. After a pair had mated on July 24, 1937 (p. 43), the male came to the feeding table and was busy picking up seeds when the female appeared. Instead of allowing her to pick up a few stray seeds, he chased her away. It was not until he had filled his pouches and departed that she came up to gather her share. A week later the female was on the table when the male appeared over the edge. This time the female chased away the male. In the chipmunk world it is first there first served, at least as far as food is concerned. During the three seasons, an old female had her home under the building where we stayed. Many times I have seen her chase other chipmunks, both male and female, that dared to enter her domain. Except for the brief periods of mating and the time spent rearing her young, this old female led a solitary life, with no welcome for others of her kind.

ACTIVITY

Chipmunks are most active in early morning and late afternoon. They are wholly diurnal in their habits and seem to spend most of their time, while abroad, in search of food. Few animals are more alert or move about with more circumspection. They always seem to be on the watch for enemies.

HOME RANGE

Records sufficient to indicate sizes of the home ranges of only four adult female and two adult male chipmunks are available. The greatest diameters of home ranges of the four females, as indicated by trapping records, were respectively 67, 70, 85, and 100 yards, with an average of 80 yards. One male ranged over an area with a diameter of 100 yards, and the other over an area 125 yards in diameter.

TERRITORIAL BEHAVIOR

Chipmunks, being wholly diurnal in their habits, are easily observed by one who is quiet and makes no sudden moves. It is best to observe them from a blind. I had an unusual opportunity to observe an old female that

held a territory around the living quarters in the center of the George Reserve. Although other chipmunks often invaded her territory, she invariably drove them away. Her protected area was about fifty yards in radius; beyond this fifty-yard limit around her nesting site she was not concerned. Her foraging range (i.e., home range) was considerably greater than the protected area (territory) and occasionally extended 100 or more yards from her nest site. The territories held by members of this species apparently are smaller than the normal home ranges of the animals. The areas in which home ranges overlap are neutral and are not protected by any one individual. Gordon (1936) has observed this in the golden-mantled ground squirrel in the Blue Mountains of eastern Oregon.

HOMING INSTINCT

While conducting a homing-instinct experiment on *Peromyscus leucopus,* I carried one chipmunk about 150 yards and released it. This animal returned to the place of capture. The one instance means very little, but it does suggest that these animals might have a homing sense. It should be tried with more of the animals at greater distances.

DISPERSAL

Movements of chipmunks from the place of original capture, according to my data, are confined to young animals and adult males. Old females probably move rarely after they have established their homes. I have records for twenty-eight individuals for periods ranging from a month to two and one-half years. Twenty of these individuals remained in the same locality (within 100 yards of place of original capture) and were grouped as follows: six adult females, four adult males, three young females, and seven young males. Eight individuals moved, respectively, 225 yards (a young female), 300 yards (one adult and two young males), 325 yards (an adult male), 375 yards (a young male), 430 yards (a young male), and 700 yards (an adult male). The average distance over which these eight individuals moved was 370 yards. One-third or more of the animals may be expected to move from the place of original capture.

POPULATIONS

My data on populations of chipmunks do not cover an area sufficiently large to represent conditions accurately. They do give a rough indication of the population per acre and for that reason are presented here. The total area of the two study plots is 5.52 acres. These are isolated wood lots and therefore the counts should be fairly accurate. I have added together the numbers of animals in the two areas in Table XII and in the graph (Fig. 8). The breeding population in the spring—old males and females

TABLE XII

POPULATIONS OF CHIPMUNKS DURING THE THREE SEASONS 1935–37 IN PLOTS 1 AND 2 COMBINED, 5.52 ACRES

Year and Month	Number of Adults	Number of Young	Total Number	Number Per Acre
1935				
May	9	0	9	1.63
June	9	11	20	3.62
July	7	6	13	2.56
August[1]	2	1	3	1.66
1936				
May	6	0	6	1.09
June	6	8	14	2.54
July	7	5	12	2.17
August[1]	3	0	3	1.66
1937[2]				
May	3	0	3	0.8
June	3	6	9	2.42
July	3	4	7	1.9
August	2	3	5	1.34

[1] Plot 2 only, 1.8 acres.
[2] Plot 1 only, 3.72 acres.

from the previous year—varied from 1.63 per acre in 1935 to 0.8 per acre in 1937. When the first litter appears in late May or early June, the population is increased in proportion to the number of young produced. It may increase to about four per acre and then gradually decrease until September, when the second litters come out of the nest. Unfortunately, I have no data on the population in the fall months and cannot say what it is then, but I suspect that it is higher than in June, since the young females of the first litter also are bringing forth young at this time.

LONGEVITY IN THE WILD

If they escape predation, chipmunks may live three or more years. I have one record of a female which was adult when marked in the spring of 1935 and was still active in September, 1937. She was at least three years old when last observed. Three animals were at least two years old, and five were one year old each at the time of their last captures. I have not carried my studies over a sufficiently long period to determine the extreme ages reached by individuals.

MORTALITY

I have seen no evidence of disease in the chipmunks during the three seasons at the George Reserve. During late summer and early fall, many of them are parasitized by the botfly larvae (*Cuterebra*). As far as I know, death never results from these parasites. Predation undoubtedly is the main cause of death in this as in other species of rodents. Marsh hawks

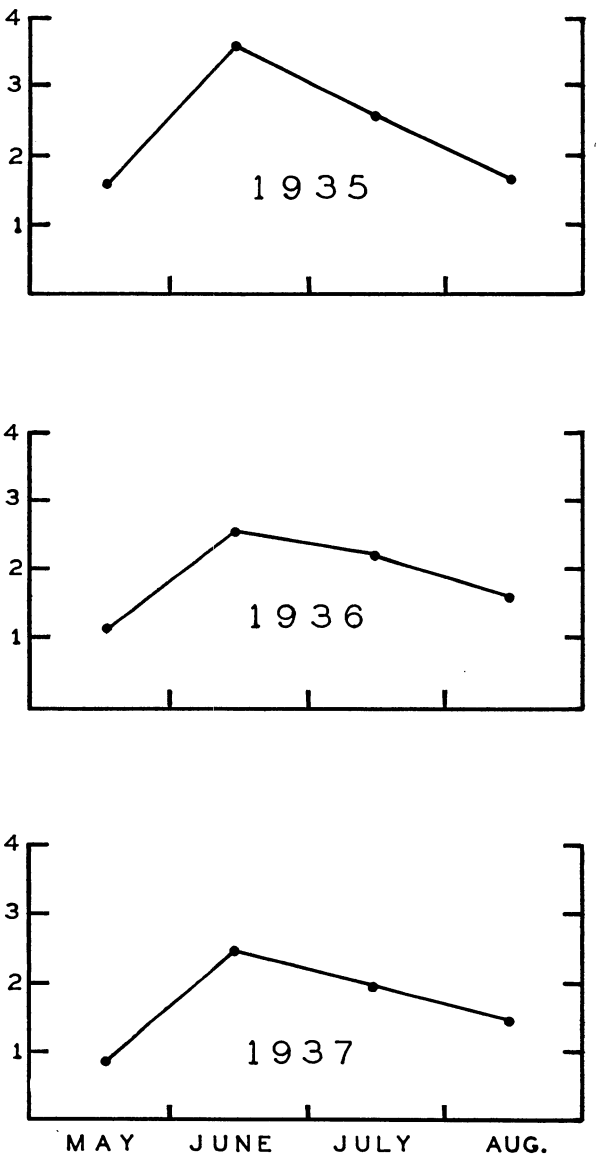


FIG. 8. Population curves for *Tamias striatus lysteri*, during the three seasons 1935–37, with number of animals per acre (ordinate) for the four months May–August (abscissa).

and foxes are probably the two most important predators of chipmunks on the George Reserve.

Glaucomys volans volans

HABITAT PREFERENCES

Flying squirrels are confined to wooded areas. Their homes and safety retreats are in trees—their principal foraging areas. They descend to the ground rather often for the purpose of gathering food, but rarely leave the cover of the woods. In passing from one isolated wood lot to another, they probably follow brushy areas where cover is available.

Nests are, as a rule, in old woodpecker holes or other cavities in trees. In summer, outside nests of leaves in the branches of trees are used by some of the squirrels. One such nest was located in Plot 1, and another near the living quarters on the George Reserve.

BREEDING

My meager data indicate that at the George Reserve the first litter is born in May or early June, and that a second litter is born in August. Old females were suckling in June and again in late August and September. Hibbard (1935) found that, in Kentucky, the young are born in March and September. He found one female with four embryos on August 22.

I have no data on the number of young in a litter. King (1883) records a nest with three young, in Wisconsin, and Hibbard (1935) records eight nests with from two to four young each, in Kentucky. Hibbard's records show an average of three young per litter.

SEX RATIO

Forty-five flying squirrels were marked on the George Reserve. Twenty-seven were males and eighteen were females, the males outnumbering the females three to two. I doubt that this represents the true sex ratio. It is possible that males enter traps more readily than do females. I trapped especially for flying squirrels only in the summer of 1937, in Plot 1, and believe that most of these animals inhabiting the area were caught. In this area the males predominated, seven males and four females were taken during the season.

SOCIABILITY

Flying squirrels are sociable animals, at least during the major part of the year. Never have I seen any indication of antagonism between individuals, either in captivity or in the wild. In the summer of 1937, three flying squirrels came to a feeding table where seeds of various kinds were supplied each evening. Here they sat and ate side by side in perfect peace —a marked contrast to the reactions of a chipmunk when another approaches the feeding table. Flying squirrels often congregate in numbers of twenty or more to spend the winter in a hollow tree (Wood, 1922).

ACTIVITY

As dusk deepens, flying squirrels come out of their nests to go about their nightly activities. By dawn they are again in their nests, where they remain during the day. I never have seen these animals abroad in the daytime except when caught in traps or otherwise disturbed.

HOME RANGE

The two areas in which I trapped especially for flying squirrels were too small to establish definitely the size of the home range. In the larger of the two areas, Plot 1, individuals of both sexes ranged over the entire 3.72 acres. This is a long, narrow wood lot; the greatest distance between traps, at the opposite ends, was 260 yards. Some individuals covered the entire area. During the 1936 season, one old female (No. 5) shifted back and forth between Plot 1 and Plot 2, a distance of 120 yards, and, in addition, ranged over areas 115 yards in diameter in Plot 1 and 100 yards in Plot 2. The dates on which she was caught, and the respective plots, are as follows: June 14, Plot 1; June 17, 21, and July 4, Plot 2; July 7 and 8, Plot 1; July 15 and August 11, Plot 2. The following year, 1937, she remained in Plot 1, where she was taken nine times in the period July 2—September 8. The greatest number of times that an individual squirrel was taken in one season was twenty-two. This was a young female that was first taken July 1, 1937. Subsequently she visited fourteen different traps, entering nine of them once each, three of them twice each, and two of them three times each. She did not go back to the same trap night after night.

POPULATIONS

It was only during the summer of 1937 that I attempted to obtain data on the populations of flying squirrels. Traps larger than those used for *Peromyscus* were placed about five feet from the ground on tree trunks in Plot 1, which has an area of 3.72 acres. One adult female, two young females, and three adult males—a total of six animals (1.6 per acre)—were caught June 29—July 3, and in the period July 13–17 the same animals were taken, except for one adult male lost by death and one not previously caught. Two adult females, two adult males, and one young female were caught June 27–31—a total of five (1.34 per acre). Five animals, one adult female, one adult male, one young female, and two young males, were taken August 10–14. In the entire period, June 29—August 14, the population ranged from 1.6 to 1.34 animals per acre.

LONGEVITY IN THE WILD

The study was not carried on long enough to determine the life span of these animals in the wild. The age of the oldest animal was two or more years at the end of the 1937 season.

Blarina brevicauda talpoides

HABITAT PREFERENCES AND ACTIVITY

The short-tailed shrew apparently prefers wood lots and low areas covered with heavy, herbaceous growths (Pl. II, Fig. 1). That it is not confined to these habitats has been shown by several authors. In southern Michigan these shrews may be found in every available type of land habitat, although they are less common on high, dry areas with a scant cover of vegetation than they are in the woods or in moist lowlands. Their nests are built underground (Shull, 1907) or under logs or stumps (Hamilton, 1929). They not only make their own burrow systems, but occasionally take over the burrows of microtines and moles. They are chiefly, but not wholly, nocturnal in their habits. They have entered my traps in the daytime; also, I have seen them abroad in daylight hours.

HOME RANGE

The data on home ranges were gathered incidentally and are meager. My technique was not worked out for shrews, and as a consequence many were lost in the traps, especially during the summer months. This difficulty, I believe, could be remedied by the use of proper traps and by the practice of visiting them more often than I did. Sixteen animals were recaptured after they were marked. The number of times that individual animals were caught ranged from two to six, and the longest period between first and last capture of an individual was sixty-three days. Three animals were retaken in the traps in which they originally had been caught. Twelve were retaken at distances of fifty-five to 360 feet from the point of original capture. The average of the distances over which these animals ranged was 153 feet. An adult female that was caught six times over a period of two weeks ranged over an area of forty yards in greatest diameter. It is possible that some of the greater distances represent shifts of range rather than extent of home range. The one that moved 360 feet was taken but twice, and the captures were forty-one days apart.

The normal home range of this species probably is about fifty yards in diameter and covers about 0.4 acres. If the animals maintain territories during the breeding season, the breeding population should be no more than about five per acre. The maximum population, including breeding adults and young, should be about twenty-five animals per acre, if eight young be the maximum per litter (Hamilton: 1929). This is in marked contrast to the 299.45 per acre estimated by Williams (1936: 363, Table 13).

Pitymys pinetorum scalopsoides

HABITAT PREFERENCES

The pine vole is considered to be a fairly rare species in southern Michi-

gan. During the summers of 1935 and 1936, I took thirty individuals on the two study plots. In 1937, however, I took but one animal. On the George Reserve, the animals are confined to the oak-hickory woods, where there is either a heavy layer of dead leaves or a fairly dense cover of grass under the trees (Pl. II, Fig. 2). The latter situation is preferred.

HOME RANGE AND DISPERSAL

The available data do not indicate any appreciable difference in the size of the home ranges of the two sexes. They have, therefore, been combined in order to yield the average home range in the species. I have used the records on seventeen individuals that were recaptured upon dates ranging from a week to thirteen months apart. The maximum home ranges, as recorded for two adult males and one adult female, were ninety-three yards in diameter for one of the males and seventy-five yards for the other male and female. The smallest range was fifteen yards in diameter. The average range of the seventeen individuals observed was thirty-eight yards in diameter. The normal home range of individuals of this species is about one-fourth of an acre in extent.

One male was caught four times in the period June 8–August 15, in one corner of Plot 1. On September 25 and on October 10, it was taken in another corner of the plot 300 yards distant from the place of original capture. This is the only record of movement I have for this species. Two individuals, a young female and a young male, were marked on June 10 and July 9, respectively. A year later they were taken in traps sixty-three yards and forty-eight yards, respectively, from the ones in which they were originally caught. They probably remained in their own small areas during the entire time.

Synaptomys cooperi cooperi

HABITAT PREFERENCES

The bog lemming, if present in an area, may be found in low, moist places that support heavy, matlike growths of grass (Pl. I, Fig. 2). In 1936, apparently a peak year for these mice on the George Reserve, they were found on high ground, and even in the midst of the larger woods. In 1937 these lemmings, from all appearances, had disappeared from the George Reserve. I did not catch one all summer, nor were their runways present in places where, only a year before, they had formed a veritable network.

HOME RANGE

I have records which are sufficient to indicate extent of the home range of but one lemming, an adult female. This animal was taken seven times in the period August 25—September 23, 1936, within an area forty yards in greatest diameter. She then moved about 115 yards, where she was last taken October 11.

TERRITORIALITY IN MAMMALS

Defense of Territory

Territorial behavior is known to exist in certain species of mammals as well as in birds, fishes, and many other animal groups (Noble, 1939). It is difficult to conceive of territorial behavior in animals without defense of the territories. This defense, as previously pointed out, is primarily against intrusion by individuals of the same species. Males of the sea lion and walrus stake out their claims and battle other males in order to retain their harems. Males of deer and elk battle others of their kind to protect what may be a shifting territory, but one which holds their attentive females. In the smaller mammals these habits are less easily observed, but are there, nevertheless. I have observed a female chipmunk repeatedly drive away both male and female chipmunks, as well as ground squirrels, that dared to enter her territory at the time she had young in her nest. Gordon (1936) has also reported this behavior in some of the western squirrels.

Of what significance is this defense of territory? What is the animal protecting? Howard (1920) believed that in certain birds this phenomenon is linked with sex and ensures mating and the rearing of young. The male, in migration, usually precedes the female, picks out his territory, and announces his presence by song. This enables the female to secure a mate without undue waste of time, and so enhances the production of young. Most mammals are nonmigratory and are already on the ground when the breeding season starts. To mammals, it seems to me, the important things are food and shelter. Such forms as squirrels, chipmunks, shrews, and mice have small home ranges, and it is necessary that they protect the food supply within the home area, especially during the breeding season. If one of these animals allows invaders to come in and carry off the available food, it is forced to seek another area where food is plentiful.

The protection of territories by established individuals tends to keep itinerants and young individuals on the move. This may be one of the contributing factors in so-called population pressures which at times bring about mass movements, of plague proportions, from certain areas. When plagues do occur, I suspect that the moving animals are mostly young. It is this pressure from within the habitat, this kicking of young individuals from pillar to post, that causes them to transcend barriers, to invade unsuitable habitats, and to disperse over the surface of the earth. I doubt that a nonmigratory animal would move voluntarily from a comfortable nesting site where there was a sufficient food supply. Animals that are moving about in search of a place to claim as their own are covering unfamiliar territory and are much more vulnerable to predators than are those in established territories.

Size of Home Range

The size of the area occupied by any animal is limited by that animal's ability to travel and its necessity for food and protection. A predatory mammal, in many instances, covers a much larger area than does the animal on which it preys. The small rodent that is ever in danger of being captured by one of its enemies must be thoroughly familiar with the area over which it travels. A female mouse (*Peromyscus leucopus*) will range over one-half acre at most. She must know her area thoroughly—every hiding place, be it a stump, a hole, or an old log. When danger approaches she knows where she can seek protection. In live-trapping these mice I always watched the routes they took when they were released. Rarely did they travel more than ten or twenty feet before they ducked into a hole, usually one that I had not seen before. In most cases they made directly for a hole, and there is no doubt in my mind but that they knew where they were going. Random traveling would on occasions lead them to a retreat, but it would not lead them to one nearly 100 per cent of the time. Flying squirrels, when released invariably went up the nearest tree, surveyed the area, and without hesitation proceeded directly toward a tree with a convenient hole in it. On several occasions I have seen them glide to a tree and disappear around the opposite side of the trunk. Upon examining the tree I found that they had landed two or three feet below, and opposite the entrance to a hole which was not visible from the tree they had left. Young individuals just out of the nest sometimes went a more or less roundabout way in finding their retreats, but old animals invariably went directly to a hole or to the nest. Ground squirrels are rarely found at any great distance from a retreat. If surprised, they unerringly go into the nearest burrow. *Microtus* and *Synaptomys* have their tunnels beneath the heavy grass; shrews and *Pitymys* tunnel beneath the floor of leaves in the woods. These are their highway systems which lead to safe retreats beneath the surface of the ground. Rarely do they come out into the open; instead, they remain for the most part in their system of tunnels, which they make as they expand their ranges.

The larger herbivores are familiar with the area they cover in search of food. Rarely are they trapped in a place where there is no known avenue of escape. Their resting sites are well selected, and their feeding areas are not so large but that they know them thoroughly. Deer (*Odocoileus*) have been known to remain "in certain areas when there appears to be more and better food only a short distance away, and easily accessible" (Bartlett and Stephenson, 1929: 415), and yet they will not move out.

We have very little definite data on the actual sizes of territories or home ranges of individuals of any species of mammal. The wolf is said to have a hunting range several miles long, and the mountain lion is likewise supposed to range over a considerable area. These large predators might travel easily

a distance of ten or more miles in a night, and they probably do, if food is scarce. Until we have more definite information on the travels of the larger animals it is best to refrain from a discussion of their hypothetical ranges. We have definite information on the size of home range of some of the smaller mammals. These data may be secured in two ways: (1) by direct observations of diurnal species, and (2) by live-trapping, marking, and releasing. We know that the female Mohave ground squirrel (*Citellus mohavensis*) will cover an area in one day with the greatest diameter of at least 130 yards, over three acres (Burt, 1930). Breeding females of *Peromyscus leucopus noveboracensis* will range over an area of one-half acre or less, while old males may cover as much as one and one-half acres, although usually they range over less than an acre. The pine mouse (*Pitymys pinetorum scalopsoides*) probably is confined to a smaller area. Our records are scanty on this species, but we do know that some individuals cover areas at least 100 feet in greatest diameter (0.25 acres). *Microtus pennsylvanicus,* according to Hamilton (1937), will range over about 0.2 acres. *Synaptomys cooperi* will range over an area about 120 feet in diameter (0.5 acres), and the short-tailed shrew (*Blarina brevicauda talpoides*) over an area at least 100 feet across (0.4 acres). The female eastern chipmunk (*Tamias striatus lysteri*) ranges over an area of about one acre. Blair (1936: 203) has found that the Florida marsh rabbit (*Sylvilagus palustris paludicola*) ranges within an area no more than 100 yards across, and Lay and Baker (1938) indicate that the home range of *Neotoma floridana attwateri* is only about eighty feet in diameter.

Significance of Size of Territory

It has been shown that the size of the home range varies greatly according to species, and, within certain species, according to sex. The size of the territory within the home range becomes important in limiting the population in an area. The wood mouse (*P. l. noveboracensis*) is an example: A breeding female, in typical woodland habitat in southern Michigan, must have for her own an area of at least one-fourth of an acre. This means that there can be no more than four breeding females per acre (and there are usually slightly less, according to the data). If the sexes are about equal in numbers—and from our data they seem to be—the population of this species is not more than eight per acre at the beginning of the breeding season in early March. Actually, I have found the areas about half filled, or with less than four mice per acre, in the spring. The beginning of the breeding season is the critical period in the population of any species, as this is the time when it is smallest. The population may swell during the summer months and reach its peak in late autumn after the last litters are born, when the maximum is ten or twelve mice per acre. By the beginning of the next breeding season the females that weathered the winter must locate nesting sites and

establish their territories to begin a new cycle of breeding activity. It is at this period that territorial behavior influences the new generation of mice to be brought forth. Only those females that can find suitable nesting sites will be successful in rearing young.

Selection of Territory

One animal does not necessarily retain the same territory for life, nor do females always stay in the same area throughout the breeding season. There are very few data on the retention of territory, and my remarks must therefore be based almost exclusively on my own work. Some breeding females of the wood mouse have been known to hold their territories throughout the entire breeding season and to remain in the same area throughout the following winter, while others have been known to move away. The breeding season of these mice is divided into two periods. The first lasts from about the first week in March until early June. There is then a rest period of about six weeks to two months, during which time no young are born. The second period begins in July and continues until about October. Thus the entire season lasts about eight months, with a rest period of nearly two months in the middle. It is during this rest period that some of the females change territories; others, however, remain in the same area throughout the eight months. If an area is vacated by an old female, either another old female or a young female born that year is likely to move in. Just how a selection is made I do not know, but it is probable that a young mouse keeps traveling until it finds an unoccupied territory. When first out of the nest the young wander a great deal, but about the time they become sexually mature they settle in one place and reside there during the remainder of the season. Selection, therefore, seems to depend on the finding of suitable shelter and food conditions. The period from the time the mouse leaves the nest, at about twenty-one days old, until it finds a territory not occupied by another, is probably the most hazardous part of the animal's life. During this time it is exploring. It must travel over much unfamiliar ground; its chance of escape if approached by a predator is markedly less than that of a mouse familiar with all the retreats. The greatest mortality apparently occurs in the searching stage. Partially to compensate for such a loss and to make the first few days that the young are out of the nest less perilous, the old female sometimes vacates the home nest and leaves it to the young. I have observed a female chipmunk do this, and our trapping records of *Peromyscus* indicate that they, too, may display the trait, especially with the last litter of the breeding period. When an old female vacates the nest site she does not necessarily move any great distance, but merely finds a new retreat within her original territory. This gives the young a chance to become able to care for themselves before they are driven into new surroundings.

Significance in Dispersal

When the population of an area becomes so great that there is not room for all the individuals—that is, that there are not enough available territories—some of the individuals are forced out. Under normal conditions those that are established may be expected to defend their respective areas. Young individuals without homes are driven from place to place until they leave the area and seek new homes elsewhere. A reasonable conclusion would be that they leave by force rather than by choice—that they are literally ejected from the area by the older, stronger individuals. This pressure from within the range of a species, this conflict for nesting sites and territories that keeps a certain percentage of the population moving, pushing in all directions, coming into contact with one another and with established individuals only to be driven on and into new areas, is important in the spread of a species.

Territorial behavior is important in limiting the populations in an area. It is influential in causing young animals to cross unsuitable habitats and barriers, thereby bringing about the dispersal of animals over a geographic area. The dispersal of young from the nest site to some extent prevents inbreeding in a population.

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PLATE I

FIG. 1. Wooden trap used during the last two seasons.

FIG. 2. Sink-hole in foreground with heavy low vegetation; *Synaptomys* and *Microtus* habitat.

PLATE I

FIG. 1.

FIG. 2.

PLATE II

FIG. 1. Oak-hickory woods with ground cover of dead leaves and small shrubs; *Blarina, Tamias,* and *Peromyscus leucopus* habitat.

FIG. 2. Open oak-hickory woods with ground cover of heavy grass; *Pitymys* and *Synaptomys* habitat. *Peromyscus leucopus,* although frequently taken here, prefers the habitat shown in Figure 1.

PLATE II

FIG. 1.

FIG. 2.

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