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MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 73

A STUDY OF SMALL MAMMAL POPULATIONS IN NORTHERN MICHIGAN

BY
RICHARD H. MANVILLE

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A STUDY OF SMALL MAMMAL POPULATIONS IN NORTHERN MICHIGAN*

INTRODUCTION

In recent years increasing numbers of studies on small mammal populations have appeared. Some of these have been estimates of numbers of animals; others have been analyses of populations with regard to habitat; and more recently there have been various studies of home range, territoriality, and behavior. Techniques, at first subject to a high degree of error, have improved with new types of traps, new methods of trapping, and different ways of interpreting data. Dice (1938, 1941) reviewed methods that have been employed and made valuable suggestions for improvements in technique and analysis of data.

The opportunity for making the present study came to me in the autumn of 1939, when I undertook a general wildlife survey for the Huron Mountain Club, a private organization. The Huron Mountain region, in the extreme northwestern part of Marquette County, in the Upper Peninsula of Michigan, represents one of the few remaining tracts of extensive primeval forest in the Lake States. It includes areas of northern conifers and eastern deciduous forest. A more detailed description, together with a list of the vertebrate fauna and notes on the meteorology of the region, has been published elsewhere (Manville, 1948).

The work on small mammal populations reported here was carried out during the summers of 1940 to 1942 inclusive. In the three seasons, a total of 1079 individuals, representing thirteen species, was taken in live traps on eight quadrats in different types of forest habitat. The kinds of mammals captured, and the number of each, were as follows: masked shrew, *Sorex c. cinereus,* 67; pygmy shrew, *Microsorex hoyi intervectus,* 1; short-tailed shrew, *Blarina brevicauda kirtlandi,* 350; short-tailed weasel, *Mustela erminea cicognanii,* 1; least chipmunk, *Eutamias minimus jacksoni,* 31; eastern chipmunk, *Tamias striatus griseus,* 28; red squirrel, *Tamiasciurus hudsonicus loquax,* 2; northern flying squirrel, *Glaucomys sabrinus macrotis,* 3; woodland deermouse, *Peromyscus maniculatus gracilis,* 462; red-backed vole, *Clethrionomys g. gapperi,* 122; meadow vole, *Microtus p. pennsylvanicus,* 7; meadow jumping mouse, *Zapus h. hudsonius,* 3; woodland jumping mouse, *Napaeozapus insignis frutectanus,* 2. Most of these species are treated separately hereinafter. In the following account, generic names alone are frequently used; unless otherwise stated, they will be understood to refer to the animals listed above.

* A part of a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the University of Michigan.

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TECHNIQUES FOR POPULATION STUDIES

In many population studies snap traps have been employed. Among such studies are those of Townsend (1935), Williams (1936), Hatfield (1938), Hanson (1944), and Quimby (1944). Bole (1939) made the most thorough study of the snap-trap method applied to quadrats for the study of small mammal populations. Much valuable information has been forthcoming from these studies, but the fact remains that an animal is killed by the snap trap. Studies of populations of live animals which are based on dead captures are necessarily subject to considerable error.

Chitty (1937) reviewed the techniques which had been used for marking small mammals. Since then, new methods have been advocated by various writers. With satisfactory methods of marking animals for identification, the use of live traps became more general. A number of efficient models have been devised by various workers. On the basis of marking small mammals caught in live traps, releasing and later recapturing them, many important studies have been made. Among them are those of Murie and Murie (1931, 1932), Hamilton (1937*a*), Burt (1940), and Blair (1940*a, b, c, d,* 1941*c, d,* 1942). Blair (1941*b*) outlined in detail the techniques he employed. Mohr (1943) summarized the results of many of these small mammal studies.

To compare the efficiency of the snap-trap and the live-trap methods, Goodnight and Koestner (1942) made studies on an Illinois prairie. They found that six or seven days were required to determine the population in an area with live traps; three days were required with snap traps. They concluded that "the two methods of trapping were equally reliable for indicating the size of populations." Stickel (1946) in a similar study in Maryland, obtained population figures three times as great with snap traps as

with live traps, and concluded that the use of live traps was the only valid method. Cockrum (1947) presented evidence, from work in Wyoming, that live traps were far more effective for capturing small mammals than were snap traps.

In the present study, live traps were employed on eight similar quadrats in different types of habitat. My original object was to make a comparative study of the small mammal populations in different types of typical northern forest. In the course of the work, additional data on the natural history of several species were accumulated. All of these findings are presented in this paper.

DEFINITION OF TERMS

Various concepts of animal distribution have been formed, and terms applied to populations in the wild have been used somewhat loosely by different writers. Burt (1943) attempted to standardize certain of these terms as applied to mammals. In my discussion, I use the expressions "home range" and "territory" in the sense defined by him.

The term "range" is applied not to an individual animal, but to a species or a subspecies, and is generally understood as that region throughout which a particular group normally occurs; "home range" refers to the area regularly occupied by an individual animal. Burt (1940) defined home range as "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 homesites." This home range may vary in size and extent with season and with the age and sex of the animal concerned. Possibly, it may further vary with population pressure from other individuals in the vicinity. The home range is not constant, but may change in size and location during the lifetime of an individual. The home range need not be occupied exclusively by one individual of a species, although part of it usually is; there may be overlapping of home ranges at their margins, the areas in common being neutral zones. Somewhere within the home range is the "homesite" of an individual, the actual nest, den, or retreat which it occupies more or less regularly. This may be shared by a family or occupied only by one individual. Animals which have no actual homesite, as juveniles moving about in search of a spot to settle, do not, strictly speaking, have a home range.

Distinguished from the home-range concept is that of "territoriality." The definition by Noble (1939) is the most comprehensive and concise: "A territory is any defended area." Territories have long been known to exist among various animals, but the classic study of Howard (1920) on the reed bunting, *Emberiza schoeniclus,* furnished the impetus for many detailed

investigations, especially on birds. Not all animals possess territories in the sense of a defended area, but this behavioristic trait has been shown to exist among certain fishes, reptiles, and mammals as well as birds. Nice (1941) listed six types of territories among birds. In mammals, Burt (1943) spoke of two fundamental types: "One concerns breeding and rearing of young, the other food and shelter." The territory of a mammal, then, is that part of its home range which is defended against trespass by other animals. This defense is usually directed against members of the same species, by intimidation, aggressive actions, or fighting when necessary. The fact that trespass does occur does not negate the existence of territorial behavior.

With the species, as opposed to the individual, in view, the "habitat" is that part of the range characterized by certain environmental factors essential or desirable for the existence in the wild of the species in question. Within this general habitat—be it woodland, desert, swamp, or prairie—the "ecologic niche" (a term coined by Joseph Grinnell) is the particular situation which provides the food, nesting sites, shelter, and other requisites of the animal.

VARIABLE FACTORS IN LIVE-TRAPPING

A population study of live mammals is more effectively made by the use of live traps than by snap traps which kill the captives, thus drastically upsetting the biotic balance. Even so, the use of live traps introduces unnatural factors which must be considered in interpreting the data. The present study was made with several views in mind. It was intended to make a comparative study of the small mammal faunas of different types of forest habitat; population figures over a period of time were desired; and various data on the life histories of the several species were expected. The technique employed was not equally well suited for achieving each of these ends.

The effects of live-trapping on a population have been discussed by various authors (Chitty, 1937; Dice, 1938; Burt, 1940). The mere laying out of a plot to be trapped and the setting and running of the trap lines disturb the natural conditions of the area to a certain extent. The use of an artificial bait changes somewhat the feeding habits of the animals lured to the trap. Some animals may be attracted way from their normal area of residence by the baits, causing an unnatural concentration of animals in the area trapped. Furthermore, the bait may be more tempting to one species than to another, which may lead to an actual or apparent change in the relative abundance of species. Some mortality in the traps seems bound to occur. In the present study, this was the case chiefly with shrews. The removal of an animal by death leaves a site available for occupancy by

another individual. If an area is near the periphery of the plot, this available site may be reoccupied almost immediately, leading to a possible exaggeration of the apparent population. Some animals may become exhausted from fighting the trap in an effort to escape; this was frequently the case with some of the red-backed voles, *Clethrionomys*. And again, nursing females may be held captive in a trap long enough to endanger their young in the nest.

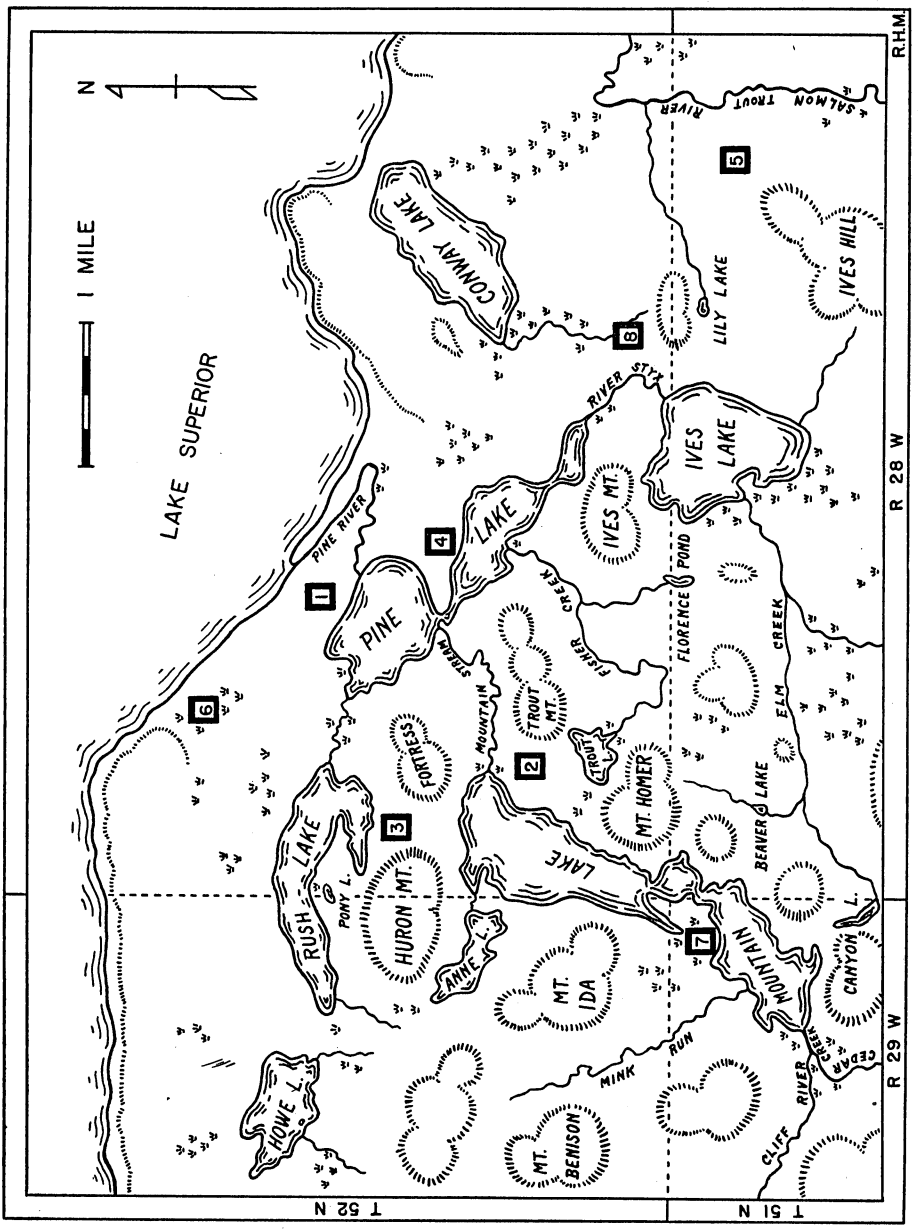
For determining populations of small mammals, Chitty (1937) pointed out the advisability of capturing individuals "as infrequently as possible" so as not to disturb unduly the natural conditions. To determine the home ranges of individuals, however, it is desirable to have as many captures in different traps as possible. Some individuals seem to develop the habit of visiting a particular trap, and thus the extent of their normal home range is not evident. Furthermore, the presence of an animal in a trap precludes the capture therein of other individuals which may be resident on adjoining areas. Some animals may become trap-shy and be captured but once. Others may escape capture altogether, although I believe that such instances are few in the course of five successive days of trapping on one plot. It cannot be safely assumed that all animals captured on a plot are necessarily residents, especially if they are captured but once; it seems likely that transients will be captured more frequently in the marginal rows of traps than in the center of the plot.

MATERIALS AND METHODS

ARRANGEMENT OF PLOTS

Ten plots, each 150 feet square (0.52 acre), were tentatively established in November and December, 1939. They were observed through the following winter. From June 8 to 20, 1940, preliminary trapping was done on Plots 1, 2, and 6. At this time it was decided to discontinue two of the ten plots and to enlarge all the rest. At the same time, Plot 3 was re-established one-half mile west of its original site. Trapping on the plots as finally established was begun on June 26, 1940.

Each of the eight plots was 300 feet square (2.07 acres). All plots were uniformly laid out, with compass and steel tape, as nearly as possible on level ground. Each plot was at least a mile distant from other plots and was well within an area of similar forest type, that is, had a marginal area of at least 500 feet of similar cover on all sides, except for Plot 4. On this plot, the south border was an average distance of 30 feet from a lake shore, roughly parallel to the border, and an area of hemlock stood 150 feet distant from the north border. The eight plots represented different types of cover as follows: 1, jack pine; 2, virgin sugar maple–basswood; 3, virgin



MAP 1. Part of the Huron Mountain region, containing the eight study plots. The size of the plots is exaggerated in this map.

hemlock; 4, white birch, burned about 1900; 5, sugar maple–yellow birch saplings, an area clean cut in 1930; 6, northern white cedar swamp; 7, black spruce swamp; 8, virgin hemlock. Plots 3 and 8 were very similar in composition. The latter was selected because it had been proposed for selective cutting, and it was desired to study the effect of this cutting on the small mammal population. The cutting, however, was delayed until after the completion of this study.

Each plot was marked by a two-inch iron pipe driven into the ground at one corner and projecting about three feet above ground. Detailed directions for reaching each plot may be found in a mimeographed report available at the Huron Mountain Club (Manville, 1942). The plots are here indicated on Map 1. After the first trapping period in 1940, the trees over one inch d.b.h. (diameter at breast height) on each plot were tallied and measured. In 1941, the ground vegetation of each plot was sampled on ten areas, each one meter square and representative of the plot. Detailed figures appear in a later section.

TRAPS AND BAITS

Four different kinds of live traps were used in this study in the following numbers: "36" trap, 89; Sherman trap, 86; Burt-Benson trap, 64; Fisher trap, 22. The "36" trap, described by Blair (1941*a*), is of wooden construction; the others are of sheet metal. The wooden traps are far more bulky to transport, but offer the advantage of added insulation against heat or cold. In all these traps the entrance is approximately two inches square and the inside length is approximately six inches. All are of the single-catch variety, and they operate on the principle of a treadle or false bottom, with the door closed either by gravity or by a spring mechanism.

The traps were generally satisfactory. In several instances, chipmunks gnawed their way out of the "36" traps; porcupines sprung some of these traps by gnawing from the outside. A dozen traps on Plot 2 were once overturned and moved several feet; one "36" trap containing a dead short-tailed shrew, *Blarina,* was completely crushed. This was thought to be the work of a bear, for one was present on the area at about that time. Red squirrels, deer, and hares were presumed to have sprung the traps in a few instances by contact with the outside. Occasionally, through faulty mechanism, an animal was caught in the door of a trap. This usually proved fatal to the captive. Such accidents happened more often with the Sherman trap, which operated by a spring, than with the other types. Sometimes, too, the door at the rear of the trap proved insecure and allowed the escape of the captive; this was the case with the "36" trap more often than with the others. With the Fisher trap, which has an outside door, some difficulty was encountered from ground vegetation that impeded the action of the door.

Animals other than those sought were sometimes captured. On Plot 3, some difficulty was caused by snails, *Polygyra albolabris,* and slugs, *Agriolimax agrestis.* Salamanders, *Plethodon cinereus,* and beetles, *Geotrupes balyi, Necrophorus vespilloides,* and *N. marginatus,* were taken occasionally in traps. Millipedes (*Saiulus canadensis*), spiders, ants, and annelids were frequently in or about the traps, but failed to spring them.

The bait initially used was a mixture of equal parts by volume of Japanese buckwheat, marquis wheat, hog millet, sunflower seeds, and dry rolled oats. Hemp seed, Japanese millet, and small pieces of dry prunes or raw bacon were added at times. There was a tendency for the smaller seeds to lodge beneath the treadle and impair the mechanism of the trap. In wet weather the rolled oats formed a soggy mass in the trap, but still seemed to present an attractive bait. Finally, a simple mixture of sunflower seeds and dry rolled oats, in equal parts by volume, was adopted; this was the only bait used during the 1942 season.

TRAPPING METHOD

Traps were laid out in a regular grid pattern, at thirty-foot intervals, with 121 traps covering a three-hundred-foot square plot. Precise measurements were first made with a steel tape and the locations marked with stakes or stones. The traps were then placed as near as practicable to these markers; some were placed one or two yards from the markers to obtain more favorable trapping sites near stumps, logs, or burrows. The outside row of traps was always on the marginal line of the plot. On all plots the traps were numbered in the same manner, according to location. Trap No. 1 was always at the northeastern corner, trap No. 121 at the southwestern corner, and trap No. 61 at the center of any plot. Sufficient traps were available to trap two plots simultaneously. Traps were baited and set during the afternoon. They were removed on the afternoon of the fifth day. Thus, each trapping period represented 605 trap-days of twenty-four hours. At the termination of each trapping period, the traps were washed and sun-dried before being used again. All traps were examined each morning and afternoon; on plots on which chipmunks were present, the traps were visited two or three additional times during the day.

Each animal, when first captured, was marked by a system of ear punching and/or toe clipping similar to that used by Burt (1940). A poultry punch was used for marking the ears, small scissors for the toes. No anesthetic was employed. Mice and chipmunks were marked chiefly by ear punches, enabling individuals to be numbered serially to 399. Shrews were marked entirely by clipping toes, by which method numbers to 99 could be achieved on the forefeet only. No infections nor ill effects due to these markings were apparent. Animals were usually removed from the trap

by dropping them into a small sack, from which they could easily be taken by hand. The docile deermouse, *Peromyscus,* was sometimes taken from the trap by a pair of long forceps or by the hand alone. All animals were carefully examined at each capture and were then released at the spot where taken.

Each of the eight plots was trapped during one five-day period in 1940; during two such periods in 1941; and during one period in 1942. The dates of trapping on each plot are given in Table I. In later discussions these trapping periods are referred to merely by year, with the two periods in 1941 indicated as 1941 (1) and 1941 (2).

TRAPPING EFFICIENCY

I believe that nearly the entire population of small mammals resident on a plot was taken at least once in the course of a trapping period. Occasional

TABLE I

DATES OF TRAPPING ON EIGHT PLOTS DURING THREE YEARS; ALL DATES INCLUSIVE

Plot	1940	1941 (1)	1941 (2)	1942
1	June 8–12	August 5–9	Sept. 23–27	May 30–June 3
2	June 12–16	July 20–24	Sept. 12–16	June 9–13
3	July 10–14	July 12–16	Sept. 3–7	June 1–5
4	July 17–21	June 17–21	Sept. 2–6	June 16–20
5	July 27–Aug. 2*	July 1–5	August 23–27	May 23–27
6	August 14–18	July 31–Aug. 4	Sept. 22–26	June 17–21
7	September 3–7	July 21–25	Sept. 14–18	June 10–14
8	August 7–11	July 3–7	August 21–25	May 24–28

* Sixty-one traps set on July 27, and 60 on August 2, each during daytime only; 121 traps set continuously from July 28 to August 1.

transients across the area might or might not be taken. Animals the size of a red squirrel, flying squirrel, or weasel were seldom caught, although they probably were resident on some of the plots. Table II lists the increase in numbers of animals previously caught through typical five-day trapping periods from July 20 to 24, 1940, on Plot 2; and from July 17 to 21, 1940, on Plot 4. These areas had not been previously trapped. Of the seven unmarked individuals caught on Plot 2 on the last day, four were taken in the outside row of traps; five of the seven were males of the genus *Peromyscus,* three of them were adults, and all probably were wandering. On Plot 4, the two unmarked individuals taken on the last day belonged to the genus *Clethrionomys;* both were in marginal traps.

RECORDS

All basic data were recorded in a file of printed three-by-five-inch cards. One card was used for each mammal; on the card were recorded the num-

ber, sex, age when first taken, plot on which caught, dates and trap numbers of each capture, data on the specimen if preserved, and general remarks. Record was kept of breeding condition, pelage, parasites, and evidence of disease, for all of which the animals were examined at each capture. On the reverse of the card was a chart of trap locations on which all captures of the individual were indicated; inks of different colors were used for different trapping periods. This system was highly satisfactory, and the cards could readily be sorted or arranged in any desired sequence. In a register kept by species in a field notebook, I recorded each individual's number, sex, date and age at initial capture, plot on which taken, and remarks. In addition, in a loose-leaf notebook, arranged by plots to show the species and individuals taken on each trapping day and the traps in which caught, a daily journal of general observations was maintained.

DETERMINATION OF HOME RANGES

From the nature of the study, the data gathered were insufficient for the calculation of a complete home range, for trapping periods of five days in extent afforded too few captures for any one individual. Many animals taken were captured at least once in the outside row of traps, which indicated that their home ranges may have extended some distance beyond the area trapped. I regard the home ranges as determined from my data to be nearly all smaller than the actual home ranges of the individuals concerned.

TABLE II

NUMBERS OF MARKED AND UNMARKED INDIVIDUALS CAPTURED ON FIVE SUCCESSIVE DAYS OF TRAPPING ON TWO AREAS NOT PREVIOUSLY TRAPPED

Trapping Day	Total Number Caught		Number Previously Marked		Number Unmarked	
	Plot 2	Plot 4	Plot 2	Plot 4	Plot 2	Plot 4
First	9	11	0	0	9	11
Second	23	11	9	9	14	2
Third	25	13	17	9	8	4
Fourth	26	17	21	12	5	5
Fifth	34	13	27	11	7	2

With traps equally spaced at ten-yard intervals, checkerboard fashion, each trap was considered to cover effectively an area of 100 square yards. Figure 1 illustrates the method by which home ranges were computed from trapping records. The four individuals selected (*Peromyscus*) were taken from three different plots so that the figure does not indicate territorial limitations in the field. Each number on the chart represents a trap location. Solid squares indicate traps in which a mouse was captured within one five-day period. Squares of broken lines which connect, in the shortest

possible distance, all areas occupied are assumed to be within the home range of the individual. The home range is calculated by adding the number of squares occupied and assumed to be occupied and multiplying by 100 square yards. This method indicates approximately the minimum home range of the individual during the five-day period. The shape of the home range may be other than indicated—certainly it is not comprised of geometrical squares—but its minimum area is probably not less than the amount obtained by this method.

CALCULATION OF POPULATIONS

Many calculations and estimates of the populations of small mammals per unit area have been made. Various methods of arriving at the figures have been employed, some fairly accurate, others subject to large error. Results obtained by various workers on different species of *Peromyscus* may be used to illustrate the diversity of the findings. Blair (1941*d*), who worked with live traps on an 18.18 acre plot of hardwood forest in northern Michigan, estimated an average population of 3.81 *P. maniculatus* per acre from August 23 to September 7, 1940. Townsend (1935), with snap traps and a combination of a stationary line and movable quadrat, covered an area in dry woods of 264 by 33 feet and recorded nineteen to thirty-three mice (*P. leucopus* and *P. maniculatus* combined) per acre. Williams (1936) made use of a quadrat only ten meters square and estimated 218.52 mice (*P. leucopus*) per acre; he himself stated that his figures were much too high. Bole (1939) employed snap traps on different-sized quadrats and found a maximum density of forty-six mice (*P. leucopus*) per acre in beech-maple forest. Burt (1940), using live traps, reported populations of *P. leucopus* ranging from 3.08 per acre on May 16, 1937, to 10.87 per acre on November 21 to 22, 1936, on two plots totaling 5.52 acres. Hanson (1944), using snap traps on fifteen different quadrats, recorded population figures as high as 13.0 (*P. leucopus*) and 24.0 (*P. maniculatus*) per acre during October, 1941.

In all figures, it is essential that one know the dates covered by the estimate; an interval of two or three days is preferable to one of a week. It is also desirable to know the composition of the population by age groups, as well as by sex, and the size of the area included in the estimate. Throughout an extensive area the population of mice might be relatively high; but if the census were for only a small part of the area it might include a section unoccupied by mice and give a population figure far from typical. A given area may appear to support vastly different populations, depending on whether the young recently out of the nests are included in the counts. Populations will vary throughout the breeding season; they may fluctuate with the amount of available food or cover, with the presence of predators

or disease conditions, or with varying weather conditions. In the so-called "cyclic" animals, violent fluctuations in population that occur from time to time lack adequate explanation.

In the present study, my three-hundred-foot square plots were well within areas of similar forest, the one exception being Plot 4, as noted previously. Dice (1941) pointed out that animals whose home ranges bor-

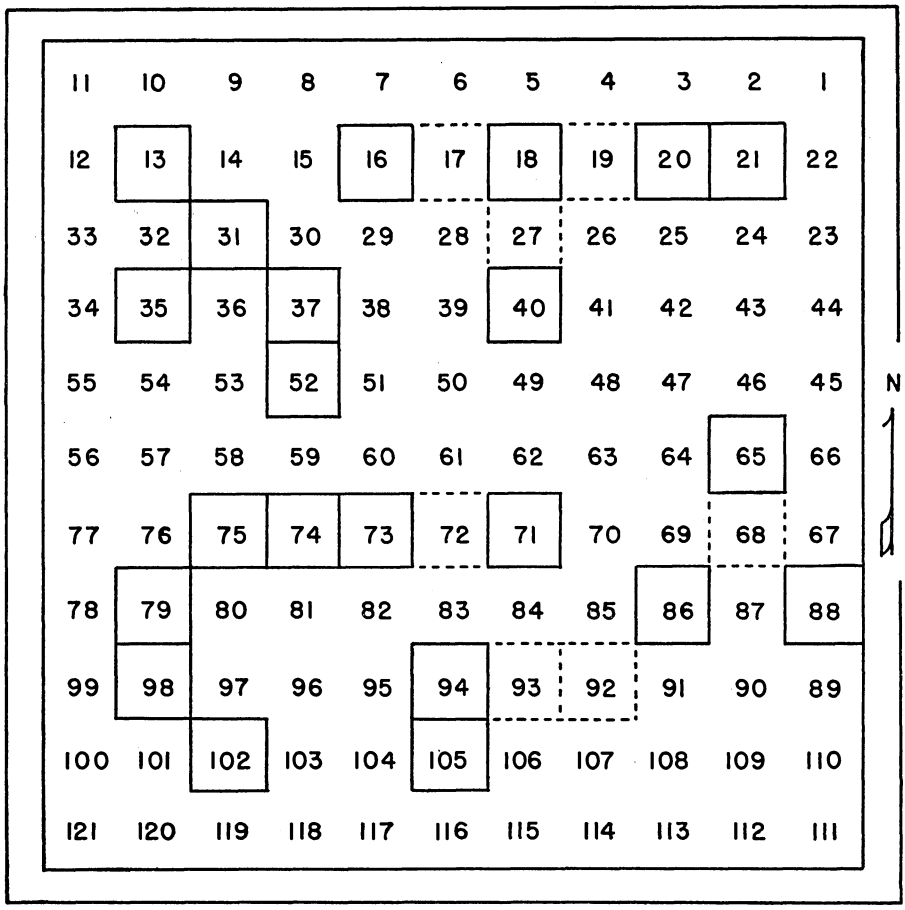


FIG. 1. Method of calculating home ranges from trapping records of four specimens of *Peromyscus*.

der the plot are likely to be taken in the traps, especially those traps in the peripheral rows. Therefore, my traps effectively covered an area greater than three hundred feet square. Dice (1938) suggested the census area should be that covered by the traps plus a marginal distance on each side equal to the radius of the home range of the animal under consideration. This is the procedure I have employed in calculating populations per acre.

I have based my calculations on what appear to be the most reliable home range figures available for each species; in each instance I have stated the width of the marginal strip considered to be within the area effectively trapped. Appropriate corrections were made in the case of Plot 4, the south border of which was near a lake shore.

DESCRIPTION OF PLOTS

The composition and distribution of ninety-seven forest cover types of the eastern United States have been enumerated by a committee of the Society of American Foresters (Hawley, 1932). These standardized names and their type numbers are appended to the descriptions of my plots, although in most instances there are slight differences between the composition of the plots and the accepted normals. Comparative data on the trees and ground cover (Tables III, IV), as well as on the small mammals trapped on each plot (Table V), are presented in later sections.

PLOT 1: JACK PINE

(Soc. Amer. For. Type 1)

Plot 1, laid out on June 20, 1940, was three hundred yards north of First Pine Lake. The plot (Pl. I, Fig. 1) was level and on dry sandy soil. An old logging road crossed the southern half of the plot. The trees were tallied on June 29, 1940, and the ground vegetation was tallied on October 4, 1941. On the area were 1700 trees, one to fourteen inches and averaging 3.6 inches d.b.h. Jack pines predominated, with white and Norway pines next in abundance. Of the latter two species, 187 stumps up to twenty-one inches in diameter represented cuttings that had been made since 1890; no cuttings have been made in recent years. A few red oaks, red maples, and white birches were encroaching on the southwestern corner of the plot. The principal ground vegetation included blueberry, reindeer moss, and bracken; trailing arbutus and other plants were generally distributed.

Both species of chipmunk were resident on the area. Red-backed voles outnumbered deermice, but in 1942 short-tailed shrews far outnumbered all other small mammals. A single flying squirrel was taken. In addition to the mammals trapped, red squirrels were common, and both gray squirrels and woodchucks were seen. Deer, bears, red foxes, and hares ranged over the plot. Flickers, robins, and chipping sparrows nested on the area. Ruffed grouse, barred owl, blue jay, nighthawk, hairy woodpecker, red-breasted nuthatch, parula, myrtle, pine, and black-throated green warblers, ovenbird, red- and white-winged crossbills, redpoll, purple finch, pine siskin, junco, wood pewee, chickadee, olive-sided flycatcher, and hermit thrush were observed. One garter snake was seen.

PLOT 2: SUGAR MAPLE–BASSWOOD
(Soc. Amer. For. Type 13)

This plot, laid out on July 1, 1940, was one quarter of a mile east of upper Mountain Lake. The plot (Pl. I, Fig. 2) was a typical area of virgin hardwood forest. It was level, with a soil of thick humus and leaf mold. No cutting or burning had occurred on the area. The trees were tallied on July 6, 1940, and the ground vegetation was tallied on September 16, 1941. On the plot were 662 trees, one to forty-four inches and averaging 7.5 inches d.b.h. The dominant tree was sugar maple, up to twenty-eight inches d.b.h., which constituted 52 per cent of the trees tallied. Hemlock, next in abundance, was limited mostly to the northwestern quarter of the plot and consisted chiefly of trees less than eight inches in diameter. Several other species in small numbers were distributed widely over the area. The largest tree on the plot was a red oak of forty-four inches d.b.h. There were twenty-seven dead trees of all these species, up to twenty-four inches d.b.h. either standing or fallen. Seedlings of most of these trees occurred on the plot, but dominant by far were sugar maple seedlings, which grew almost everywhere and which, in places, reached a density of over a million per acre (Anon., 1929). Hardly 20 per cent of these maple seedlings survive their second year, and only 3 per cent ever reach a height over five feet or a diameter greater than one-half inch (Anon., 1929). Various other herbaceous plants appeared on the area in lesser numbers.

In 1940, only three deermice were caught. Several other species were represented during 1941; deermice were the most plentiful. In 1942, however, short-tailed shrews far outnumbered deermice (the only other species taken). Other mammals that ranged over the plot included deer, bear, bobcats, porcupines, and red squirrels. Robins nested on the area. Other birds observed were: ruffed grouse, downy, hairy, and pileated woodpeckers, yellow-bellied sapsucker, black-billed cuckoo, red-breasted and white-breasted nuthatches, parula, blackburnian, and black-throated green warblers, ovenbird, red and white-winged crossbills, redpoll, pine siskin, wood pewee, chickadee, red-eyed vireo, rose-breasted grosbeak, and olive-backed thrush. The red-backed salamander, American toad, spring peeper, green and wood frogs, and one garter snake were observed.

PLOT 3: HEMLOCK
(Soc. Amer. For. Type 11)

This plot, two hundred yards south of Rush Lake, was laid out on July 9, 1940. The area (Pl. II, Fig. 1) was, for the most part, nearly level. A rocky bluff about twenty feet high crossed the plot approximately twenty yards from and parallel to the south margin; in it were a number of small caves and crevices. Two footpaths crossed the center of the plot and con-

verged near the west margin. The trees were tallied on July 15, 1940, and the ground vegetation was tallied on September 10, 1941. This was practically a virgin stand of timber; thirteen hemlock stumps, six to sixteen inches in diameter, represented the only cutting, made many years ago. There were 553 trees on the plot, one to forty-six inches and averaging eleven inches d.b.h. Hemlocks constituted 73 per cent of these trees. The largest individual tree was a white pine, the only one of its species, measuring forty-six inches d.b.h. A few hardwoods of several species were distributed over the plot. Scattered over the area were ninety-five snags of most of these trees, up to twenty-six inches d.b.h. Ground vegetation was varied and generally sparse; some spots had only a thick cover of dead hemlock needles. Seedlings of most of the trees were present; sugar maple was most abundant, although not so numerous as on Plot 2. Mosses, ferns, and several small flowering plants grew in small numbers over the area.

Deermice were the principal small mammals resident during the first two years. Only the least chipmunk was trapped, but one eastern chipmunk was seen on the plot in September, 1941. In 1942, only two species were captured; 60 per cent were short-tailed shrews and 40 per cent were deermice. In 1942, also, the total population of small mammals taken (81) was far greater than that in the other trapping periods (12 to 47). Porcupines regularly occupied several of the small caves along the bluff. Deer and red squirrels were the only other mammals observed on the plot. Of the birds present, the ovenbird and blackburnian warbler nested on or near the area. Other birds seen here included the ruffed grouse, blue jay, downy and pileated woodpeckers, red-breasted nuthatch, pine, parula, and black-throated green warblers, red crossbill, redpoll, pine siskin, wood pewee, chickadee, and hermit thrush. Amphibians present included the red-backed salamander, American toad, spring peeper, common tree toad, and wood frog. One garter snake was seen.

PLOT 4: WHITE BIRCH

(Soc. Amer. For. Type 6)

Plot 4, laid out on July 16, 1940, was immediately north of Second Pine Lake. This plot (Pl. II, Fig. 2) sloped very gradually toward the shore of the lake, which was roughly ten yards beyond the south margin of the area. This was part of an area swept by fire about 1900; burns remained on a few stumps up to thirty inches in diameter. The trees were tallied on July 22, 1940, and the ground vegetation was tallied on September 6, 1941. The plot contained 1327 trees, one to thirty-two inches and averaging 4.1 inches d.b.h. White birch comprised 61 per cent of the trees; poplar and red and striped maple were next in abundance. The largest tree on the plot was a red oak of thirty-two inches d.b.h. Formerly poplar was more

abundant, but beaver cuttings left only stumps up to twelve inches in diameter. There were many fallen dead trees, chiefly birches. The principal ground cover was bracken; in a few spots there were thick clumps of blueberry. Seedlings of most of the trees on the plot were represented. Immediately to the south, but not on the plot, were such shore forms as tag alder, sweet gale, and leatherleaf.

The deermouse population was relatively high at all times, but was surpassed by that of short-tailed shrews in 1942. Both species of chipmunk were present in small numbers. The total number of small mammals taken was much greater in 1942 (113) than at any other time (24 to 44). Deer, hares, otter, red squirrels, gray squirrels (the black phase only), and porcupines were observed on the plot; beaver, muskrats, and mink occasionally ranged along the shore near by. Kingbirds nested on or near the plot. Other birds on the area were ruffed grouse, downy, hairy, and pileated woodpeckers, flickers, black-throated green warbler, ovenbird, winter wren, black-billed cuckoo, chickadee, red-eye vireo, song sparrow, robin, and olive-backed thrush. Loons, pied-billed grebes, and great blue herons occurred near the shore. Spring peepers and garter snakes were present on the plot.

PLOT 5: SUGAR MAPLE–YELLOW BIRCH

(Soc. Amer. For. Type 12)

This plot, three-eights of a mile southwest of the Five Forks, was laid out on July 26, 1940. The plot (Pl. III, Fig. 1) was level, except for a gully about ten feet deep which crossed the northwest corner and included three trap sites. A thick layer of leaf mold covered the ground. An old logging road, no longer used, diagonally crossed the southern half of the plot. This area was clean cut about 1930; many large stumps and much decaying slash remained. The area had never been burned. This plot was a veritable jungle of hardwood reproduction, the stems being somewhat smaller and more dense wherever standing trees afforded shade. A sample tally of the trees on the southeast 900 square feet of the plot was made on August 1, 1940; ground vegetation was tallied on September 3, 1941. On the basis of the corner sampled, the plot contained over 27,000 stems, one to thirty inches and averaging two inches d.b.h. Of these, 88 per cent were sugar maple and 10 per cent yellow birch, averaging less than two inches d.b.h. A few larger trees were scattered over the area; these included sugar maples, yellow birches, and hemlocks that were spared by the loggers. Various plants comprised the ground cover; chief among these were mosses, aster, wood fern, grasses, and sugar-maple seedlings.

The majority of small mammals trapped on this plot were deermice, although in 1942 short-tailed shrews slightly surpassed them in numbers.

Both species of chipmunk and both species of jumping mouse were present in small numbers. A star-nosed mole and a short-tailed weasel were seen. Other mammals that occasionally frequented the area were deer, bear, skunks, porcupines, and hares. Birds that bred on or near the plot at various times were the ruffed grouse, blue jay, robin, rose-breasted grosbeak, chickadee, chestnut-sided warbler, redstart, and ovenbird. Other birds observed here were the woodcock, downy, hairy, and pileated woodpeckers, flicker, white-crowned, chipping, and song sparrows, hermit and wood thrushes, junco, red-eyed vireo, black-billed cuckoo, scarlet tanager, parula, black-throated green, and black and white warblers. The American toad, wood frog, and garter snake were present.

PLOT 6: NORTHERN WHITE CEDAR

(Soc. Amer. For. Type 24)

This plot, in a typical, tangled northern cedar swamp, one-fourth mile north of Hans Jensen's clearing, was laid out on August 12, 1940 (Pl. III, Fig. 2). A few small streams flowed into the area from the west. The moist, porous, acid soil supported a heavy growth of sphagnum moss. There had been no cutting or burning on the area. Trees on the plot were tallied on October 1, 1940, and ground vegetation was tallied on September 29, 1941. The white cedar count was made only on the southwest quarter of the plot. Based on this sample, the entire plot contained 1280 trees, one to thirty-two inches averaging 7.7 inches d.b.h. In addition to these, there were 368 down cedars, averaging twelve inches d.b.h. White cedar comprised 51 per cent of the standing timber; balsam fir, tag alder, and mountain maple together comprised 36 per cent In the northeast quarter of the plot were concentrated a few hemlocks and black ash; most of the tag alders were along the north margin; other trees were about equally distributed over the whole area. Many species comprised the ground vegetation; sphagnum and other mosses, goldthread, violets, grasses, and yellow-birch seedlings were the most conspicuous elements.

Eight species of small mammals were captured; the pygmy shrew and short-tailed weasel were each taken once. Masked shrews were captured in 1940 and 1941, but not in 1942. Short-tailed shrews were not taken in 1940, one was taken in 1941, and fifty-seven (78 per cent of all mammals captured) in 1942. Deermice and red-backed voles were taken consistently, the latter in greater numbers except in 1942. A few least chipmunks and meadow voles were captured. Deer, bear, porcupines, red squirrels, and hares were observed. Ruffed grouse, blue jays, winter wrens, and magnolia warblers bred on or near the plot. Other birds seen were barred owl, downy and hairy woodpeckers, yellow-bellied sapsucker, red-breasted nuthatch, chickadee, red crossbill, redpoll, pine siskin, purple finch, junco, wood

pewee, black and white warbler, black-throated green warbler, northern yellow-throat, white-crowned sparrow, robin, and veery. Amphibians on the plot included the American toad, green and wood frogs, spring peeper, and common tree toad. Garter snakes were also present.

PLOT 7: BLACK SPRUCE

(Soc. Amer. For. Type 23)

This spruce swamp lies south of Lumberman's Bay on Mountain Lake. The plot was laid out on September 2, 1940, in a nearly pure stand of black spruce (Pl. IV, Fig. 1). It was a level, moist area almost entirely covered with sphagnum moss. The acid soil dried out only after protracted periods of heat. There had been no burning on the area, and the only cutting was a clearing ten yards wide, made in 1896, that crossed the plot diagonally in a southeasterly direction. A sample tally of the trees on the northeast quarter of the plot was made on October 4, 1940; ground vegetation was tallied on September 17, 1941. On the basis of the sample, the entire plot contained 2434 trees, one to sixteen inches and averaging four inches d.b.h. Except for three trees, two white pines and one tamarack, the plot contained only black spruce. Sphagnum moss was the most abundant species of ground cover; pale laurel, Labrador tea, leatherleaf, and bog rosemary were generally distributed, as were such species as blueberry, pitcher plant, cotton grass, cranberry, and goldthread. In the clearing were seedlings of tamarack; black-spruce seedlings occurred generally throughout the area.

Only six species of small mammals were trapped on the plot, all in relatively small numbers except for the short-tailed shrews (68) in 1942. Red-backed voles consistently outnumbered deermice. Of the chipmunks, only a few least chipmunks were present. Other mammals that ranged across the area were deer, bear, coyotes, bobcats, porcupines, and hares. No birds were noted as breeding on the plot, but observed were ruffed grouse, downy, hairy, pileated, and Arctic three-toed woodpeckers, blue jay, cedar waxwing, red and white-winged crossbills, redpoll, pine siskin, purple finch, ruby-throated hummingbird, red-breasted nuthatch, wood pewee, chickadee, black-throated green warbler, golden-crowned kinglet, pine grosbeak, junco, and chipping sparrow. The leopard frog and garter snake both occurred on the area.

PLOT 8: HEMLOCK

(Soc. Amer. For. Type 11)

This plot, laid out on August 5, 1940, was one-eighth of a mile south of Oscar Webster's clearing. The area (Pl. IV, Fig. 2) greatly resembled Plot 3; it sloped very gently toward the north and had not been burned or cut. An old wood road crossed the plot from east to west, leading to an area 400 yards distant that was clean cut about 1930. Midway on the

western margin was a "blow-down" of recent years which included five trap sites. The trees were tallied on September 14, 1940, and the ground vegetation was tallied on August 26, 1941. On the plot were 816 trees, one to thirty inches and averaging 7.4 inches d.b.h. Hemlocks comprised 64 per cent of these trees; yellow birch and sugar maple were the next most abundant species. Ground cover was generally sparse, much of the forest floor being covered merely with dead hemlock needles. Mosses, starflower, partridge berry, and sugar-maple seedlings were the most conspicuous elements.

Masked shrews were taken only in 1940 and 1941; short-tailed shrews only in 1941 and 1942, and relatively few the last year as compared with their occurrence elsewhere. Deermice and red-backed voles were both taken, the former predominating at all times. One eastern chipmunk was seen on the area and one least chipmunk in hemlock cover near by, both in August, 1941. Deer, bear, porcupines, and red squirrels were observed. The ovenbird and pileated woodpecker bred near by. Other birds observed were ruffed grouse, blue jay, hairy woodpecker, red-breasted and white-breasted nuthatches, chickadee, parula, black-throated green, and pine warblers, wood pewee, golden-crowned kinglet, and olive-backed and hermit thrushes. The American toad, wood frog, spring peeper, common tree toad, and garter snake also were present.

COMPARISON OF PLOTS

It was evident that the eight plots, with the exception of Plots 3 and 8, represented distinctly different plant associations. Plots 6 and 7 were lowland areas of cedar and spruce swamps, respectively; the other six plots were areas of well-drained upland forest. Tree counts, either *in toto* or on a sample of the area, were made of all trees over one inch d.b.h. Table III lists, for those species comprising at least 1 per cent of the trees on the plot, the total trees per acre and the percentage of each on the eight plots individually. The plots differed vastly in numbers as well as in species of trees present.

The occurrence of species of ground vegetation was noted on ten one-meter square quadrats situated throughout each of the eight plots. Table IV summarizes these data and, for each plot, gives the number of quadrats on which each species was present. It is apparent that the plots varied widely both in the species composition and in the density of ground vegetation represented.

A complete listing of all plants mentioned, trees as well as herbaceous species, appears in the Appendix.

It was to be expected that these areas would support different sorts of animal populations, as reflected by the small mammals taken on the different plots.

TABLE III

COMPARISON OF PRINCIPAL TREES ON EIGHT STUDY PLOTS

Species	Total Trees Per Acre								Per Cent of Trees on Plot							
	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6	Plot 7	Plot 8	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6	Plot 7	Plot 8
White pine	75	.....	1	8	11,520	.....	1	.....	9	.....	.....	1	88	.....	.....	.....
Jack pine	620	.....	.....	.....	.....	.....	.....	.....	76	.....	.....	.....	.....	.....	.....	.....
Norway pine	61	.....	.....	3	.....	.....	.....	.....	7	.....	.....	.....	.....	.....	.....	.....
White spruce	.....	.....	.....	.....	.....	29	.....	.....	.....	.....	.....	.....	.....	5	.....	.....
Black spruce	.....	.....	.....	.....	.....	.....	1173	.....	.....	.....	.....	.....	.....	.....	99	.....
Balsam fir	1	4	.....	30	.....	109	.....	5	.....	1	.....	4	.....	16	.....	1
Hemlock	.....	67	196	5	11	26	.....	254	.....	21	73	1	.....	4	.....	65
White cedar	.....	.....	.....	2	.....	328	.....	15	.....	.....	.....	.....	.....	51	.....	4
Poplar	.....	.....	.....	125	.....	.....	.....	.....	.....	.....	.....	12	.....	.....	.....	.....
Ironwood	.....	34	4	2	4	.....	.....	6	.....	10	2	.....	.....	.....	.....	1
Yellow birch	.....	27	.....	.....	1,351	11	.....	48	.....	8	.....	.....	10	2	.....	12
White birch	10	.....	18	394	.....	.....	.....	.....	1	.....	6	61	.....	.....	.....	.....
Tag alder	.....	.....	.....	.....	.....	85	.....	.....	.....	.....	.....	.....	.....	14	.....	.....
Red oak	35	1	.....	5	.....	.....	.....	.....	4	.....	.....	1	.....	.....	.....	.....
Striped maple	.....	4	3	51	147	1	.....	11	.....	1	1	8	.....	.....	.....	3
Mountain maple	.....	.....	.....	.....	.....	45	.....	.....	.....	.....	.....	.....	.....	7	.....	.....
Sugar maple	.....	168	37	4	.....	.....	.....	41	.....	53	14	1	.....	.....	.....	10
Red maple	18	.....	.....	56	.....	.....	.....	11	2	.....	.....	9	.....	.....	.....	3
Basswood	.....	15	7	.....	1	.....	.....	2	.....	5	3	.....	.....	.....	.....	.....
All species	820	320	266	685	13,034	634	1174	393	99	99	99	98	98	99	99	99

TABLE IV

COMPARISON OF GROUND VEGETATION ON EIGHT STUDY PLOTS

Species	Occurrences on Ten Quadrats							
	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6	Plot 7	Plot 8
Reindeer moss	9	.....	.....	.....	.....	.....	3	.....
Liverwort	.....	.....	.....	.....	.....	3	.....	.....
Sphagnum moss	.....	.....	.....	.....	.....	8	10	.....
Unidentified moss	5	4	7	7	5	9	5	5
Shining clubmoss	.....	.....	2	.....	1	2	.....	2
Flatbranch groundpine	.....	.....	1	.....	.....	.....	.....	.....
Running clubmoss	.....	.....	.....	2	.....	.....	.....	1
Groundpine	1	.....	.....	1	.....	.....	.....	.....
Common polypody	.....	.....	1	.....	.....	1	.....	.....
Bracken	7	.....	.....	7	1	.....	.....	.....
Wood fern	.....	3	3	.....	4	3	.....	2
Long beech fern	.....	.....	.....	.....	.....	2	.....	.....
Oak fern	.....	4	1	.....	.....	2	.....	.....
Rattlesnake fern	.....	1	.....	.....	.....	1	.....	.....
White pine seedling	1	.....	1	1	.....	.....	.....	.....
Jack pine seedling	2	.....	.....	.....	.....	.....	.....	.....
Norway pine seedling	1	.....	.....	.....	.....	.....	.....	.....
Tamarack seedling	.....	.....	.....	.....	.....	.....	1	.....
White spruce seedling	.....	.....	.....	.....	.....	1	.....	.....
Black spruce seedling	.....	.....	.....	.....	.....	.....	2	.....
Balsam fir seedling	1	.....	.....	1	.....	4	.....	.....
Hemlock seedling	.....	1	1	.....	.....	3	.....	.....
White cedar seedling	.....	.....	.....	.....	.....	2	.....	.....
Unidentified grass	4	3	1	5	4	6	8	2
Cotton grass	.....	.....	.....	.....	.....	.....	3	.....
Jack-in-the-pulpit	.....	.....	.....	.....	.....	1	.....	.....
Yellow clintonia	.....	.....	2	.....	.....	3	.....	1
Canada mayflower	.....	1	3	.....	.....	.....	1	3
Twisted-stalk	.....	2	1	.....	1	.....	.....	1
Hairy Solomon's seal	.....	.....	1	.....	.....	.....	.....	.....
Moccasin flower	1	.....	.....	.....	.....	.....	1	.....
Hooker's orchis	.....	.....	.....	.....	.....	1	.....	.....
Round-leaved orchis	.....	1	.....	.....	.....	.....	.....	.....
Lesser rattlesnake plantain	1	.....	.....	.....	.....	.....	.....	1
Menzies' rattlesnake plantain	.....	.....	2	.....	.....	.....	.....	1
Heart-leaved twayblade	.....	.....	.....	.....	.....	1	1	.....
Large coral root	.....	.....	1	.....	.....	.....	.....	1
Striped coral root	.....	.....	1	.....	.....	.....	.....	1
Calypso	.....	.....	1	.....	.....	.....	.....	.....
Poplar seedling	.....	.....	.....	1	.....	.....	.....	.....
Ironwood seedling	.....	.....	.....	1	.....	.....	.....	1
Yellow birch seedling	.....	3	2	.....	.....	6	.....	2
White birch seedling	.....	.....	.....	2	.....	.....	.....	.....
Red oak seedling	.....	1	.....	.....	.....	.....	.....	.....
Slender nettle	.....	.....	.....	.....	2	.....	.....	.....
Hepatica	.....	1	.....	.....	1	.....	.....	1
Goldthread	.....	.....	.....	.....	.....	9	1	1
White baneberry	.....	.....	.....	.....	.....	2	.....	.....
Mandrake	.....	.....	.....	.....	.....	1	.....	.....
Pitcher plant	.....	.....	.....	.....	.....	.....	4	.....
Mountain ash seedling	.....	.....	.....	.....	.....	1	.....	.....

TABLE IV (*Cont.*)

Species	Occurrences on Ten Quadrats							
	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6	Plot 7	Plot 8
Wood strawberry	.....	.....	.....	.....	1	.....	.....	.....
Cinquefoil	.....	.....	.....	.....	1	.....	.....	.....
Red raspberry	.....	.....	.....	.....	2	1	.....	.....
Thimbleberry	.....	.....	.....	.....	.....	1	.....	1
Dewdrop	.....	.....	.....	.....	.....	4	.....	.....
White clover	.....	.....	.....	.....	2	.....	.....	.....
Wood sorrel	.....	.....	.....	.....	.....	1	.....	.....
Striped maple seedling	.....	3	6	5	.....	2	.....	.....
Mountain maple seedling	.....	3	2	.....	.....	.....	.....	.....
Sugar maple seedling	.....	10	9	1	4	4	.....	4
Red maple seedling	.....	.....	.....	1	.....	1	.....	3
Jewelweed	.....	.....	.....	.....	.....	2	.....	.....
Basswood seedling	.....	.....	2	.....	.....	.....	.....	.....
Blue violet	.....	1	1	.....	1	8	.....	1
Sundrops	1	.....	.....	.....	.....	.....	.....	.....
Wild sarsaparilla	.....	.....	2	.....	1	.....	.....	1
Sweet cicely	.....	.....	1	.....	.....	.....	.....	.....
Bunchberry	.....	.....	.....	.....	.....	3	.....	1
Pipsissewa	1	.....	.....	.....	.....	.....	.....	.....
One-flowered pyrola	.....	.....	.....	.....	.....	1	.....	.....
Indian pipe	.....	1	.....	1	.....	.....	.....	1
Labrador tea	.....	.....	.....	.....	.....	.....	9	.....
Pale laurel	.....	.....	.....	.....	.....	.....	7	.....
Bog rosemary	.....	.....	.....	.....	.....	.....	3	.....
Leatherleaf	.....	.....	.....	.....	.....	.....	8	.....
Trailing arbutus	6	.....	.....	2	.....	.....	.....	.....
Wintergreen	1	.....	.....	4	.....	.....	4	.....
Bearberry	1	.....	.....	.....	.....	.....	.....	.....
Creeping snowberry	.....	.....	.....	.....	.....	4	5	1
Huckleberry	2	.....	.....	.....	.....	.....	2	.....
Blueberry	10	.....	.....	2	.....	.....	7	.....
Cranberry	.....	.....	.....	.....	.....	.....	2	.....
Starflower	1	6	2	2	.....	1	.....	5
Black ash seedling	.....	.....	.....	.....	.....	1	.....	.....
Self-heal	.....	.....	.....	.....	.....	1	.....	.....
Bedstraw	.....	2	4	.....	3	6	.....	2
Partridge berry	.....	3	3	1	.....	.....	.....	4
Fly honeysuckle	.....	1	2	.....	.....	1	.....	2
Twinflower	.....	.....	.....	.....	.....	1	.....	.....
Goldenrod	1	.....	.....	.....	.....	.....	.....	.....
Large-leaved aster	.....	.....	.....	.....	5	.....	.....	.....
Cat's foot	.....	.....	.....	2	.....	1	.....	.....
Pearly everlasting	.....	.....	.....	.....	1	.....	.....	.....
Thistle	.....	.....	.....	.....	.....	1	.....	.....
Dandelion	.....	.....	.....	.....	1	.....	.....	.....
Number of species on each plot	20	21	29	20	19	43	21	28

COMPARISON OF SMALL MAMMAL POPULATIONS

Of the 1079 different individuals captured in the three years, over 98 per cent belonged to six species. Table V lists the numbers of these six species captured on the various plots during each trapping period; also

included in Table V is a summary of the numbers of all thirteen species caught. The only small mammals captured or observed on all of the eight plots were members of the genera *Tamiasciurus, Peromyscus, Clethrionomys,* and *Blarina* (the last in 1942 only). Specimens of *Sorex* were taken and those of *Erethizon* were observed on seven different plots (all but Plot 1, jack pine). Specimens of *Eutamias* occurred on seven and those of *Tamias* on six different plots. Other forms were captured or observed too seldom to permit generalizing. It is of interest, however, that specimens of *Microsorex* and *Microtus* were captured only on Plot 6 (cedar swamp), those of *Condylura* and *Napaeozapus* were noted only on Plot 5 (hardwood saplings), those of *Glaucomys* were taken only on Plots 1 (jack pine) and 5 (hardwood saplings), those of *Mustela* were observed only on Plots 5 (hardwood saplings) and 6 (cedar swamp), and those of *Zapus* were caught only on Plots 4 (white birch) and 5 (hardwood saplings). Plot 5 (hardwood saplings) appeared to support the greatest number of species (fourteen), and Plot 2 (virgin hardwoods) the least (seven). Plots 3 (hemlock), 7 (spruce swamp), and 8 (hemlock) each contained eight different species of the small mammals taken or observed.

The habitat and home range requirements of the more abundant species are discussed in later sections. It is patent that different habitats support different populations. Plot 4 (white birch) yielded the greatest number of individuals (113) taken in one five-day period, in 1942 (Table V). In 1941, no plot contained so great a number, but sixty-three or more individuals were taken in one five-day period on each of Plots 2 (virgin hardwoods), 5 (hardwood saplings), and 6 (cedar swamp). The fewest individuals (3) taken in one five-day period were on two plots in 1940: on Plot 2 (virgin hardwoods), three animals (*Peromyscus*); on Plot 7 (spruce swamp) one representative each of three genera (*Sorex, Eutamias,* and *Peromyscus*). The increase from 1940 to 1941 on Plot 2 is noteworthy. The next smallest number of individuals taken in one five-day period was on Plot 1 (jack pine): ten in 1940, nine in 1941.

Table VI lists, for the eight plots and the several trapping periods, the percentage of the total catch on all plots during that period of eleven kinds of small mammals (*Sorex, Microsorex, Blarina, Eutamias, Tamias, Glaucomys, Peromyscus, Microtus, Clethrionomys, Zapus,* and *Napaeozapus*). If each plot were equally desirable for all members of the small mammal fauna, and if there were a purely random distribution of the small mammals taken in any one trapping period, one would expect each of the eight plots to contain 12.5 per cent of the total population of small mammals caught. But such is not the case. No one plot at any time contained less than 2 per cent, nor more than 22 per cent, of the total population of small mammals taken. Only two plots were consistently above or below the 12.5 per cent

TABLE V

COMPARISON OF SMALL MAMMAL POPULATIONS TRAPPED ON EIGHT STUDY PLOTS

Species and Trapping Period	Total of Individuals Captured							
	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6	Plot 7	Plot 8
All species caught*								
1940	10	3	12	24	26	24	3	15
1941 (1)	20	44	43	36	36	40	17	48
1941 (2)	9	63	47	44	63	67	22	40
1942	29	97	81	113	34	73	73	19
Sorex cinereus								
1940	.....	.....	1	1	6	5	1	1
1941 (1)	.....	.....	.....	.....	.....	2	3	2
1941 (2)	.....	2	.....	1	5	20	15	1
1942	.....	.....	.....	.....	2	.....	.....	.....
Blarina brevicauda								
1940	.....	.....	.....	.....	.....	.....	.....	.....
1941 (1)	.....	6	2	.....	3	.....	1	1
1941 (2)	.....	4	.....	.....	7	1	.....	1
1942	18	61	49	57	14	57	68	2
Eutamias minimus								
1940	6	.....	.....	.....	1	1	1	.....
1941 (1)	5	.....	5	.....	.....	3	3	.....
1941 (2)	1	.....	2	3	2	1	.....	.....
1942	.....	.....	.....	1	.....	.....	.....	.....
Tamias striatus								
1940	2	.....	.....	.....	6	.....	.....	.....
1941 (1)	3	3	.....	.....	6	.....	.....	.....
1941 (2)	2	.....	.....	2	8	.....	.....	.....
1942	1	.....	.....	1	4	.....	.....	.....
Peromyscus maniculatus								
1940	1	3	11	20	13	5	.....	14
1941 (1)	3	34	34	31	25	12	3	41
1941 (2)	.....	49	41	33	34	15	.....	32
1942	7	36	32	52	13	11	1	15
Clethrionomys gapperi								
1940	1	.....	.....	3	.....	13	1	.....
1941 (1)	9	1	2	5	.....	19	6	4
1941 (2)	5	8	4	4	4	26	7	6
1942	3	.....	.....	2	1	4	4	2

* This includes captures of *Microsorex, Mustela, Tamiasciurus, Glaucomys, Microtus, Zapus,* and *Napaeozapus* not otherwise included in this table.

mark: Plot 1 (jack pine) varied from 2 to 9 per cent and Plot 6 (cedar swamp) from 14 to 20 per cent of the total population. For ready comparison, these figures from Table VI are presented graphically in Figure 2.

The small mammal populations on most plots fluctuated widely, sometimes above and sometimes below the 12.5 per cent mark. Whether these fluctuations were caused by varying availability of food supply, local abundance

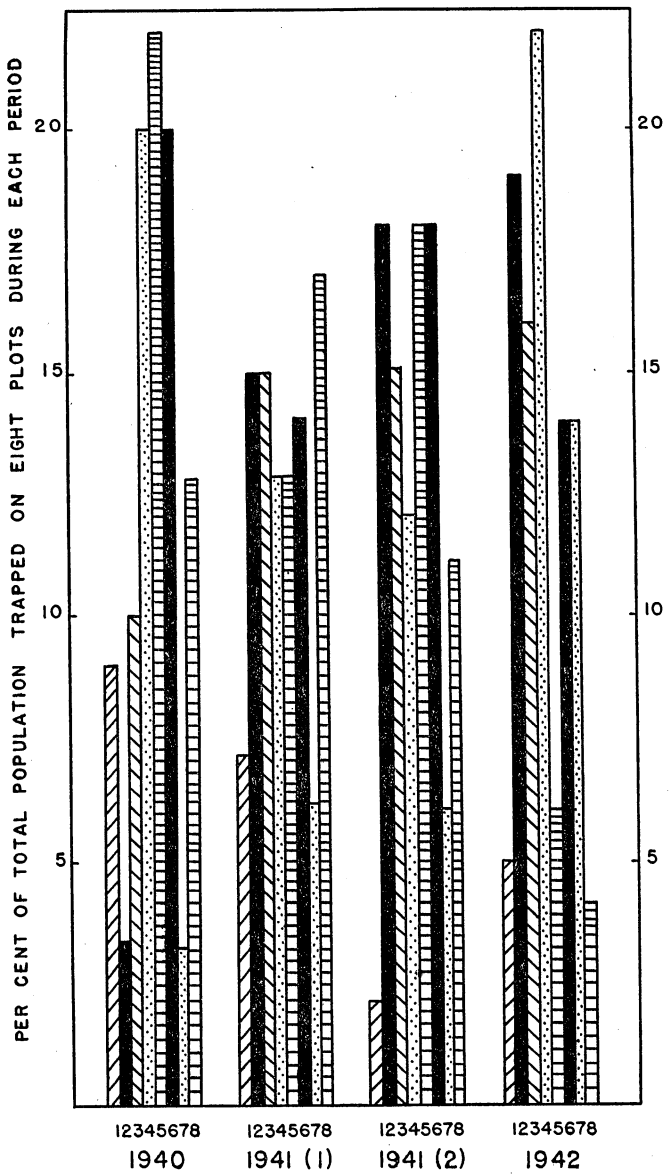


FIG. 2. Percentage of small mammals captured on each of eight plots during four trapping periods.

of predators, available shelter and/or homesites, weather conditions, or other controlling factors could not be determined.

The calculated populations per acre of eleven species (as deduced in later species accounts) on each of the eight plots are likewise summarized in Table VI, and presented graphically in Figure 3. In general, there was a gradual increase in the populations represented on the plots during the three-year period, as evidenced by the average populations per acre. Plot 4 (white birch), and to a lesser extent Plot 3 (hemlock), ranked high during each period; Plot 2 (virgin hardwoods) also ranked high except during 1940. Plot 1 (jack pine) was at or near the bottom as regards populations supported during most periods. These figures serve well to indicate trends, but minor fluctuations as between plots or between trapping periods may merely reflect differences in the time of trapping. The data on each plot

TABLE VI

RELATIVE POPULATIONS OF ELEVEN SPECIES OF SMALL MAMMALS CAPTURED ON EIGHT STUDY PLOTS

Plot	Percentage of Total Catch				Total Population Per Acre			
	1940	1941(1)	1941(2)	1942	1940	1941(1)	1941(2)	1942
1	9	7	2	5	1.3	2.9	1.3	4.5
2	3	15	18	19	0.3	7.3	10.8	16.5
3	10	15	15	16	2.1	6.9	8.0	13.9
4	20	13	12	22	5.1	7.6	9.2	23.4
5	22	13	18	6	4.3	5.6	10.4	5.7
6	20	14	18	14	3.7	7.0	8.0	12.4
7	3	6	6	14	0.5	2.7	4.3	12.3
8	13	17	11	4	2.6	8.4	6.9	3.1
Total of all plots	100	100	100	100	19.9	48.4	58.9	91.8
Average of all plots	12.5	12.5	12.5	12.5	2.5	6.1	7.4	11.4

are not altogether comparable during the three seasons; indeed, varying weather conditions would have made this impossible even had any one plot been trapped on the same dates each year. Therefore, some variables, such as number of young that were trapped after leaving the nest, have been introduced into the data.

In general, Plot 7 (spruce swamp) was the least desirable habitat for small mammals, considering both species and numbers. The moist acid nature of the soil and the presence of only one species of tree in any numbers doubtless were influential factors. Plot 1 (jack pine) likewise appeared to be a relatively undesirable habitat for small mammals; it supported seven species, but only small numbers were present. On the other hand, Plot 2 (virgin hardwoods) appeared to be far from the "biological desert"

which this type of habitat has sometimes been called. Plots 5 (hardwood saplings) and 6 (cedar swamp) were both highly favorable for small mam-

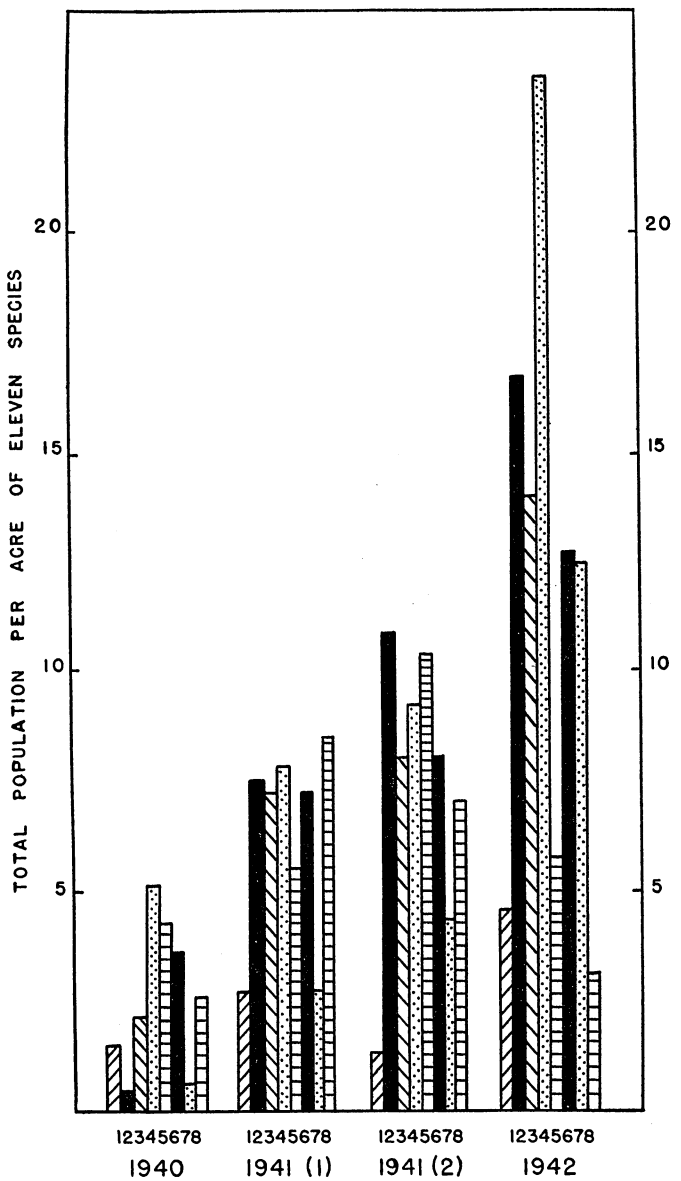


FIG. 3. Relative populations of small mammals captured on each of eight plots during four trapping periods.

mals; species occurred in different relative numbers on the two areas. On all plots the small mammal populations varied considerably from season

to season, not only (as would be expected) with the stage of the breeding cycles of the resident mammals, but also with the fluctuation in numbers of *Blarina,* which rose strikingly in 1942.

Hatfield (1938) suggested that there might be a correlation between the numbers of *Peromyscus* caught and the presence on the area of plants such as *Clintonia Maianthemum, Diervilla, Rubus,* and *Vaccinium,* the fruits of which are game foods of some value. I can find no such correlation. Food plants certainly have a bearing on the distribution of the herbivorous mammals but, as Hatfield stated, numerous other factors are also involved. The whole appears to be far too complex for analysis in the light of present knowledge. After working with two species of *Peromyscus,* Johnson (1926) concluded—rightly, I believe—that "the whole biotic association type, rather than any single factor of the environment, is of primary importance in the distribution of these mice."

THE SPECIES

Peromyscus maniculatus gracilis Le Conte

HABITAT PREFERENCES.—The ubiquitous deermouse appears to be the most abundant mammal of the Huron Mountains in most years. Although taken on all plots, it varied in abundance on different areas. On Plots 1 (jack pine) and 7 (spruce swamp) it was not captured during several trapping periods; at other times a maximum of five and three animals, respectively, was taken on these two plots. On the remaining six plots, it was captured during all trapping periods, but was least common on Plot 6 (cedar swamp). All major upland forests of the region support deermice. In addition they occur in and about buildings, in meadows and pasture lands, and one was taken in a leatherleaf bog. It is probable that the amount of ground water influences local distribution of this species.

Homesites for these mice are readily available. All the mature forests offer a variety of retreats, and mice have been seen to utilize holes in the ground, crevices beneath or among rocks, fallen logs, stumps, brush piles, and cavities in trees. Lack of suitable retreats may account for the small numbers of *Peromyscus* on Plot 1. The ground was sandy, not well suited for burrows, and with little accumulated litter; the nearly pure stand of jack pines consisted largely of small, healthy trees with few cavities.

BEHAVIOR.—When released after capture, most mice immediately hurried for shelter, hiding in the nearest available retreat. In three instances, this shelter was a trap. After several captures, most mice lost much of their timidity and were more leisurely about retreating when released. Sometimes they stayed in the open, preening themselves for a few minutes before running off. One female remained in sight for eight minutes; she washed her face with her paws, poked about among the dry leaves, caught

and ate a carabid beetle, and finally scurried off along a runway and disappeared beneath a stump twenty-five feet from where she had been trapped.

It was apparent that most mice, certainly all adults, were entirely familiar with the territory about them. They made their way unerringly along runways, across logs, around rocks, or over the ground surface to some retreat. It was not always the same retreat, but the mice always seemed to know where one was available. Often it was in a tree; thirty-three mice, of which twenty-five were adults, climbed near-by trees when released. A large oak tree was used regularly by a male in 1941 and by a female the following year. Sugar maples, basswoods, and hemlocks were also climbed. Occasionally, mice disappeared into cavities about twenty feet from the ground; one male ascended a hemlock until he was lost to view at a height of approximately thirty feet. Another male climbed high into a tree during a moderately heavy rain.

These mice are active throughout the year; their trails in the snow were frequently seen. They are usually considered to be nocturnal, and although they generally are, they may occasionally venture outside of their retreats during the daytime. I have records of nine individuals (five adults, four juveniles) that were taken between the hours of 9:00 A.M. and 1:00 P.M. All except two were males; one was taken a second time the same day between 2:00 and 5:00 P.M.

LONGEVITY.—In the wild, few if any mice attain the age of eight years that they may reach in the laboratory (Dice, 1933). The turnover in the population in an area from year to year is high due either to movement away from the area or to death from predation or other causes. Of sixty-seven mice first captured in 1940, twenty-three (34 per cent) were recaptured in 1941 and seven (10 per cent) in 1942; of 290 mice captured in 1941, forty-two (14 per cent) were recaptured in 1942. Six mice, all juveniles when first taken, were captured in both 1940 and 1942; if they be considered one month old at the time of initial capture, they were twenty-four months old when last taken. My oldest specimen was lactating when first captured on July 17, 1940; it is unlikely that she was born that spring. If it be assumed that she was of a late litter of the previous fall (mid-September), her age when last taken on June 18, 1942, was approximately thirty-three months. These seven specimens, when last captured, were in apparent good health.

SEX RATIO.—The sex ratio of these mice in three years seldom departed by more than 10 per cent from the hypothetical 50-50 ratio. The slight disparity in numbers between the sexes may be caused by the relatively small number of individuals captured or by the greater tendency of the males to wander, and thus their greater frequency of capture (Townsend, 1935;

Burt, 1940). In considering mice of all age classes, I found the males in the majority each year, ranging from 53 per cent in 1941 to 59 per cent in 1942. For the three seasons combined, on the basis of 540 individuals captured, the males constituted 56 per cent and the females 44 per cent.

Perhaps a truer indication of the sex ratio is to be obtained by comparing individuals within a particular age class. In considering only the juveniles, males were in the majority in 1940 (59 per cent) and in 1942 (63 per cent);

TABLE VII

BREEDING ACTIVITY OF *Peromyscus* IN THREE SEASONS, GROUPED INTO APPROXIMATELY TEN-DAY PERIODS

Dates	Adult Females		Adult Males		Juveniles First Captured, Both Sexes
	Captured	Breeding	Captured	Breeding	
1940					
June 8–10	0	0	1	0	0
June 11–20	1	1	2	0	0
June 21–30	1	0	1	0	0
July 1–10	1	1	0	0	3
July 11–20	5	4	4	0	20
July 21–31	2	0	7	0	6
Aug. 1–10	2	2	5	0	11
Aug. 11–20	1	1	1	1	6
1941					
June 17–20	3	3	11	6	15
June 21–30	0	0	4	0	1
July 1–10	9	6	16	3	42
July 11–20	8	8	11	1	23
July 21–31	14	9	14	4	8
Aug. 1–10	2	2	4	0	9
Aug. 11–20	0	0	0	0	17
Aug. 21–31	6	2	13	0	22
Sept. 1–10	8	6	15	0	17
Sept. 11–20	16	7	13	2	12
Sept. 21–27	2	0	5	0	3
1942					
May 23–31	10	10	19	4	0
June 1–10	22	21	27	8	8
June 11–20	18	14	24	1	47
June 21–30	0	0	0	0	2

in 1941, however, females were more numerous (53 per cent). Over the three years, on the basis of 277 specimens, males were but slightly in the majority (52 per cent). It is possible that the differential tendency between the sexes to wander is less pronounced in juveniles than in adults. If so, sex ratios based on juveniles alone should give a more nearly correct picture.

For comparison, sex ratios based on numbers of adults alone show males predominating as follows: 1940, 57 per cent; 1941, 63 per cent; 1942, 57

per cent. Over the three-year period, 60 per cent of 262 adult mice taken were males. Males were relatively more abundant on the basis of adults only than was the case when juveniles only or all age classes combined were considered. It is patent that the sex ratio may vary considerably with season as well as with age class. Temporal deviations from the hypothetical 50-50 ratio may have a bearing on seasonal fluctuations of populations.

Breeding.—At each capture all mice were examined for evidence of breeding activity. A well-advanced pregnancy or state of lactation is apparent and the position of the enlarged testes in the scrotum is indicative of sexual activity. Unfortunately, my records of three years do not cover altogether comparable periods in each season, nor do they include a sufficiently large number of individuals to permit generalizations concerning the breeding cycle. Data on adult mice captured during ten-day periods in each of the three seasons are presented in Table VII. Breeding females are those in late pregnancy or lactating; breeding males are those with testes in the scrotum.

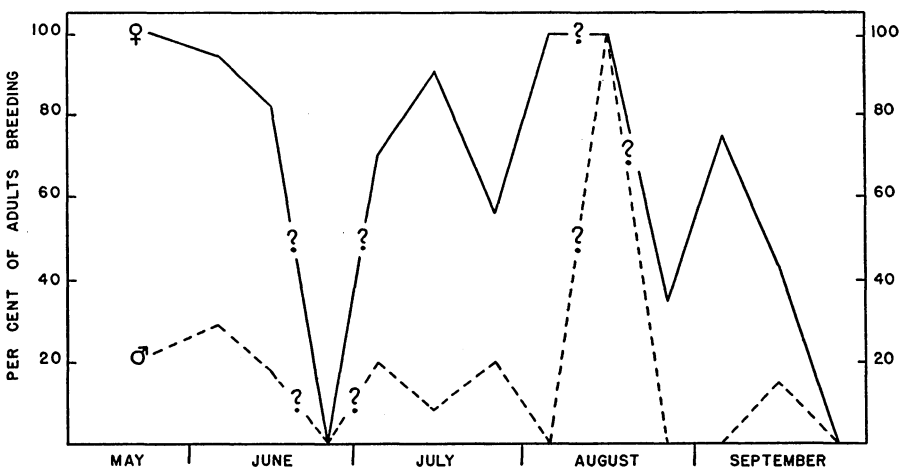


Fig. 4. Breeding activity of adult specimens of *Peromyscus*, 1940 to 1942.

If the data from each season are plotted separately, the lines fall nearly together. From this it is inferred that environmental differences during the three seasons made but slight changes in the breeding cycles of the mice, at least as relates to the duration of the breeding season. The data from the three seasons combined are shown graphically in Figure 4. I believe that the trough about June 21, and the peak about August 11, may be apparent rather than real, because of the small number of individuals. Actually, there appears to be no such midsummer lull or resting period during the breeding season as was reported by Coventry (1937) in Ontario or in

related species farther south by McNair (1931), Burt (1940), and Blair (1940*d*). Such a lull, however, might exist if the activity of any particular female were followed throughout the breeding season. This was not done in the present study.

The earliest trapping in any season was on May 23, 1942, and the latest on September 27, 1941. In 1942, from May 23 to June 4, both dates inclusive, thirty-four mice were taken. All were adults; ten of them were lactating females and the rest were males. The first juvenile was taken on June 5, and sixteen more juveniles were caught within the following week. It is apparent that these juveniles were of the first spring litter. If one assumes that these juveniles were a month old when first captured and a twenty-five-day gestation period is postulated, it appears that the first spring mating

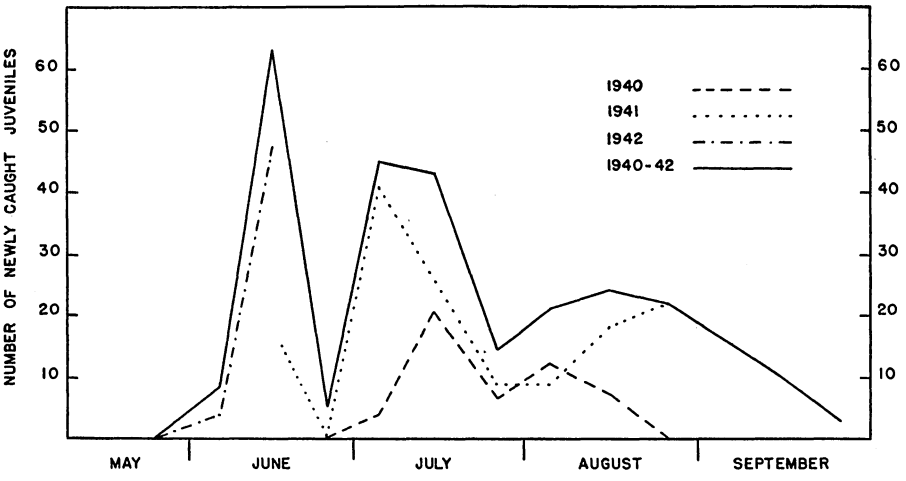


FIG. 5. First appearance of litters of *Peromyscus* away from the nest, as judged from dates of first captures of juveniles.

took place about April 11. In 1941, the last lactating female was taken on September 16 and no young juveniles, that is, those which had not begun molting, were taken after September 15. From this it appears that the last mating took place about August 23. It may be inferred from an adult male with testes in the scrotal position, taken on September 12, 1941, that some breeding continues at least until this date. The breeding season among these mice, during the years 1940 to 1942, therefore extended approximately from the first week in April until early October, with the first spring litters born in early May.

Females in this locality did not appear to breed until after their first winter. Twenty-six females first captured as juveniles in the summers of 1940 and 1941 and recaptured the same season with no indication of breeding, had bred when taken the season after their initial capture. Be-

tween June 17 and July 21, 1941, I first captured eleven juvenile females; they were recaptured between August 22 and September 12, 1941, when none were breeding. If one assumed them to be thirty days old when first taken, their ages ranged from seventy-eight to 110 days when last taken. In northern Michigan the rigors of the weather apparently preclude the breeding of females that become sexually mature in the late fall.

In the last column of Table VII are listed 272 individuals of both sexes which were juveniles when first captured. In Figure 5, these data are plotted for each year separately and for the three years combined. In this locality young appear away from the nest in numbers in mid-June, early

TABLE VIII

CALCULATED HOME RANGES OF *Peromyscus*

Adults				Juveniles			
Individuals	Times Caught	Dates	Home Range (sq. yd.)	Individuals	Times Caught	Dates	Home Range (sq. yd.)
24 ♂	5	June 1942	700	7 ♂	3	July 1941	600
41 ♂	7	July 1940	800	44 ♂	5	July 1940	900
70 ♂	5	June 1941	800	102 ♂	5	Aug. 1941	800
208 ♂	4	June 1942	1100	19 ♂	5	July 1940	800*
234 ♂	5	May 1942	500	43 ♂	5	July 1940	1200*
279 ♂	4	Sept. 1941	800	63 ♂	4	Aug. 1940	1300*
20 ♂	5	July 1940	900*	277 ♂	4	Sept. 1941	1300*
37 ♂	7	July 1940	1500*	419 ♂	4	June 1942	900*
42 ♂	6	July 1940	800*	.....	.....	.....	.....
74 ♂	3	Sept. 1941	1000*	53 ♀	4	Aug. 1940	600
107 ♂	4	July 1941	1000*	79 ♀	4	June 1941	800
231 ♂	4	June 1942	900*	114 ♀	5	July 1941	500
				156 ♀	3	July 1941	600
54 ♀	4	Aug. 1941	600	161 ♀	4	July 1941	700
6 ♀	3	July 1940	800*	427 ♀	5	June 1942	1000
21 ♀	5	July 1940	1200*	23 ♀	6	July 1940	1100*
150 ♀	5	July 1941	900*	421 ♀	6	June 1942	500*
183 ♀	5	July 1941	800*	424 ♀	5	June 1942	800*

* Based in part on one capture in marginal row of traps.

July, and mid-August; a few late litters appear through September. These three peaks may indicate that a breeding female raises three, or possibly four, litters during one season in this area. In a related species (*P. leucopus*) some three hundred miles farther south, Burt (1940) found that "each old female that lives throughout the breeding season has four, or possibly five, litters."

Two pregnant females, found dead in traps, each contained five well-developed embryos. Those taken from one female on June 19, 1942, averaged 18 mm. in length; those from the other, taken on July 7, 1941, averaged 16 mm. By assuming that all adult females are breeding, and that all adult females as well as juveniles present were captured, one may approxi-

mate the litter size by the ratio of young per adult female. This figure was 5.1 in 1940, 3.6 in 1941, and 1.2 in 1942. The low ratio in the last year is doubtless due, at least in part, to the short period covered by trapping early in the season when many juveniles had not yet ventured away from the nest. Over the three years the ratio was 2.6 young per adult female.

HOME RANGE.—Such home ranges as were calculated from the data available are listed in Table VIII. They vary from 500 to 1500 square yards (0.11 to 0.31 acre) for adult males, from 600 to 1200 square yards (0.12 to 0.25 acre) for adult females, and from 500 to 1300 square yards (0.11 to 0.27 acre) for juveniles of both sexes. My figures are considerably lower than those for *P. leucopus* given by Burt (1940), whose mice were taken more often during a month's time. Likewise, my figures are lower than those of Blair (1942) for *P. maniculatus*. I feel, however, that Blair indicated the maximum possible, rather than the actual, home range as reflected by trapping data. By using his data, my calculated home ranges are one-half to two-thirds the figures he reaches. Probably, the actual home range lies somewhere between his figures and mine.

DISPERSAL.—No planned experiments were made relating to homing instinct, dispersal, or distances traveled by mice, yet some data pertaining to dispersal were accumulated. From trapping records on the same or successive days, I have data on fifty-four mice known to have traveled at least 150 feet in twenty-four hours or less; many may have gone so far as to depart entirely from the area trapped. Thus, the figures only indicate how far a mouse may travel in a day or less. Of the adult males, twenty-two mice moved 200 to 340 feet and averaged 253 feet; six adult females moved 180 to 305 feet and averaged 239 feet; among the juveniles there was little difference as between the sexes; twenty-six mice moved 150 to 305 feet and averaged 214 feet.

Mice are known to establish new home ranges from time to time. Juveniles in particular may move a considerable distance from their place of birth to establish homesites of their own. Burt (1940) considered dispersal as the permanent movement of a mouse a distance of 100 yards or more from the place of original capture, and regarded 23 per cent of 287 animals as having dispersed after an interval of two weeks or more. Such movements, in this study, would usually remove the individual from the area trapped. Some mice, however, remained on the same plot for several seasons or years. Examples are given in the accounts of longevity in this species; all recaptures of mice in different years were on the same plot on which originally taken. Three females in particular appeared to remain in very restricted parts of their respective plots for two or three years.

POPULATIONS.—For lack of precise data on the size of the home range of *Peromyscus* in this locality, I have assumed 0.75 acre (Burt, 1946: 271)

TABLE IX

Peromyscus POPULATIONS ON EIGHT PLOTS, 1940 TO 1942

Plot	Ages	1940				1941 (1)				1941 (2)				1942			
		♂	♀	Total	Pop./A	♂	♀	Total	Pop./A	♂	♀	Total	Pop./A	♂	♀	Total	Pop./A
1	Juvenile	1	.....	1	0.17	.....	1	0.17	.....	.....	.....	.....	.....	5	.....	5	0.85
	Adult	.....	.....	.....	.....	1	1	2	0.34	.....	.....	.....	.....	.....	.....	.....	.....
	Total	1	.....	1	0.17	1	2	3	0.51	.....	.....	.....	.....	5	.....	5	0.85
2	Adult	1	1	2	0.34	12	12	24	4.10	13	16	29	4.94	12	5	17	2.90
	Juvenile	.....	.....	.....	.....	7	3	10	1.70	11	9	20	3.40	10	9	19	3.24
	Total	1	1	2	0.34	19	15	34	5.80	24	25	49	8.36	22	14	36	6.14
3	Adult	1	2	3	0.51	8	3	11	1.88	7	3	10	1.70	13	18	31	5.29
	Juvenile	6	2	8	1.36	9	13	22	3.76	10	21	31	5.29	1	.....	1	0.17
	Total	7	4	11	1.88	17	16	33	5.64	17	24	41	6.99	14	18	32	5.46
4	Adult	3	3	6	1.27	12	3	15	3.18	8	5	13	2.76	11	11	22	4.67
	Juvenile	6	8	14	2.97	7	9	16	3.39	10	10	20	4.25	17	13	30	6.37
	Total	9	11	20	4.25	19	12	31	6.58	18	15	33	7.01	28	24	52	11.04
5	Adult	5	.....	5	0.85	8	2	10	1.70	6	4	10	1.70	9	4	13	2.22
	Juvenile	5	3	8	1.36	7	8	15	2.56	9	15	24	4.10	.....	.....	.....	.....
	Total	10	3	13	2.22	15	10	25	4.27	15	19	34	5.80	9	4	13	2.22
6	Adult	1	1	2	0.34	4	1	5	0.85	5	2	7	1.19	2	3	5	0.85
	Juvenile	3	.....	3	0.51	4	3	7	1.19	6	2	8	1.36	6	.....	6	1.02
	Total	4	1	5	0.85	8	4	12	2.05	11	4	15	2.56	8	3	11	1.88
7	Adult	.....	.....	.....	.....	1	2	3	0.51	.....	.....	.....	.....	.....	.....	.....	.....
	Juvenile	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	1	.....	1	0.17
	Total	.....	.....	.....	.....	1	2	3	0.51	.....	.....	.....	.....	1	.....	1	0.17
8	Adult	.....	2	2	0.34	8	7	15	2.56	8	2	10	1.70	8	6	14	2.39
	Juvenile	6	6	12	2.05	15	12	27	4.61	8	13	21	3.58	.....	.....	.....	.....
	Total	6	8	14	2.39	23	19	42	7.16	16	15	31	5.29	8	6	14	2.39

and have included a marginal strip of one hundred feet about the plot as within the area effectively trapped. My calculations of population per acre are, therefore, based on a three-hundred-foot square plot plus a one-hundred-foot strip on each side, equaling 5.86 acres (4.71 acres for Plot 4). In Table IX the plot population and the population per acre are given for each five-day trapping period, broken down into sex and age groups, and tabulated separately for each year. Juveniles taken in any year are not considered as adults until the following year, since evidence indicates that in this locality they do not breed until after their first winter.

The most consistently low populations of *Peromyscus* were on Plot 7, where in two periods no mice at all were taken, and in two other periods the maximum number was three (0.51 per acre). Plot 1 likewise supported a small population, the maximum number at any one time being five mice (0.85 per acre). All other plots, at one time or another, supported a total population of at least 2.56 mice per acre. The highest population, including all *Peromyscus* present, was 11.04 per acre on Plot 4 from June 16 to 20, 1942; of these, the juveniles reached a density of 6.37 per acre and the adults 4.67 per acre. Following the population on one particular plot at different periods throughout the season (though not in one year) I find that on Plot 5 there were 2.22 mice per acre (all adults) from May 23 to 27, 1942; 4.27 mice per acre (40 per cent adults) from July 1 to 5, 1941; 2.22 mice per acre (39 per cent adults) from July 27 to August 2, 1940; and 5.80 mice per acre (29 per cent adults) from August 23 to 27, 1941. Throughout the three years, the populations of all *Peromyscus* present on a plot in one five-day period ranged to 4.25 per acre in 1940, to 8.36 per acre in 1941, and to 11.04 per acre in 1942.

TERRITORIALITY.—My data are insufficient to demonstrate conclusively whether territoriality actually exists in this species. A five-day trapping period was not ample for securing records of any one individual throughout all of its home range. An analysis of my records indicates that adult females, during the periods trapped, occupied more circumscribed areas than did either adult males or juveniles of either sex. Adult males wandered widely, crossing the ranges of other adults of each sex. Juveniles appeared almost anywhere and probably were wandering at random in search of available homesites.

My findings may be illustrated by the mice on Plot 2, which supported a larger population of *Peromyscus* (sixty-five of all ages) than did any other plot during 1941. I have excluded as nonresidents those individuals caught but once during the trapping period or caught only in the outside row of traps (unless repeatedly caught there). Such individuals are considered to be wanderers from homes at varying distances outside the plot. From July 20 to 24, 1941, this plot contained ten resident adult females and

seven resident adult males. Sketching in possible home ranges on the basis of actual captures, in much the same manner as used for the determination of home ranges (Fig. 1), discloses only two instances of overlap among the females and three among the males. From September 12 to 16, 1941, this same plot contained six resident adult females and seven resident adult males. There were no apparent instances of overlap among the females, and there were only two among the males.

Populations of *Peromyscus* were smaller on the other plots, but the same general trend was evident. Adult females occupied specific areas, larger in some cases than on Plot 2, but with even less overlapping. Adult males were also localized in their ranges, but traveled far more widely than did the females; their ranges overlapped those of other adults of both sexes far more frequently than was the case with the adult females.

I suspect that territorial behavior does exist in this species. Adults, and females in particular, usually occupy isolated territories upon which others seldom trespass. How these territories are defended—if, indeed, they are, for mice may instinctively recognize the property rights of others —I cannot state. There may well be disputes, at least during the initial occupancy of a territory. Intolerance appears to be greater between adults, especially of the same sex, than between adults and juveniles.

In my conclusions, I am at variance with Blair (1942), who worked on this same subspecies also in northern Michigan. He stated: "The calculated home ranges of all sex and age classes broadly overlapped one another. Thus there was no occupation of exclusive home ranges by breeding females." Blair's method of calculating home ranges exaggerates the areas of overlapping that may exist. The presence of overlapping does not in itself disprove the existence of territorial behavior. Areas of overlap may represent "neutral" zones between two or more territories or may simply indicate instances of trespass upon an adjoining territory.

SOCIABILITY.—I had ten multiple captures of specimens of *Peromyscus* in one trap. All traps used were single-catch so that the mice had to enter at nearly the same time and may have been traveling together. These catches occurred from June 17 to September 6. Six instances involved only juvenile mice: two males, once; a male and a female, twice; and two females, three times. The four other instances involved adult males: with another adult male, once; with a juvenile male, once; and with a juvenile female, twice. These multiple catches consisted of two animals in all but one case—that of an adult male and two juvenile males caught at the same time. There was no evidence of intolerance on the part of any of the captives.

There is indirect evidence of some fighting among these mice. Eighteen specimens bore various scars. All of them had the ears more or less lacer-

ated and punctured, some severely, and a few had additional bruises or scars on the tails or near the eyes. These marks were present before the animals were initially identified by punching the ear. Of these animals 66 per cent were males, half adults and half juveniles. One badly injured juvenile female was apparently blind in the left eye. There was swelling about the eye, the eyeball had a whitish cast, and the lids would not close. The injury appeared to be completely healed when the animal was retaken the following year.

PELAGE ABNORMALITIES.—Skin collections contain scattered specimens with small spots of white in their pelage, frequently on the head. These whitish areas may be several millimeters in extent. Much of the literature on spotting characters and their heredity in *Peromyscus maniculatus* was summarized by Clark (1938). In the present study I noted several instances of this condition in wild populations. In 1941 each of five mice captured had a small white patch in the center of the forehead. These mice occurred on three different plots: all were juveniles; two were males and three females. Only one of these individuals was retaken in 1942; he still had this characteristic marking. Two other individuals, juveniles of each sex, were also taken in 1942 on still a fourth plot. The mutation would seem to have appeared independently on the four areas.

Another type of marking, a white patch in front of each ear, was observed in 1942. This condition existed in fifteen mice of both sexes and all age groups. An adult female on Plot 2, an adult male on Plot 3, and thirteen individuals on Plot 4 had these markings. Of the thirteen, four were adult females, six adult males, and three juvenile males. No juvenile females were observed with the markings, but the numbers concerned were so small that this may be of no significance. On Plot 4, the condition was present in 25 per cent of the fifty-two animals trapped in June. This points to its being accentuated by inbreeding among this population.

A partial albino (Museum of Zoology No. 86393) was collected in a cabin at the Huron Mountain Club on June 25, 1941. This was a young female (total length, 111 mm.) still in its juvenile pelage. It was uniformly white except for a grayish zone down the length of the back, dark ears, and dark eyes. It was one of eight young that had been taken in this cabin in a period of three days, but was the only one to exhibit albinistic traits.

PARASITES.—By far the most common parasite was the flea, *Orchopeas leucopus*. Probably all animals were infected. The incidence of fleas noted was as follows: in 1940, 19 per cent of the mice were parasitized; in 1941, 54 per cent; and in 1942, 82 per cent. In 1941 the fleas were unusually abundant on the mice parasitized. Infestation by mites, possibly *Trombicula harperi,* was noted in 1940 and 1941. Barely visible to the

naked eye, they always occurred on the inside of the pinna of the ear and occasionally about the eye. They were so numerous as to give the appearance of a light orange or pinkish encrustation on the affected spot. These mites were always noted on the surface, never buried in the skin. No traumatic effects or evidences of infection were noted. In 1940 this condition was observed only once (August 18), on an adult male on Plot 6. In 1941 the infestation was more widespread (from July 1 to August 24), occurring on 9 per cent of the mice taken, and being present on all plots except 3 and 4. Six of these parasitized mice had been captured the previous year, and no evidence of the mites was then apparent. Two others, when recaptured in 1942, showed no evidence of this condition. There was no correlation between age or sex of the host and presence of the mites; all groups were similarly affected.

Specimens of the tick *Ixodes marxi* were found on five individuals. Each time there was one seed tick present, on the ear, neck, or side of the face. The incidence of this parasite during the three years was as follows: 1940, 1.5 per cent; 1941, 1.0 per cent; 1942, 0.6 per cent. In all instances the condition was noted during June and July. Both sexes and age groups were affected. No botfly infections were observed during the three years.

MORTALITY.—Evidence of mortality, except for nine mice that were killed when caught in a trap door, was difficult to detect in the field. Some individuals bore injuries that may have been due to unsuccessful attacks by predators. Three mice had had their tails broken and healed so as to present several stiff vertebrae near the base. Two mice had their tails completely broken off about an inch from the body, and the stumps had healed. Three other mice had their tails broken off near the tips. One of these had recently suffered the injury when caught on June 20; when retaken on September 2 the stump was completely healed. One adult male, when taken on June 4, had lost both feet on the right side. The stumps were well healed, and the mouse was able to stumble along on them fairly well. He was not taken again.

On September 5 and 6, 1941, I found a peculiar condition present among the mice of Plot 4. It was an inflammation of the eyelids, with some swelling, so that the lids were closed with difficulty or not at all. Numerous small whitish pustules were present on both upper and lower lids. Both eyes were affected in the mice with this condition. Aside from one adult male, the nine mice with this inflammation were juveniles, both males and females. Fleas were numerous on all and were especially abundant near the site of the inflammation. These nine mice constituted 18 per cent of those present on Plot 4 and 3 per cent of all specimens of *Peromyscus* taken in 1941. Of the nine, three were retaken the following year—a survival rate which indicated that the condition was not fatal.

Clethrionomys gapperi gapperi Vigors

HABITAT PREFERENCES.—The red-backed vole, although less common than is the deermouse in the Huron Mountains, is generally distributed. At one period or another it was taken on each of the eight plots. It was most numerous on Plot 6, where, in 1941, it outnumbered any other species. On this plot specimens of *Peromyscus* were least common. There appeared to be a tendency for these two species to complement each other in point of numbers. During the period of this study these voles were far more common in the white cedar than they were in the black spruce swamp. During the three seasons, they were consistently more abundant in these swamps than in any of the upland areas. They were also taken in buildings on three occasions.

Nest sites and retreats, such as logs, stumps, deserted burrows of other animals, or piles of litter on the ground, are readily available in the Huron Mountains. The vole's food consists of a variety of leaves and stems, young shoots of grasses, fruits, and the bark of trees and shrubs. Possibly the year-round availability of food and the greater ease of procuring it by tunneling beneath the snow are factors favoring the greater abundance of this species in swamps.

BEHAVIOR.—This vole is far less docile than is the deermouse. When captured, it invariably struggled to escape. It bit viciously and often uttered a shrill chattering "churr-r-r." When released, the vole usually remained in the same spot for several seconds and sniffed the air in different directions while its whole body quivered; then with a sudden dash it disappeared into some near-by retreat. This vole appears to be well acquainted with the territory it occupies. In one instance an adult female, perhaps confused after being handled, returned to the trap when released; she had been captured once the previous day.

This vole has a very nervous temperament and is extremely liable to shock. This is illustrated by a common reaction when a vole is first caught and marked by ear-punching. During this operation the animal was grasped with the thumb and index finger by the nape of the neck, its body cradled in the palm of the hand. The process did not appear to distress either deermice or chipmunks handled in the same manner. But fifteen voles, when thus handled, apparently became unconscious after struggling for a few seconds. In one case there was even some bleeding from the mouth. The voles which reacted in this way represented both sexes and both adults and juveniles in nearly equal numbers. After marking, the animals were placed on the ground. They recovered consciousness after one or two minutes and dashed for cover. There appeared to be no permanent aftereffects, for each of these individuals, in apparent good

health, was recaptured on subsequent days. One juvenile female was accidentally dropped from a height of two feet upon a floor of pine needles; she was stunned and remained unconscious for half a minute, then recovered and scurried off. An adult male, originally caught on August 6, 1941, had a fresh, slight wound on the back of the neck when taken the following September 27; he died while being examined.

Clethrionomys is active the year round; even severe winter weather does not prevent its excursions above ground. Fresh tracks of this vole were common in the snow in the winter months of the study.

The diurnal habits of this species have been mentioned by various writers. I captured eight different individuals between the hours of 8:00 A.M. and 5:00 P.M. Some were repeatedly captured during the same day, and others as often as six times during different days. Five of these individuals were adult males; three were females, and of these one was a juvenile. On several other occasions voles were seen by day on areas away from the plots.

I had no instances of multiple captures in my traps. The indications are that members of the species are rather intolerant toward others of their kind.

LONGEVITY.—My limited data indicate that this vole has a shorter normal life span in the wild than does the deermouse. Of fifteen voles first captured in 1940, two (13 per cent) were recaptured in 1941, none in 1942. Of ninety-two voles captured in 1941, one (2 per cent) was recaptured in 1942. Of the 104 different voles captured in the first two years, only three (3 per cent) are known to have lived for more than one year; these included two adult females and a juvenile male. If the juvenile be considered one month old and the adults three months at the time of initial capture, their ages when last taken would be fourteen months or more. One of the females was lactating when first taken on August 5, 1941; she was, therefore, probably born not later than the previous September. This would fix her age when last captured at approximately twenty months.

SEX RATIO.—Throughout the three-year period, of the 123 individuals of all age classes captured, 54 per cent were females. The males were in the majority in 1940 (53 per cent) and in 1942 (56 per cent), and the females predominated in 1941 (57 per cent). At no time did one sex deviate by more than 7 per cent from the 50–50 ratio. The males constituted 75 per cent of thirty-seven juveniles in 1940, the females 76 per cent in 1941; no juveniles were captured in 1942. This disparity is regarded as a result of the small number of individuals considered rather than an indication of a differential tendency of the sexes to wander. In comparing eighty-six adults taken in the three years, females predominated in 1940 (55 per cent), males in 1941 (54 per cent) and in 1942 (56 per cent). Although

based on a relatively small number of individuals, this is taken as indicative of practical equality in numbers between the sexes.

BREEDING.—Few data have been published on the breeding habits of this vole in the wild. In this study 122 voles were captured during three seasons. No individual was followed throughout its breeding cycle, but some information on the breeding habits was forthcoming. Breeding begins early in May in the Huron Mountains. The earliest date on which juveniles were trapped was June 20, 1941. The first young of the year may have appeared long before this date. In 1942, one female on May 26 and two others on May 30 were lactating. On the basis of a seventeen- to nineteen-day gestation period (Svihla, 1930), breeding must have taken place not later than the second week in May.

The last juveniles (not yet molting) trapped during the season were taken on September 7, 1940, and on September 26, 1941. I have a record of one female lactating on September 22, 1941. The latest breeding record was of a litter born in a trap between the hours of 9:00 A.M. and 1:00 P.M. on September 23, 1941. To judge by other individuals caught in September, this one late breeding record is the exception rather than the rule. Criddle (1932) found in southern Manitoba that with favorable weather the breeding season ran from early April until the middle of September. Coventry (1937) believed the breeding habits of *Clethrionomys* and *Peromyscus* to be very similar in Ontario, except that the vole might breed until mid-September, somewhat later than the mice breed. In the Huron Mountains the voles breed from early May until late September.

Criddle (1932) believed that red-backed voles in southern Manitoba raised at least four litters a year. I do not know the number of litters raised in one season in the Huron Mountain region. The size of the litter is variously given as from two to eight (Svihla, 1930; Criddle, 1932; Townsend, 1935; Coventry, 1947). I have definite data on three individual females: one bore three young in a trap on August 17, 1940; another contained five embryos (average length, 8 mm.) on July 23, 1941; the third contained five embryos (average length, 20 mm.) on June 14, 1942.

Svihla (1930) found that both sexes in captivity became sexually mature in about four months, at which time females might bear young. I have records of two voles that bred during their first year. One was obviously a young of the year when first captured on August 17, 1940; his testes were then in the scrotal position. The other was a juvenile beginning to molt when first taken on July 25, 1941; she was lactating when retaken on September 14, 1941. In contrast to these two instances, I have records of one male and seven females first taken as juveniles which showed no evidence of having bred when later recaptured in the same season. If they be considered as thirty days of age when first captured, they ranged from

seventy-nine to one hundred and eight days of age without having bred. Breeding by young of the year evidently does occur, but is not the normal procedure in the Huron Mountains. This agrees with the findings of Blair (1941*c*) in Alger County, northern Michigan. He concluded that "voles born during the summer may breed in late summer or early fall."

HOME RANGE.—Blair (1941*c*) calculated the home ranges of six red-backed voles in northern Michigan and found them to vary from 0.49 to 3.56 acres. My captures of an individual vole did not exceed seven in any five-day trapping period. I have calculated that the home ranges of fifteen individuals listed in Table X varied from 600 to 1100 square yards (0.12 to 0.23 acre) for adult males, from 600 to 1000 square yards (0.12 to 0.21 acre) for adult females, and from 500 to 700 square yards (0.10 to 0.15

TABLE X

CALCULATED HOME RANGES OF *Clethrionomys*

Adults				Juveniles			
Individuals	Times Caught	Dates	Home Range (sq. yd.)	Individuals	Times Caught	Dates	Home Range (sq. yd.)
45 ♂	4	Aug. 1941	1100	39 ♂	4	Sept. 1941	700*
67 ♂	3	Aug. 1941	600	.....	.....	.....	.....
20 ♂	3	Sept. 1941	800*	.....	.....	.....	.....
56 ♂	4	Aug. 1941	600*	.....	.....	.....	.....
58 ♂	6	Aug. 1941	900*	.....	.....	.....	.....
3 ♀	3	June 1941	800	93 ♀	5	Sept. 1941	500
7 ♀	4	Aug. 1940	1000	21 ♀	5	Sept. 1941	600*
29 ♀	5	Sept. 1941	900	35 ♀	3	Sept. 1941	700*
49 ♀	3	Aug. 1941	600	74 ♀	3	Sept. 1941	500*
55 ♀	4	May 1942	600	.....	.....	.....	.....

* Based in part on one capture in marginal row of traps.

acre) for juveniles of both sexes. Additional captures would probably have increased the size of these calculated home ranges.

DISPERSAL.—From captures of eighteen individuals on the same or successive days, I have figures on the distance that voles may travel in a day's time. These individuals include only those known to have covered at least one hundred feet. The figures should not be construed as maximum distances that voles travel. Nine adult males moved 125 to 260 feet and averaged 183 feet; five adult females moved 150 to 310 feet and averaged 202 feet. Two juvenile males moved 270 and 310 feet, and two juvenile females 135 and 150 feet, respectively.

POPULATIONS.—The populations of red-backed voles were computed in the same manner as for *Peromyscus*. Lacking definite figures, I have assumed the same home range of 0.75 acre and have included a one-hundred-

TABLE XI

Clethrionomys POPULATIONS ON EIGHT PLOTS, 1940 TO 1942

Plot	Ages	1940				1941 (1)				1941 (2)				1942			
		♂	♀	Total	Pop./A	♂	♀	Total	Pop./A	♂	♀	Total	Pop./A	♂	♀	Total	Pop./A
1	Adult	1	.....	1	0.17	5	2	7	1.19	2	2	4	0.68	.....	3	3	0.51
	Juvenile	.....	.....	.....	.....	.....	2	2	0.34	.....	1	1	0.17	.....	.....	.....	.....
	Total	1	.....	1	0.17	5	4	9	1.53	2	3	5	0.85	.....	3	3	0.51
2	Adult	.....	.....	.....	.....	.....	1	1	0.17	4	1	5	0.85	.....	.....	.....	.....
	Juvenile	.....	.....	.....	.....	.....	.....	.....	.....	.....	3	3	0.51	.....	.....	.....	.....
	Total	.....	.....	.....	.....	.....	1	1	0.17	4	4	8	1.36	.....	.....	.....	.....
3	Adult	.....	.....	.....	.....	2	.....	2	0.34	2	2	4	0.68	.....	.....	.....	.....
	Juvenile	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
	Total	.....	.....	.....	.....	2	.....	2	0.34	2	2	4	0.68	.....	.....	.....	.....
4	Adult	.....	2	2	0.42	3	1	4	0.84	2	1	3	0.63	1	.....	1	0.21
	Juvenile	1	.....	1	0.21	.....	1	1	0.21	.....	2	2	0.42	.....	1	1	0.21
	Total	1	2	3	0.63	3	2	5	1.05	2	3	5	1.05	1	1	2	0.42
5	Adult	.....	.....	.....	.....	.....	.....	.....	.....	1	.....	1	0.17	1	.....	1	0.17
	Juvenile	.....	.....	.....	.....	.....	.....	.....	.....	1	2	3	0.51	.....	.....	.....	.....
	Total	.....	.....	.....	.....	.....	.....	.....	.....	2	2	4	0.68	1	.....	1	0.17
6	Adult	4	4	8	1.36	5	4	9	1.53	5	3	8	1.36	3	1	4	0.68
	Juvenile	2	.....	2	0.34	2	8	10	1.70	5	13	18	3.06	.....	.....	.....	.....
	Total	6	4	10	1.70	7	12	19	3.23	10	16	26	4.42	3	1	4	0.68
7	Adult	.....	.....	.....	.....	1	2	3	0.51	1	3	4	0.68	3	1	4	0.68
	Juvenile	.....	1	1	0.17	1	2	3	0.51	.....	3	3	0.51	.....	.....	.....	.....
	Total	.....	1	1	0.17	2	4	6	1.02	1	6	7	1.19	3	1	4	0.68
8	Adult	.....	.....	.....	.....	2	.....	2	0.34	2	3	5	0.85	1	1	2	0.34
	Juvenile	.....	.....	.....	.....	.....	2	2	0.34	.....	1	1	0.17	.....	.....	.....	.....
	Total	.....	.....	.....	.....	2	2	4	0.68	2	4	6	1.02	1	1	2	0.34

foot marginal strip around each plot as within the area effectively trapped, except in the case of Plot 4. The populations by sex, by age group, and per acre, on the eight plots during each period are listed in Table XI.

Plots 3 and 5 supported no *Clethrionomys* during two of the four trapping periods; the greatest total population at any time on these two plots was four voles (0.68 per acre). All other plots, at one period or another, supported at least 1.02 voles per acre. The highest population was reached on Plot 6, where there was a total population of twenty-six (4.42 per acre) from September 22 to 26, 1941, near the end of the breeding season; of these, the juveniles reached a density of 3.06 per acre and the adults 1.36 per acre. Throughout the three years, the range of populations on any plot in one five-day period was to 1.70 per acre in 1940, to 4.42 per acre in 1941, and to 0.68 per acre in 1942. During the latter year, all trapping was done prior to June 21.

Blair (1941*c*) found an average population of 0.18 voles per acre on an 18.2 acre plot in a beech-maple forest, between August 23 and September 7, 1940. This is nearly identical with my figure (0.17 per acre) on Plot 2, a virgin hardwood area, from July 20 to 24, 1941.

TERRITORIALITY.—The same difficulty for determining territoriality obtains in this species as did in *Peromyscus*—the paucity of captures in a five-day trapping period. Furthermore, the number of individuals taken was much smaller; in some cases so few voles inhabited a plot that competition between them was practically nil, and no need for territorial behavior seemed to exist.

Plot 6, which supported thirteen voles in 1940 and thirty-eight in 1941, serves to illustrate my findings. By excluding as transients those individuals which were caught only once, or only in the outside row of traps, there remain seven resident adults on the plot during both 1940 and 1941. Of the seven resident adult females on the plot during the two periods, only one was taken in traps in common with other adult females. The same applies to the seven resident adult males, of which only one appeared to overlap the range of other adult males. The juveniles of both sexes on this plot showed no apparent patterns in their distribution; they were caught in almost any trap and appeared to be wandering in search of homesites of their own.

PARASITES.—No fleas were noted on these voles during either 1940 or 1942. In 1941 specimens of *Orchopeas* sp. were observed on seventeen (18 per cent) of the voles taken. The infestation was light on those individuals parasitized. Sexes and age groups were about equally affected. Fleas were present on some voles in all areas except one specimen in Plot 5. This vole was parasitized by mites, possibly *Trombicula harperi,* which occurred also on specimens of *Peromyscus.* As in the deermice, the mites were always on

the inside of the pinna of the ear. No ill effects from their presence were evident. There appeared to be no correlation between presence of these mites and sex or age of the host. In 1940 the mites occurred on 56 per cent of the voles taken; they were noted only from August 14 to 18, and only on Plot 6 (as was also the case with *Peromyscus*). Of the ten individuals parasitized, only one was retaken the following year, when no mites were evident on it. This condition was far more widespread in 1941, when it occurred on 70 per cent of the voles captured; it was noted from June 20 to September 24 and was present on all eight plots. Thirty (47 per cent) of the voles so parasitized were on Plot 6; the other seven plots each had two to eight cases. None of the individuals parasitized in 1941 was retaken the next year. In 1942 only two cases were observed, both on Plot 8; the hosts were an adult male and an adult female, taken on May 28 and May 26, respectively. The progress of this infestation through the three years was similar in populations of *Peromyscus* and *Clethrionomys,* but was much more prevalent in the latter.

Red-backed voles were also parasitized by the tick *Ixodes marxi.* The incidence of this parasite was 11 per cent in 1940, 7 per cent in 1941, and 19 per cent in 1942. In six cases the seed ticks were on the ear, in five cases on the shoulder or neck. Two parasitized individuals (both adult males) each carried two ticks. These ticks were noted from June 13 to September 7 on five of the eight plots. Seven of the hosts were adult males, three were adult females, and one was a juvenile male.

MORTALITY.—Since voles appear to travel somewhat shorter distances than do deermice, one would expect, other factors being equal, to find more repeats from year to year among the vole population. As this is not the situation, I am forced to conclude that mortality is greater among the voles than among the deermice. This might be a result of the vole's greater diurnal activity, for it is exposed more frequently to predators; or it might be a consequence of the vole's nervous temperament whereby a sudden shock (such as an unexpected attack) proves fatal. The vole's greater breeding potential helps somewhat to maintain the balance but even so in an apparently "stable" situation the population of *Peromyscus* consistently outnumbers that of *Clethrionomys.*

In the course of three seasons' trapping thirty-seven (30 per cent) of the voles captured were ultimately found dead in the traps. This happened most frequently after the vole had been confined by captures on several previous nights. It may again be associated with the animal's nervous temperament, an inability to withstand close confinement; or it may be a low tolerance for cold or rainy conditions. Fewer deermice died in the traps.

I observed eight injuries among the voles captured. These ranged from

bad tears in the ears, possibly the result of fighting among the voles themselves, to missing limbs. The worst injury was in an adult female whose right hind leg was nearly torn off; the femur was broken and the limb was attached merely by a few ligaments; this vole appeared in good health otherwise during four days after the injury was first noted. Another adult female was injured on the face and had apparently lost the sight of one eye, when first captured on September 4, 1941; the eye seemed somewhat improved the following day, although the vole was in a weakened condition. Of the eight injured individuals, only two are known to have died. These were a juvenile female, with a tear in the right ear, and an adult male bruised on the back of the neck.

Tamias striatus griseus Mearns

HABITAT PREFERENCES.—The eastern chipmunk occurred on all plots except 6 (cedar swamp) and 7 (spruce swamp). It was by far most common on Plots 5 (hardwood saplings) and 1 (jack pines). This animal is generally distributed throughout the Huron Mountains, where it ranges vertically to the summit of Mount Homer and other mountains. Its burrows have been found beneath logs and stones and in the bare ground among birch and aspen, dense hemlock, cedar, balsam fir, and virgin hardwood cover. It also occurs about buildings in forested areas.

Deep shade and a dry habitat seem to be determining factors in the distribution of this chipmunk in the Huron Mountains. It seldom frequents open lake shores, rocky outcrops, small unshaded openings in forests, or swamps, although it does occur among mature trees along streams or lakes, and it was twice seen on old beaver dams now deeply shaded. On five occasions I noted specimens of *Tamias* in heavy cover, while near by in unshaded openings were specimens of *Eutamias*.

BEHAVIOR.—The eastern chipmunk, known locally in the Huron Mountains as the "gopher," is the larger and less numerous of the two species of chipmunks in this region. It is less conspicuous than its smaller relative because of its different habits. When taken in a live trap, for instance, the eastern chipmunk was never known to chirp; the least chipmunk nearly always did so. The call note of the eastern chipmunk was seldom heard in the course of the three seasons; only occasionally when alarmed did it chirp before fleeing. It was not easily alarmed. On several occasions I observed one for about ten minutes from a distance of approximately ten feet; the chipmunk proceeded with its foraging, uttering not a sound. This species runs with the tail flowing straight out behind and in line with the body, unlike the least chipmunk. Usually considered a ground dweller, the eastern chipmunk can climb with agility. I observed it several times in low shrubs and once at a height of about twelve feet in a large sugar maple.

The chipmunks are diurnal species. They hibernate through most of the winter. The latest date on which I noted individuals of *Tamias* in the autumn was on October 16, 1939; the earliest spring appearance noted was on March 30, 1940. There appeared to be a tendency for males to emerge from hibernation earlier than females. Of four specimens which I captured in May, 1942, three were males. This accords with the findings of Schooley (1934) in Indiana and of Allen (1938) in New York.

This species in the Huron Mountains has been observed feeding on the seeds of sugar maple and on red raspberries; one specimen had its stomach crammed with finely comminuted green foliage, apparently bracken. Many other plants and fruits contribute to its diet.

During much of its life the eastern chipmunk lives a solitary existence. Burt (1946: 183) stated: "Except for the period when young are in the nest and about a week after they come above ground, they lead solitary lives interrupted only for the brief periods of mating. I cannot imagine less sociable animals." On nine occasions, however, I have seen pairs of these animals, well grown and not apparently antagonistic toward each other, active in the same small area of perhaps ten yards diameter. This was in June, July, September, and October. Lone individuals were observed much more frequently.

Longevity.—Allen (1938) mentioned individuals known to have lived five years in the wild and nearly eight years in captivity, although in the wild "probably two or three seasons is nearer the average length of life." In southern Michigan Burt (1940) recorded one individual at least three years old and eight others at least one year old (two years, in three instances). Of twenty-eight different chipmunks which I marked, only six were taken in two different years. Each of these was an adult when first taken and thus at least two months old. The oldest chipmunk, a male, was captured in 1940 and 1942 and was at least twenty-four months old when last taken. The other five, of which only one was a female, achieved known ages of eleven to fifteen months.

Sex ratio.—The number of eastern chipmunks captured was insufficient for determining the true sex ratio. Only three juveniles were taken, all females, in 1941. The ratios during the three seasons, based on adults only, were as follows: 1940, 50 per cent males; 1941, 53 per cent males; 1942, 83 per cent males. In the last year only six chipmunks were taken; the trapping was done entirely during May and June, at which time the females were presumed to be occupied with their new-born litters and subsisting largely on stored food preserves. The figures during 1940 and 1941 point toward practical equality of numbers between the sexes.

Breeding.—My data on the breeding of this chipmunk in the Huron Mountains are scanty. I have records of females lactating as early as May

27, and as late as August 26. Breeding males were captured only between May 23 and June 2. Most of my captured specimens were full-grown, although possibly young of the year. Only three specimens taken were obviously juveniles, probably less than two months old; these were captured on July 2, July 5, and September 23. I believe that in the Huron Mountains, as elsewhere, mating begins in April; one, or possibly two, litters may be raised during the season; the second litter, probably born in late July or early August, leaves the nest by late September. I doubt that females or males breed before they are a year old in this locality.

HOME RANGE.—Klugh (1923) computed the home range of an adult female in early autumn as an area one hundred by seventy-five yards in extent, or 1.6 acres. Burt (1940) reported the home ranges of four adult females to average eighty yards in greatest diameter (1.04 acres) and of

TABLE XII

CALCULATED HOME RANGES OF ADULT *Tamias*

Individuals	Sex	Times Caught	Captures in Outside Row	Dates	Home Range (sq. yd.)
3	♂	4	2	July 1940	900
5	♂	5	2	July 1940	1200
18	♂	8	4	Aug. 1941	1000
27	♂	5	4	May 1942	900
4	♀	14	6	July 1940	2100
7	♀	8	4	July 1940	1300
17	♀	9	6	Aug. 1941	1200

two adult males, 112 yards (2.04 acres). Blair (1942) reported the home ranges of sixteen adult females to average 2.15 acres, and of sixteen adult males 2.31 acres; he believed there was no significant difference in size of home range between any of the sex and age classes.

Such records as I have are listed in Table XII. The computed home ranges are in all instances smaller than the actual ones, inasmuch as each individual was taken at least twice in the outside row of traps; furthermore, additional captures would have increased the calculated size of the home range in most instances. All seven specimens listed in Table XII were adults. Their calculated home ranges vary from 900 to 2100 square yards (0.19 to 0.43 acre) and average 1230 square yards (0.25 acre). The home ranges of the four males average 1000 square yards, of the three females 1533 square yards.

DISPERSAL.—Allen (1938) noted that two individuals trapped and removed distances of 350 and 500 paces returned to the spot at which they had been trapped on the same or the next day; two individuals transported one mile failed to return. Burt (1940) had one individual that

returned to its place of capture after being released 150 yards away; he believed that extensive movements were confined chiefly to juveniles and adult males. I recorded six adults which were known to have moved distances of 150 feet or more in one day's time. Two females moved 165 and 306 feet; four males moved from 210 to 303 feet and averaged 256 feet. Of twenty-six specimens first captured in 1940 or 1941, only six (23 per cent) remained on the same plot the following year; five of these were males.

In the Adirondacks of New York local migrations which were apparently correlated with the crop of beechnuts, have been noted by several authors. Merriam (1883) recorded an unusual migration of unknown extent in which, during the first week of July, "a multitude of chipmunks passed through Lewis county, Northeastern New York." Such mass movements certainly are exceptional, but indicate that on occasion individuals may move considerable distances.

TABLE XIII

Tamias POPULATIONS PER ACRE ON SIX PLOTS, 1940 TO 1942

Plot	1940		1941 (1)		1941 (2)		1942	
	No.	Pop./A	No.	Pop./A	No.	Pop./A	No.	Pop./A
1	2	0.24	3	0.36	2	0.24	1	0.12
2	.....	.....	3	0.36	.....	.....	.....	.....
3	.....	.....	.....	.....	1	0.12	.....	.....
4	.....	.....	.....	.....	2	0.30	1	0.15
5	6	0.72	6	0.72	6	0.72	4	0.48
8	.....	.....	.....	.....	1	0.12	.....	.....

POPULATIONS.—In Table XIII are listed the numbers of eastern chipmunks and their calculated populations per acre on each plot where they occurred during a trapping period. Specimens of *Tamias* were captured only on Plots 1, 2, 4, and 5; individuals were also seen, however, on Plots 3 and 8 during the periods indicated. I have assumed a two-acre home range (Burt, 1946: 271), and have accordingly included a marginal strip of 150 feet around each plot, so that the area considered as effectively trapped amounted to 8.26 acres (6.61 acres in the case of Plot No. 4). Because of the small number of individuals concerned (28) it has seemed advisable to consider only the total population of chipmunks known to occur on each plot. The sexes were nearly equal in number; over 89 per cent of the chipmunks captured were full grown. Plots 6 (cedar swamp) and 7 (spruce swamp) contained no eastern chipmunks during any trapping period. The highest populations during each of the periods trapped occurred on Plot 5 (hardwood saplings). During the three years the populations per acre on one plot reached 0.72 in 1940 and 1941, and 0.48 in 1942.

The low figure in 1942 may reflect the fact that trapping was done prior to June 20, and young of the year were not taken.

My figures are much lower than those of Burt (1940), who studied *T. s. lysteri* (= *rufescens*) on two isolated woodlots totaling 5.52 acres in southern Michigan. He found populations of 0.8 to 3.62 chipmunks per acre, with a marked peak in June when the spring litter first appeared outside the nests. In a large uninterrupted tract of similar habitat, such as my plots represented, it is possible that chipmunks do not reach the concentrations that they may on isolated patches of woodland.

TERRITORIALITY.—In New York, Allen (1938) stated that the chipmunk did not display territorial behavior. In southern Michigan, Burt (1940) decided that territories do exist, but that only a part of the normal home range of an individual is protected against trespass. In northern Michigan, Blair (1942) found considerable overlapping of the home ranges of all sex and age groups, but also observed frequent cases of antagonism toward other chipmunks. In my study the plots were too small and the captures too few to reach any definite conclusion. On Plot 5, from July 27 to August 2, 1940, there were three resident adults of each sex. In seven instances different individuals were caught in the same trap but at different times. The home ranges obviously overlapped broadly; still there were spots where only one chipmunk appeared to range. Instances of one chipmunk's chasing another were observed, and this indicates that some antagonism between individuals does exist. Such antagonism as a feature of territorial behavior appears to be common among the squirrels, as has been noted for several species by Gordon (1936) and others.

PARASITES.—External parasitism was light in the eastern chipmunks captured. Fleas were noted on a few individuals, with incidence as follows: 1940, 13 per cent; 1941, 15 per cent; 1942, 17 per cent. A tick, *Ixodes marxi,* was found on the ear of one chipmunk, in 1941. Two well-developed larval bots, *Cuterebra* (*Pseudobogeria*) sp., were present in the inguinal region of an emaciated adult female on July 23, 1941; she died in the trap.

MORTALITY.—The greatest apparent cause of mortality was exposure while confined in traps. This occurred chiefly in June and July when the sun's heat produced an unbearable temperature within a metal trap. During the three years, eight (29 per cent) of the specimens of *Tamias* captured were dead in the traps. At least one of these was thought to have died from the effects of two well-developed bots. Three chipmunks, unconscious in the traps after exposure on cold, rainy days, were taken indoors and carefully tended for several hours; two of them recovered and were returned to the plot, where they were later recaptured in good health. The third individual rallied after half a day, then suffered a

relapse and died, probably from pneumonia; a subcutaneous injection of 3 cc. of caffeine and adrenalin immediately before death had no apparent effect.

Eutamias minimus jacksoni Howell

HABITAT PREFERENCES.—The least chipmunk was present on or near all plots, but was most abundant on Plots 1 (jack pine), 3 (hemlock) and 6 (cedar swamp). This species occurs widely throughout the region, from the shores of Lake Superior to the summits of Huron Mountain and Mount Homer. Its burrows have been found in the ground beneath logs and among birch, aspen, hemlock, and virgin hardwood cover. It is a frequent visitor about buildings, dumps, and places of human habitation.

Unlike the eastern chipmunk, this species seems to be but slightly influenced in its distribution by dense cover or moisture. Not only does it occur in dense upland forest, hardwoods and conifers alike, but it also frequents swamps of white cedar, black spruce, alder, and leatherleaf, as well as rocky and sandy shores, recently burned or cutover areas, rocky mountain-tops, cleared lands, and openings in the forest grown up to brambles and brush.

BEHAVIOR.—The least chipmunk is the smaller and the more common of the two species of chipmunks in the Huron Mountains. Its habits also differ from those of its larger relative. When captured in a live trap, this species nearly always chirped and when disturbed in the wild, it usually uttered at least a few chirps, if not a prolonged chatter. Its call note and song are frequently heard. The least chipmunk, unlike the eastern species, runs with the tail rigid and straight up in the air, at a right angle to the body. This chipmunk is an able climber and is often seen sunning itself in low bushes. I have observed it at a height of twelve feet in tag alders and some thirty feet high in jack pine.

The period of hibernation appears to be about the same for the two kinds of chipmunks in the Huron Mountains. My latest autumn record of the least chipmunk was for October 20, 1939, and my earliest spring record for April 18, 1940. It may be that males appear earlier than do the females in the spring, as seems to be the case with *Tamias*. I captured five specimens of *Eutamias* on April 21, 1940, of which four were males.

Many foods are utilized by the least chipmunk. It was seen in the Huron Mountains feeding on sugar maple seeds, acorns, the leaves and seeds of dandelion, alder cones, leaves of the early saxifrage, and red raspberries. It is a frequent and fearless visitor about campsites, where it industriously disposes of crumbs and other leavings.

LONGEVITY.—The least chipmunk may have a shorter normal life span in the wild than does the eastern chipmunk. Of thirty-one different in-

dividuals captured, only two (6 per cent) were taken in two different years. Both were adult females when first taken. One was marked on September 5, 1940, and was last taken on July 24, 1941, when her age was at least thirteen months; the other was marked on September 2, 1941, and was last taken on June 17, 1942, at which time she was at least twelve months old. There is the possibility that movement of chipmunks to new areas precluded their captures in successive years.

SEX RATIO.—Too few individuals were captured to indicate the true sex ratio in the wild. In 1941, eight juveniles were taken, of which five were females. Of twenty-four adults taken in 1940 and 1941, males comprised 67 per cent in 1940 and 47 per cent in 1941. Equality of numbers between the sexes is indicated. In 1942, when only one individual (a female) was captured, the trapping was done only during May and June. Over the three-year period, thirteen (52 per cent) of the adults captured were males.

TABLE XIV

CALCULATED HOME RANGES OF ADULT *Eutamias*

Individuals	Sex	Times Caught	Captures in Outside Row	Dates	Home Range (sq. yd.)
4	♂	5	2	June 1940	1100
18	♂	4	1	Aug. 1941	1300
31	♂	7	4	Sept. 1941	700
9	♀	4	4	July 1941	600
13	♀	4	1	Aug. 1941	1100
19	♀	6	4	Aug. 1941	1200
26	♀	6	0	Sept. 1941	1500

BREEDING.—My records indicate that the breeding cycle of this species is much like that of *Tamias* in this locality. Breeding probably begins in April, soon after emergence from hibernation. On April 21, 1940, I captured and preserved four males and one female; in each male the testes were enlarged and scrotal in position; the female showed no evidence of pregnancy. Lactating females were taken from June 9 until August 5. Breeding males were taken on April 21 and July 13. Eight juveniles were captured between July 13 and September 22. One of these, first taken on July 13, was retaken the following September 3 when he showed no evidence of breeding. Two breeding females that were captured in June and July had been taken as adults the preceding September, when they had shown no indications of breeding activity. I believe that in this region the least chipmunk breeds from April to July or early August; one or two litters may be raised in a year. It is doubtful if the young breed until after their first winter.

HOME RANGE.—My data, although insufficient for calculating the complete

home ranges, are comparable for the two species of chipmunks. In Table XIV are listed my records for *Eutamias*. All but one of the seven individuals were taken at least once in the outside row of traps, indicating that the calculated home ranges are smaller than the actual ones. All seven specimens were adults. Their calculated home ranges vary from 600 to 1500 square yards (0.12 to 0.31 acre) and average 1070 square yards (0.22 acre). The home ranges of the three males average 1033, of the four females 1100 square yards.

In addition to these adult specimens, I have records of one juvenile female chipmunk which was captured ten times, once in the outside row of traps, during August, 1941. Her calculated home range was 1700 square yards or 0.35 acre.

DISPERSAL.—I have data on six adults which traveled 150 feet or more in one day's time. The greatest distance covered was 248 feet; the average for the six individuals was 191 feet. Two males moved distances of 210 and

TABLE XV

Eutamias POPULATIONS ON SEVEN PLOTS, 1940 TO 1942

Plot	1940		1941 (1)		1941 (2)		1942	
	No.	Pop./A	No.	Pop./A	No.	Pop./A	No.	Pop./A
1	6	0.72	4	0.48	1	0.12	.....	.....
3	.....	.....	5	0.60	2	0.24	.....	.....
4	.....	.....	.....	.....	3	0.45	1	0.15
5	1	0.12	.....	.....	2	0.24	.....	.....
6	1	0.12	3	0.36	1	0.12	.....	.....
7	1	0.12	3	0.36	.....	.....	.....	.....
8	.....	.....	.....	.....	1	0.12	.....	.....

248 feet; four females moved 150 to 235 feet, and averaged 171 feet. Of the thirty-one specimens first captured in 1940 or 1941, only two (7 per cent) were recaptured on the same plot in successive years; both of these were females. From this scanty evidence one might conclude that, although least chipmunks travel shorter distances than do the eastern chipmunks, a larger percentage of the least chipmunks are removed from the original area in a year's time, either by death or by movement. In both species the males usually travel somewhat farther than do the females. No data are at hand as to the relative distances traveled by juveniles and adults.

POPULATIONS.—In Table XV are listed the populations of least chipmunks on the several plots during each trapping period. None was captured on Plot 8; the specimen listed represents a sight record. In calculating populations per acre, I have assumed the same home range of two acres as for *Tamias*, that is, each plot is regarded as representing 8.26 acres effectively trapped, except for Plot 4.

No least chipmunks were observed on Plot 2 (virgin hardwoods) at any time. The largest populations, through the three-year period, were on Plot 1 (jack pines). During the three years, the populations per acre on any plot reached 0.72 in 1940, 0.60 in 1941, and 0.15 in 1942. The animal was conspicuous for its scarcity in 1942. This reverses the situation observed by Quimby (1944) in northeastern Minnesota during April and May of the same year; he reported specimens of *Eutamias* more abundant in 1942 than in 1941, whereas those of *Tamias* were less abundant in 1942.

TERRITORIALITY.—The least chipmunk did not appear as intolerant in its attitude toward other individuals of the same species as was the case with the eastern chipmunk. I did observe several instances of one individual pursuing another. Gordon (1936) noted this in individuals of *E. quadrivittatus* in Colorado and attributed it to social dominance evidenced by a chase order rather than to defense of territory. My data are to meager to indicate whether there is territoriality in this species. Four individuals were resident on Plot 1 from August 5 to 9, 1941; two of these were adult males, one an adult female, and one a young adult female. In only one instance were two individuals caught in the same trap, but not at the same time. The young adult female appeared to travel more widely than the others; she was captured in nine different locations, whereas four captures were the most for any other individual.

PARASITES.—Parasitism was most general among the least chipmunks in 1941. These chipmunks were hosts to an undetermined species of flea, the incidence of which was 30 per cent in 1941; the only individual captured in 1942 was also parasitized by fleas. One tick, *Ixodes marxi,* occurred on the ear of one chipmunk each in 1940 and 1941. The same kind of mite, possibly *Trombicula harperi,* which was found on specimens of *Peromyscus* and *Clethrionomys* occurred also on six different least chipmunks in 1941, an incidence of 26 per cent. These parasites were present on the ears and about the anus and were found among the chipmunks of Plots 3, 6, and 7. This mite was reported on chipmunks in New York state by Allen (1938) and others.

MORTALITY.—As in the eastern chipmunk, the greatest apparent cause of mortality among the least chipmunks captured was exposure during confinement in traps. During the three seasons, ten (32 per cent) specimens of *Eutamias* captured died in the traps; these deaths occurred from June until August and were attributed to the heat inside the metal traps. Three individuals trapped on August 23 and September 5, 1941, both cold and rainy days, were unconscious in the traps; all recovered after several hours' attention in a warm room and were released at the spots where captured. Two captured females apparently had been attacked by some other animal; in one, about one-third of the tail was missing; in the other, the skin was

lost from most of the tail, though the vertebrae remained. Neither of these specimens appeared to suffer any ill effects from its injuries. A third individual was observed which had lost about half of its tail. Another chipmunk suffered a broken foreleg and an injured eye when caught by a dog. It was cared for indoors and became rather tame. After a week it had recovered sufficiently to be released.

Sorex cinereus cinereus Kerr

HABITAT PREFERENCES.—The masked shrew occurred on all plots except No. 1 (jack pine). As a rule it was most abundant on Plots 6 (cedar swamp) and 7 (spruce swamp). Moisture is undoubtedly an important factor in the distribution of this species. Only two specimens were taken in 1942, both on Plot 5 (hardwood saplings), but in late May when the forests were still generally moist. In addition masked shrews were taken near buildings among mixed conifers as well as in or near marshes of leatherleaf, iris, and rushes.

This primarily terrestrial animal may occasionally construct its own burrows in sphagnum moss or loose soil. For the most part it probably appropriates the burrows of other small animals (Blossom, 1932). My findings agree in general with those of Quimby (1943), in Minnesota, where this species "prefers a semi-aquatic habitat, especially coniferous swamps and marshy areas along streams and lakes where there is an abundance of sedges and grasses." Bole (1939) reported a somewhat different situation in Ohio, of which he wrote: "During favorable (i.e., cool, wet) years, this species is found chiefly in old fields and on fallow land; during droughts the species retires to sedge meadows, cat-tail marshes and swamp forests."

BEHAVIOR.—This shrew is active both day and night throughout the year. In the present study all but two of the sixty-seven individuals taken died in the trap after one capture. This may have been due to exposure, to lack of food for an extended period, or to shock. The high-strung nervous temperament of this shrew is well-known. Blossom (1932) kept two masked shrews in captivity, one for seventy-seven days. An adult female consumed an average of 3.3 times her own weight in food each day for a week. Mere confinement without food for several hours in a trap may have been the cause of death of the shrews I captured.

SEX RATIO.—The determination of sex in shrews is often extremely difficult from a cursory examination, except in the case of a breeding male or a female that is lactating or in an advanced stage of pregnancy. I have only determined the sex of those individuals which were actively breeding or which were examined internally after death. Over the three-year period 68 per cent of the sixty-six individuals definitely sexed were females. These shrews included all age groups, but only during 1941 were any obvious

juveniles taken—five males and six females. At all periods the females were more numerous, comprising 93 per cent in 1940, 59 per cent in 1941, and 100 per cent in 1942. The preponderance of females in 1940 and 1942 is possibly accounted for by the small number of individuals examined (fifteen in 1940, two in 1942).

BREEDING.—Very little is known of the breeding habits of this species. Burt (1946: 92) stated that it probably breeds from March to September and that there are from four to ten young per litter. I found only four individuals that were definitely breeding; these were lactating females captured on July 6 and September 16, 1941, and on May 23 and 26, 1942. Only eleven individuals captured were easily recognized as juveniles; they were taken between September 16 and 25, 1941. This slight evidence indicates that in the Huron Mountains there are three litters raised per year, in the

TABLE XVI

Sorex POPULATIONS PER ACRE ON SEVEN PLOTS, 1940 TO 1942

Plot	1940		1941 (1)		1941 (2)		1942	
	No.	Pop./A	No.	Pop./A	No.	Pop./A	No.	Pop./A
2	.....	.....	.....	.....	2	0.41	.....	.....
3	1	0.21	.....	.....	.....	.....	.....	.....
4	1	0.23	.....	.....	1	0.23	.....	.....
5	6	1.24	.....	.....	5	1.03	2	0.41
6	5	1.03	2	0.41	20	4.12	.....	.....
7	1	0.21	3	0.62	15	3.09	.....	.....
8	1	0.21	2	0.41	1	0.21	.....	.....

spring, summer and early autumn. The young apparently are well grown before they venture far from their nests.

MOVEMENT.—I have records of but one individual that was captured twice. This was an adult female originally taken on July 24, 1941, and recaptured at a point eighty-five feet away on September 14, 1941. Seton (1909: 1101) reported observations made by Nelson in the Yukon Valley of Alaska, indicating that an individual of this species may travel a mile beneath the snow; this distance would seem to be exceptional. The home range of this shrew is not known, but I should expect it to be about half an acre.

POPULATIONS.—In Ohio, where this species was at a peak in 1937, Bole (1939) recorded populations of one to eleven per acre, but stated that there were normally less than one per acre, except where drought had caused local concentrations of these shrews in swamps and marshes.

In Table XVI are listed the populations of this species on the plots at different times. I assumed a home range of one-half acre and included a marginal strip eighty feet wide in making my calculations. No specimens

were taken on Plot 1 (jack pine) at any time. The highest populations were on Plot 6 (cedar swamp, 4.12 per acre) and on Plot 7 (spruce swamp, 3.09 per acre). Both of these figures were obtained during late September and probably included most of the young of the year. Throughout the three years, populations extended to 4.12 shrews per acre. The highest population computed in each season was 1.24 in 1940, 4.12 in 1941, and 0.41 per acre in 1942. During the latter year only two shrews were captured, both adults, in late May.

Blarina brevicauda kirtlandi Bole and Moulthrop

HABITAT PREFERENCES.—Bole (1939) reported the short-tailed shrew to be "the most widely distributed and most abundant mammal in Ohio." Burt (1946: 102) wrote: "This shrew is most common in heavy forests and low, damp, swampy areas, but may be expected in practically every land habitat. . . . This is probably the most common mammal in Michigan." These statements apply generally to the Huron Mountains as well, where I took this shrew on each of the eight plots as well as in other habitats, during 1942 in particular. In this year it was especially common on Plots 2 (virgin hardwoods), 3 (hemlock), 4 (white birch), 6 (cedar swamp), and 7 (spruce swamp). Moisture seems to have somewhat less influence on the distribution of this species than on that of specimens of *Sorex*.

The distribution of the short-tailed shrew is complicated by the marked fluctuations in its numbers. None was captured on any of my plots in 1940; in 1941, it was taken in small numbers on each of the plots except Plots 1 (jack pine) and 4 (white birch). This may have been the situation in Wisconsin in 1941, when Hanson (1944) found these shrews "apparently chiefly limited in their distribution to areas of bluegrass and woodlands having numerous fallen logs and a thick layer of leaf mold."

The species is largely terrestrial in its habits, but it can and does construct extensive burrows. Frequently, the burrows of other animals are appropriated. Its nests, situated along an underground burrow and often beneath a log or stone, have been described by Shull (1907) and by Hamilton (1929). There are abundant nest sites available in the Huron Mountains. The scarcity of individuals on Plot 1 may be the result in part of the dry, sandy soil, poorly suited to burrowing.

BEHAVIOR.—The short-tailed shrew is active all of the year and both by day and night. I captured three specimens and observed at least twelve others along roads and trails in broad daylight. This amount of activity is probably correlated with the need for much food as well as with the nervous temperament of the animal.

Hamilton (1930) listed the food of this species as largely insects, with annelids, mollusks, crustaceans, arachnids, centipedes, millipedes, verte-

brates, and vegetable matter utilized to a lesser extent. He stated that "one-half the weight of the animal is a sufficient daily diet." These shrews sometimes store food for future use. Merriam (1884: 66, 71) discussed the hoarding of beechnuts for use during the winter, and Shull (1907) described the hoarding of snails, likewise in winter. During the summer of 1942, when this shrew was particularly abundant in the Huron Mountains, I observed along a quarter-mile of wood road literally hundreds of small holes, one to two inches deep, dug by these shrews; they presumably represented captures of insects or earthworms for food.

Although this shrew's eyes are only capable of distinguishing light from shadow, its senses of touch, smell, and hearing are acute (Shull, 1907). When handled, a specimen invariably utters a series of shrill chirps and tries viciously to bite its captor. This shrew never lost consciousness when marked, as high-strung red-backed voles did frequently. Once, after a lively chase, a captured specimen died within a minute after being caught, apparently from shock. When released this shrew often remains for several seconds in the same spot, its nose quivering while it tests the air in all directions, then it scurries for shelter, usually in an obscure runway or burrow just beneath the ground litter near by. On one occasion, when released, an adult female returned to the same trap in which it had been captured.

It is difficult to conceive of this voracious creature as being social in its habits. I have two instances of multiple captures which indicate that the animals at least entered the trap at the same time; they may have been traveling together, or the situation may have been the result of pursuit. In one instance an adult male and an adult female were captured together; both were dead and apparently uninjured when found. The other case involved two adults of unknown sex; one survived, having almost completely consumed the other.

Longevity.—Few figures on the life-span of this shrew have been published. Hamilton (1930) reported three which lived in captivity for "not quite three months." Pearson (1945) reported one, and perhaps more, that was over four hundred days old. I have records of but two individuals which were taken in successive years; both were adults when first captured. A female was marked on July 4, 1941, and was last taken on May 27, 1942; a male was marked on July 23, 1941, and was recaptured on June 9, 1942. Thus, allowing one month of age at their initial captures, these shrews were each approximately twelve months old when last taken. Each was dead in the trap on the last date.

Sex ratio.—Unless in a breeding condition, these shrews are difficult to sex in the field. I have considered figures only of those individuals actively breeding or dissected. No specimens of *Blarina* were trapped on any of the plots in 1940, but away from the plots three adults were cap-

tured: a male on June 11 and a male and female on September 17. In 1941, 50 per cent of twenty-two shrews were females; in 1942, 56 per cent of 239 shrews were females. My figures indicate approximate equality in numbers between the sexes. Townsend (1935), in studies made in New York, recorded 45 per cent females among 438 specimens taken; Blair (1940*b*) stated that among forty specimens examined in southern Michigan 49 per cent were females.

Hamilton (1929), however, reported 69 per cent males among ninety-two specimens taken in New York state and concluded that "the males far outrank the females in numbers." This disparity in numbers between the sexes may be connected with the fluctuations in numbers of the species observed from time to time or it may be illusory. Blair (1940*b*) pointed out that "the home ranges of male short-tailed shrews tend to be larger than those of the females. Therefore, a line of traps set at random in any given area should cross the home ranges of more males than females," and a preponderance of males would naturally be indicated "even though the two sexes are approximately equal in abundance in the area."

BREEDING.—According to Hamilton (1929), the gestation period in this shrew is twenty-one days or longer, and five to ten (six or seven on the average) young are born per litter. They may be weaned at about twenty-six days. This author found, in New York, that the first young were born from mid-April until the end of May and the second litter in late summer or early autumn. There appeared to be no breeding in July or August.

My data indicate the same general breeding cycle in the Huron Mountains. I captured three adult males with enlarged testes, indicative of breeding, on the following dates: May 31, 1942, June 11, 1940, and September 25, 1941. Lactating females were taken as follows: one each on July 4 and 5 and one on September 16, 1941; fifteen from May 26 to June 20, 1942. I noted no breeding activity in the latter half of July or during August. It appears that two litters are raised during a season; the first appears during May or June and, after a midsummer resting period, a second litter may appear in September.

HOME RANGE.—Hamilton (1931) stated that "the range of any *Blarina* is probably restricted to an acre of ground." Blair (1940*b*) found that among twenty-six individuals the home ranges varied from less than 0.25 to 4.43 acres, those of males usually being larger. Burt (1946: 268) gave the home range as one-half to one acre in extent. In the present study I have only two individuals that were captured in three different locations. Each was an adult. One (sex unknown) ranged over at least one thousand square yards (0.21 acre) from June 9 to 13, 1942; the other (a male) had a home range of at least five hundred square yards (0.10 acre) from June

10 to 12, 1942. These two instances are obviously far too few and too incomplete for any conclusion.

MOVEMENT.—Of the 350 short-tailed shrews captured during this study, only 130 were alive after their first capture; of these, forty-six were recaptured so as to give an indication of the distance they may travel. Four of these individuals were retaken in the same trap after one to four days. Three individuals were recaptured on the same plot after a considerable lapse of time: a female was retaken 280 feet distant after ten months; a male was caught thirty feet away after two months; another male was recaptured, after eleven months, eighty-five feet away from where it had originally been caught.

The distances covered by adult shrews in a period of three days or less were as follows: fifteen females moved thirty to two hundred feet, averaging

TABLE XVII

Blarina POPULATIONS ON EIGHT PLOTS, 1941 AND 1942

Plot	1941 (1)		1941 (2)		1942	
	No.	Pop./A	No.	Pop./A	No.	Pop./A
1	.....	.....	.....	.....	18	3.04
2	6	1.01	4	0.68	61	10.31
3	2	0.34	.....	.....	49	8.48
4	.....	.....	.....	.....	57	11.63
5	3	0.51	7	1.18	14	2.37
6	.....	.....	1	0.17	57	9.63
7	1	0.17	.....	.....	68	11.49
8	1	0.17	1	0.17	2	0.34

seventy-five feet; thirteen males moved from thirty to 150 feet, averaging seventy feet; and ten individuals (sex unknown) moved from thirty to 315 feet, averaging 144 feet. Incomplete as these figures are, they indicate that the sexes may travel approximately equal distances.

POPULATIONS.—Various writers have made estimates of the abundance of *Blarina* at different times and places. Shull (1907) found "at least two pairs to the acre over the region studied," and Seton (1909: 1122) estimated fifty shrews to an acre of woodland. Hamilton (1931) believed that "there could exist about four pairs of shrews to an acre in a choice locality," whereas Bole (1939) calculated populations up to forty-eight per acre in various types of habitat in Ohio. Blair (1940*b*), in southern Michigan, reported populations of 2.2 per acre in September, 1938, and 0.8 in August, 1939.

In Table XVII are recorded the *Blarina* populations on the plots during 1941 and 1942. These figures are computed on the basis of a home range of 0.75 acre, with a peripheral zone one hundred feet wide about each

plot. Thus each plot was regarded as covering 5.9 acres, except for Plot 4 (4.9 acres).

No short-tailed shrews were captured on any plot in 1940. Small numbers were taken in 1941 on all plots except 1 and 4; in this year populations ranged up to 1.18 individuals per acre. In 1942 this species was abundant and widespread, occurring on all eight plots. The lowest populations, ranging from 0.34 to 3.04 shrews per acre, were on Plots 1, 5, and 8; these three plots were trapped in late May, before the first spring litter had appeared in great numbers away from the nests. On the other five plots, trapped during June, populations ranged from 8.48 to 11.63 shrews per acre; these doubtless included many young of the year, although all were nearly full-grown when taken.

The increase in abundance of this shrew over the three years is impressive. This phenomenon has been recorded by various writers. For example, Harper (1929) wrote: "At Indian Lake in July 1925 these shrews were amazingly abundant in the forest. . . . They filled the traps by day as well as by night. . . . No other Adirondack mammal showed such a striking fluctuation in numbers between 1925 and 1926 as did *Blarina*. I did not secure a single specimen during several weeks of trapping in 1926." Among possible causes of the scarcity in 1926, Harper mentioned failure of the beechnut crop during the previous autumn and the comparative scarcity of mice during 1926. Hamilton (1943: 60) wrote: "Some years the woods fairly swarm with these shrews, while at other times they are quite scarce."

It is of interest to compare other figures on the abundance of this shrew in the same general region as the Huron Mountains during the years of this study. During August and September, 1940, in Alger County in northern Michigan, Blair (1941*c*, *d*) captured twenty-eight specimens of *Blarina* among 396 individuals of six species. During September and October, 1941, in Columbia County in central Wisconsin, Hanson (1944) captured fifteen specimens of *Blarina* among 181 individuals of nine species. During April and May, 1941, in Carlton County, northeastern Minnesota, Quimby (1943) captured no specimens of *Blarina* in 7254 trap nights; at the same locality one year later, during April and May, 1942, he again captured none in 3946 trap nights. In the Huron Mountains, I captured none on any of the eight plots in 1940; at near-by locations I collected one on June 11, 1940, and two on September 17, 1940. My catches during 1941 and 1942 are evident from Table XVII. A few quotations from my journal in 1942 report the general trend: "June 4—Have had surprisingly large catches of *Blarina* on my plots so far. . . . June 12—Lots of *Blarina* on both plots (2 and 7). They rival *Peromyscus* in numbers. . . . June 14—It may be that this year's abundance of the carnivorous *Blarina* is associated with last year's abundance of rodents. At present, with mice

down, they are digging, apparently, for worms and grubs. Still this does not account for the paucity of *Sorex* unless they, being smaller, are eaten."

It appears, from these comparisons, that the *Blarina* population did not undergo the same fluctuations simultaneously throughout the general region; rather, this was a more local phenomenon. In northeastern Minnesota they were fewer in both 1941 and 1942, but they were increasing steadily from 1940 to 1942 in the Huron Mountains. The figures of Hanson and Blair scarcely admit of comparison, for they show no general trend from year to year. Unfortunately, I was unable to follow the population trend after June 21, 1942. My data do not appear to throw any light on the mechanics of this fluctuation in numbers.

Since the time of my study, I have had verbal reports of a peak in *Blarina* populations over a more general area in 1947. Stuart C. Downing and C. David Fowle reported these shrews abundant in Algonquin Park in northern Ontario, where they were low in 1942; W. Robert Eadie reported their increase at Laurentian Park in southern Quebec; they were at a high point in New York state according to W. J. Hamilton, Jr., and in Pennsylvania according to J. Kenneth Doutt.

PARASITES.—Few parasites were evident on these shrews from field examinations. Fleas undetermined as to species were noted on six different individuals. One adult male, on June 5, 1942, had a nymphal tick (*Ixodes* sp.) near the base of the tail. Three individuals had unidentified mites at the same location. In the Adirondacks, Harper (1929) found one specimen similarly parasitized by mites (*Haemogamasus* sp.). I captured one adult female on July 21, 1941, which had lost all the hair on her body except about the face and on the rump. No external parasites were then evident. This shrew was dead in an adjacent trap on the next day.

MORTALITY.—The greatest mortality among short-tailed shrews in my study was caused by confinement in traps. Of the 350 shrews taken, 63 per cent were dead in the trap after one capture. Of the 130 which survived their initial capture, forty-six were subsequently recaptured; thirty-four of the forty-six were found dead in the trap after their second or third capture. My findings do not agree with those of Blair (1940*b*) who concluded that "it generally could be expected, therefore, that if a shrew survived the first night it would survive subsequent nights in the traps. It seems evident . . . . that there is considerable variation in the ability of the individual shrews to survive the conditions of confinement in the traps." Blair's conclusions were based on forty shrews taken in 1938 and nineteen taken in 1939.

Shrews were caught together twice in the same trap. In one instance, on June 19, 1942, the two shrews, an adult male and an adult female, were each dead, apparently from exposure or lack of food, though neither had

been attacked. In the second instance, of two adults captured together on June 9, 1942, one was completely consumed except for the skin, feet and legs, and part of the skull; the remaining shrew was still alive and active. On July 12, 1941, I found an adult male *Blarina* and an adult female *Peromyscus* lying dead, side by side, along a woodroad through hemlock and hardwoods. They may have been struck by a passing vehicle, but it seems more likely that they were engaged in a struggle which proved fatal to them both; in each the base of the skull was broken.

Microsorex hoyi intervectus Jackson

The pygmy shrew, the smallest mammal in the Huron Mountains, is also one of the least common. It is known from three specimens, one of which I captured in a live trap on Plot 6 (cedar swamp) on June 19, 1942; this specimen, an adult male, was dead in the trap. From inference, I assume a home range of 0.50 acre which, with a marginal strip eighty feet wide, gives a population figure of 0.21 per acre on Plot 6.

Glaucomys sabrinus macrotis Mearns

The northern flying squirrel is seldom seen, but is probably not uncommon in the Huron Mountains. I captured three, as follows: a juvenile female on Plot 5 on July 3, 1941; an adult female on the same plot on August 23, 1941; and another adult female on Plot 1 on September 25, 1941. Each was captured only once.

The third specimen was parasitized by two species of flea, *Opisodasys pseudarctomys* and *Orchopeas wickhami*. The second of these fleas is usually found on *Sciurus* sp.

Although no figures on the home range of this species are available, Burt (1946: 271) listed the home range of *G. volans* as four acres or more. Using this same figure, and hence a peripheral zone 235 feet wide about the plots, I arrive at population figures of 0.07 squirrels per acre on each of Plots 1 and 5 during the periods trapped. Other flying squirrels probably were present on these plots but were not taken, perhaps because of the small size or prior occupancy of the traps. The figure of 0.07 per acre is, therefore, probably smaller than is actually the case.

Microtus pennsylvanicus pennsylvanicus Ord

The meadow vole was captured in live traps only on Plot 6 (cedar swamp), where seven adults (five females) were taken in 1941. On other areas, seven adults (three females) were collected in damp meadows and grassy bogs during 1940 and eleven (eight females) in 1941.

This prolific vole has been reported as breeding in all months of the year and as having as many as nine young per litter. I found males in

breeding condition from April 22, 1940, to October 2, 1941. Only one pregnant female was taken; she contained five embryos, averaging 18 mm. in length, on July 17, 1941. Two lactating females were collected on July 31 and August 3, 1941.

An adult male collected on April 22, 1940, was heavily infested with red mites, thought to be *Trombicula harperi,* on the ears. These same mites were present on the ears of six of the seven voles taken on Plot 6 during August and September, 1941. One vole collected was parasitized by fleas.

Hamilton (1937*a*) stated that "the home range of an individual seldom encompasses an area in excess of one-fifteenth of an acre." Blair (1940*a*) found the home ranges to vary from one-fifth to one-half acre, those of males being larger. For calculating population density, I have used a home range of 0.25 acre with a marginal strip of 60 feet around the plot. On this basis, *Microtus* reached a population of 0.98 per acre from July 31 to August 4, 1941, and of 0.74 per acre from September 22 to 26, 1941, on Plot 6.

Zapus hudsonius hudsonius Zimmermann

The meadow jumping mouse was trapped on only two plots. An adult female and an adult male were taken on Plot 5 on August 24 and 26, 1941, respectively. A juvenile male was captured on Plot 4 on September 2, 1941. Four other specimens were collected in meadows of deep grass and in swamps of leatherleaf, alder, and sedges.

One specimen, an adult female, was captured in two different locations on Plot 5. She was taken on successive days in traps 180 feet apart.

The earliest date on which I caught this species was July 15, 1941. The latest Huron Mountain record is a specimen collected by W. P. Harris, Jr., on September 20, 1924. I took one on September 16, 1940, which had much subcutaneous fat, indicative of approaching hibernation.

On the basis of sixty-four jumping mice taken in southern Michigan in 1939, Blair (1940*c*) determined the home ranges of males to average 0.89 acre, those of females 0.92 acre, and reported populations as high as 5.0 mice per acre. In the present study I use a home range of 0.9 acre for this species, and add a 110-foot marginal strip to the plot as the area effectively trapped. Thus, this species attained a population of 0.19 per acre on Plot 4, and of 0.38 per acre on Plot 5, during late August and early September, 1941.

Napaeozapus insignis frutectanus Jackson

The woodland jumping mouse is known in the Huron Mountains from two adults captured on Plot 5 on August 23 and 24, 1941. Each was taken but once. One was parasitized on the ears by red mites, presumably *Trom-*

bicula harperi, which was present on other species in the region. This mite was reported on specimens of *Napaeozapus* in the Adirondacks of New York by Harper (1929).

Blair (1941*c*), on the basis of fifty-two specimens trapped in northern Michigan, reported the home ranges to vary from 1.0 to 9.0 acres. Burt (1946 : 237) stated that "the home range averages one to two acres in area, and the populations in the fall are about three per acre." I have based my calculations on a 1.5 acre home range; with a 145-foot strip around the plot, I have arrived at a population of 0.26 mice per acre on Plot 5 during the period trapped.

DISCUSSION OF POPULATIONS

RELATIVE ABUNDANCE OF SPECIES

The relative abundance of different species of small mammals is constantly changing. Some species appear to be always present. Other rare species, such as the star-nosed mole, water shrew, pygmy shrew, bog lemming, and woodland jumping mouse in the Huron Mountains, may be trapped or observed only a few times in several years, partly because some species are more restricted than others to a particular habitat. The areas trapped in this study were all northern forest types; only two of these areas were in lowland swamps. Further trapping in marshes, meadows, and other habitats would probably have netted additional species. As it is, the plots trapped are believed to represent a typical composite of the Huron Mountain region. The species captured on these eight plots in four trapping periods, and the numbers and percentages of each, are listed in Table XVIII.

Of the thirteen species taken, six comprised at least 97 per cent of the total catch during any one trapping period. Of the seven other species, none ever comprised more than 1 per cent of the total catch. Specimens of *Microsorex, Microtus, Zapus,* and *Napaeozapus* were either rare in this region or were largely restricted to habitats not included in the plots trapped. *Mustela, Tamiasciurus,* and *Glaucomys,* although not uncommon in the Huron Mountains, were of a size for which the traps used were not designed. The few catches of these last three mammals may be considered accidental.

The relative populations of the six species which, at one or more of the four trapping periods, comprised over 1 per cent of the total catch are graphically represented in Figure 6. The "normal" situation seems to be that presented during 1940 and 1941, with specimens of *Peromyscus* comprising over 50 per cent of the small mammal population. Discussion with old residents of the country corroborates this view. Harris (1929) wrote of

TABLE XVIII

SMALL MAMMALS TRAPPED ON EIGHT PLOTS, 1940 TO 1942

Species	Individuals Caught				Per Cent of Total			
	1940	1941(1)	1941(2)	1942	1940	1941(1)	1941(2)	1942
Sorex cinereus	15	7	44	2	15	2	12.0	1.0
Microsorex hoyi	0	0	0	1	0	0	0.0	0.5
Blarina brevicauda	0	13	13	326	0	5	4.0	62.0
Mustela erminea	0	0	1	0	0	0	0.2	0.0
Eutamias minimus	9	16	9	1	8	6	3.0	0.5
Tamias striatus	8	12	10	6	7	4	3.0	1.0
Tamiasciurus hudsonicus	0	2	0	0	0	1	0.0	0.0
Glaucomys sabrinus	0	1	2	0	0	1	0.4	0.0
Peromyscus maniculatus	67	183	204	167	57	64	57.0	32.0
Clethrionomys gapperi	18	46	64	16	15	16	18.0	3.0
Microtus pennsylvanicus	0	4	3	0	0	1	1.0	0.0
Zapus hudsonius	0	0	3	0	0	0	1.0	0.0
Napaeozapus insignis	0	0	2	0	0	0	0.4	0.0
Total	117	284	355	519	100	100	100.0	100.0

this species: "This little mouse is the most abundant of all of our mammals. The woods are full of them." Next in abundance is *Clethrionomys*,

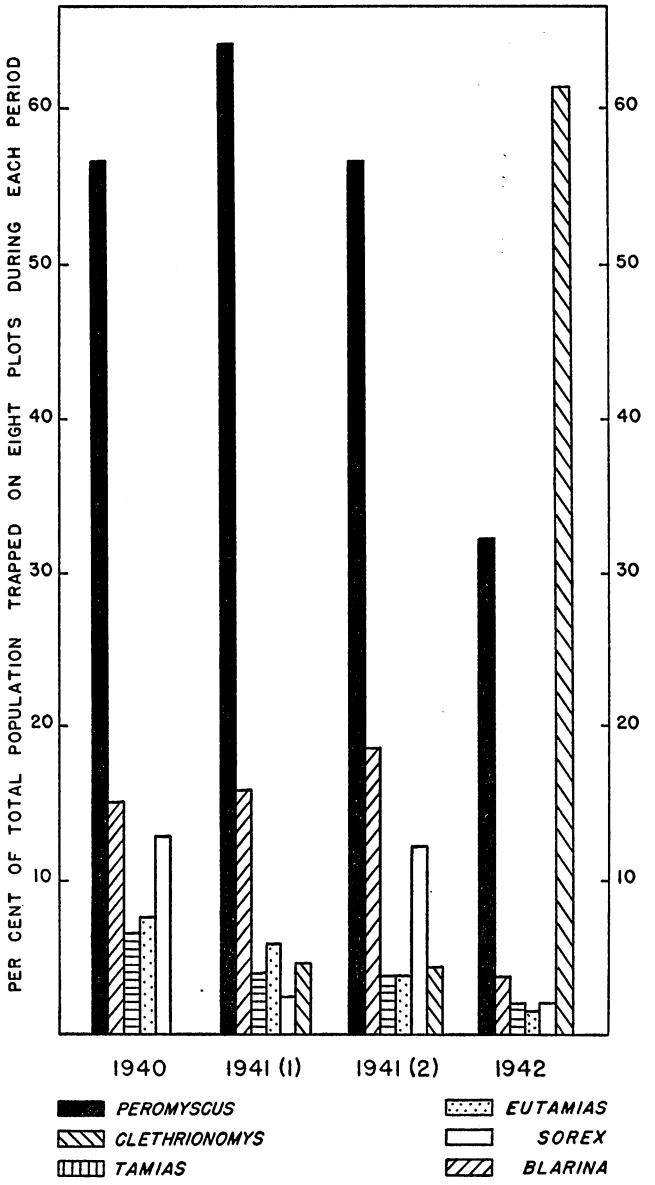


FIG. 6. Relative abundance of six species of small mammals captured on eight plots during four trapping periods.

of which Harris (1929) stated: "The red-backed mouse is very abundant in the Huron Mountain region. They are found in both wet and dry forests

and also in swamps and sphagnum bogs." The two species of chipmunks each comprise a small but relatively constant part of the fauna; of the two, *Eutamias* is the more abundant. *Sorex cinereus* and *Blarina* are the principal shrews of the region; they normally comprise a low percentage of the small mammal population, but their numbers fluctuate markedly. Specimens of *Sorex* were taken by me at all trapping periods. Harris (1929) wrote: "This common shrew . . . . leads so secluded and hidden an existence that it is rarely seen." Of *Blarina,* Harris stated: "No specimens of this species have been taken, but the region is well within its range." On the eight plots, I captured no specimens of *Blarina* in 1940; during 1941 they comprised 4 to 5 per cent of the total catch; in 1942 they outnumbered all other species combined, totalling 62 per cent of the entire catch. With this unprecedented rise in numbers of *Blarina,* the relative populations of all other species dropped considerably in 1942.

FLUCTUATIONS IN POPULATIONS

Considerable fluctuations in populations from year to year have long been known to exist among many mammals as well as among certain birds, fishes, and insects. In many species these fluctuations are thought to be cyclic in nature. A definite periodicity in rise and fall of numbers has been demonstrated in *Microtus* (Hamilton, 1937*b*) and in other species (Elton, 1924; Wing, 1935). It was stated by Howell (1923) that "there is a pronounced periodic fluctuation in the numbers of most, if not all, small mammals." Writers on this subject generally agree that it is the herbivorous species which are primarily cyclic while carnivorous species may be secondarily so, that violent fluctuations in populations occur especially in the north temperate and arctic regions, that these fluctuations are more pronounced on continental than on insular land masses, and that migratory species exhibit these fluctuations slightly, if at all.

Evidence has been presented of a fluctuation in the numbers of certain small mammals in the Huron Mountains; there have been similar fluctuations in the numbers of snowshoe hares and ruffed grouse in this region in the past. The time occupied by this study was far too brief to establish any periodicity to these fluctuations. A tendency was noted for many species to become more numerous at the same time. This is illustrated by an entry in my journal under date of September 29, 1941: "Many people have remarked, and I have been impressed by, the greater numbers of small animals this year. There are at least ten red squirrels around the Club buildings; snowshoe hares are more frequent; many more mice and shrews have been taken in my traps; grouse are on the increase; chipmunks appear more numerous; in fact I have even seen more gray squirrels, foxes, and bears than heretofore." It was not until the following summer, how-

ever, that the *Blarina* population in the Huron Mountains reached its high point; it may have continued to rise following the termination of this study.

Of the small mammals whose numbers fluctuated in the Huron Mountains during this study, *Blarina* was most noteworthy; my catch on eight plots rose from none in 1940 to 327 in 1942. The *Peromyscus* population rose to a peak in 1941 and dropped off slightly in 1942. The *Clethrionomys* population behaved much the same but on a smaller scale. For comparing the levels of these three species, the numbers of each captured and their

TABLE XIX

POPULATIONS, BREEDING CAPACITIES, AND SURVIVAL RATES OF THREE SPECIES ON EIGHT PLOTS, 1940 TO 1942

	Year	*Peromyscus*	*Clethrionomys*	*Blarina*
Individuals captured on 8 plots	1940	67	18	.....
	1941	306	92	25
	1942	167	16	327
Average population per acre on 8 plots	1940	1.51	0.33	0.00
	1941	4.28	1.20	0.28
	1942	3.77	0.35	7.16
Per cent of females among adult population	1940	43	55	.....
	1941	37	46	50
	1942	43	44	56
Per cent of adult females breeding	1940	100	50	.....
	1941	66	73	27
	1942	94	100	12
Ratio of number of juveniles to adult females	1940	5.11	1.33	.....
	1941	3.48	2.00	.....
	1942	1.21	0.17	.....
Survival rate, ♀ : per cent recaptured of those still alive last year	1940	.....	.....	.....
	1941	44	20	.....
	1942	25	3	50
Survival rate, ♂ : per cent recaptured of those still alive last year	1940	.....	.....	.....
	1941	39	13	.....
	1942	15	0	50

average populations per acre during the three seasons are shown at the head of Table XIX. I doubt that this apparent wholesale increase in numbers of animals in the Huron Mountains was part of a general increase over a wider area. Grouse seemed to be on the rise throughout a large part of Michigan at this time. As was pointed out, however, *Blarina* appeared to show no corresponding peak in numbers in Wisconsin, Minnesota, or Ontario during the period.

Many possible reasons for such increases in populations come to mind. Could decreased predation be a controlling factor? Do moderations in weather conditions affect the population level directly or indirectly through

improved food supply? Are there changes in the breeding potential as reflected by number of litters, size of litters, proportion of females in the population, number of breeding adults, or longevity of individuals? In an attempt to discover answers to some of these questions I have analyzed the data, presented in earlier sections, on the three species here considered. This is included in Table XIX. It should be borne in mind that my figures, although comparable for the three species (that is, representing the same areas trapped for the same length of time during the same periods), do not reflect the same conditions in each of the three years. For example, the trapping in 1942 was done much earlier in the season than in the other years, resulting in an increased percentage of breeding adults and a lower ratio of juveniles to adult females. Since no specimens of *Blarina* were captured on my plots in 1940, figures are unavailable for comparison.

In the case of *Peromyscus,* the greatest breeding capacity, as indicated by percentage of females among the adult population, percentage of adult females breeding, and size of litters (roughly approximated by the ratio of juveniles to adult females captured), preceded by one year the period of greatest population density. Also the rate of survival in both sexes was greater before than after the peak in population, although in all cases the females appeared to have a greater survival rate than did the males. All this is exactly what would be expected in a pyramiding population. Corresponding figures on *Clethrionomys* and *Blarina* appear somewhat contradictory and do not reflect the same trend, a situation which may be due to incomplete data. Much further material is desirable, for example on the number of litters during one season and on the earliest age of breeding. Other factors, as yet unknown, may be concerned in these fluctuations. During these three years in the Huron Mountains there did not appear to be any severe fluctuations in numbers of the larger predatory animals. Available plant foods appeared to be about the same during the three seasons, except for an abundant crop of pine cones following the 1940 season. Weather conditions were nearly normal for all three years, except that the winters of 1939–40 and 1941–42 were comparatively mild. Parasitism, as was noted under the separate species accounts, was more widespread in 1941 than at other periods.

Study of fluctuations in populations has evoked much speculation as to the cause or causes of this phenomenon. Various workers have interested themselves in the problem for many years. As yet no general agreement has been reached as to the reasons for this behavior nor, indeed, as to the intrinsic nature of the fluctuations in themselves. There have been many hypotheses aimed at explaining this phenomenon in terms of a few major controlling factors, such as parasites and diseases, predators, food supply, varying fertility, climatic cycles, sunspots, or ultra violet radia-

tion. None of these factors alone adequately explains the fluctuations in even one species. It seems to me that many investigators have gone to unnecessary lengths in attempts to oversimplify the situation. Elton (1942: 84) confessed the complexity of the problem and our ignorance of the factors involved when he wrote: "Population densities . . . . are the product of the operation during some past period of three things, all variable within certain limits characteristic of the species. These are movements, reproduction, and mortality."

I prefer to consider population levels in the light of the old concept of balance of nature. Nicholson (1933) stated: "That there is a relation between the population densities of animals and environmental conditions can be explained only in terms of balance." He felt that, in order to produce balance, there must be a controlling factor which is in turn governed by the density of the population controlled—that there is a reciprocal action between the population and the environmental factor which controls its density. This controlling factor he considered to be competition. When control is effected by competition, there is for each species a particular density at which balance exists: "Competition always *tends* to cause animals to reach, and to maintain, their steady densities." Important as competition is in regulating numbers, I doubt that it alone plays the predominating role that Nicholson assigned to it.

Chapman (1931: 182) conceived of "biotic potential" as "a sort of algebraic sum of the number of young produced at each reproduction, the number of reproductions in a given period of time, the sex ratio of the species, and their general ability to survive under given physical conditions. It is the potential power that an organism has to reproduce and survive in its environment." This biotic potential is divided into "reproductive potential" (the ability to produce high numbers) and "survival potential" (the ability to maintain high numbers). The biotic potential of a fauna is continually pitted against its environmental resistance; between these two factors a balance is maintained if the fauna survives. Chapman stated (1931: 186) that "in accordance with this hypothesis, biotic potential is a constant; and if environmental conditions were to remain constant the population should also be constant." Such constant conditions seldom if ever prevail in nature; hence the fluctuations in populations.

The breeding potential of any species is its capacity to produce living offspring; this potential differs between species; it is variable among individuals of any one species; and even within one individual it may change with age, physical condition, or other determining factors. I consider that, within broad limits, the breeding potential of a species may remain about the same in one locality over the years. In a distant, or a distinctly

different, locality it may not be the same. The breeding potential of *Peromyscus,* normally preyed upon by many other animals, is much higher than that of the porcupine, for instance. The breeding potential of each is designed to maintain the population of the species on the same level, other factors being equal. But other factors are not equal; the environment is constantly changing, with the resulting fluctuations of the animal populations. The same environmental factors are not necessarily responsible for these fluctuations at all times, although there is a continual interplay of all factors involved. At one period it may be abundant food, at another abundant predators, severe competition, or especially inclement weather, which exerts a predominant effect on the numbers of animals. The animal population in itself is an important factor in the environment of the individuals of the population. Nor does one dominant environmental factor always affect different species in the same manner or to the same extent.

This explanation seems to fit the facts as I observed them in the Huron Mountains during three years. A relaxation of certain unfavorable factors in the environment, whether it was the mild winter of 1939–40, the presence of more than normal amounts of food, a scarcity of predators, or, as is more likely, a combination of these and other unknown determinants, led to a rise in the populations of *Peromyscus, Clethrionomys,* and *Blarina* in 1941. The abundance of rodents was then, at least in part, responsible for the continued rise of the *Blarina* population to a peak in 1942. In the case of both the herbivorous rodents and the carnivorous shrews it was a temporary ascendancy of favorable (to the species concerned) over unfavorable environmental factors which promoted the rise of animal populations, although somewhat different factors were involved and their effects were not the same on the different species. In the case of a declining population, the accumulated unfavorable environmental factors outnumber the favorable ones, so that the breeding potentials of the species are not realized.

I propose that such an ecological explanation of fluctuations in animal populations may have a far wider application. Many exceptions, or apparent exceptions, will come to mind, notably among such "cyclic" species as the lemmings of both the Old World and the New World, the microtines, the grouse, and others. In these examples, however, it may develop that some single environmental factor, through the years, plays a dominant part and so causes the recurrent rhythm in animal numbers. Different factors may be at work in different cases, resulting in the apparent three- to four-year cycle among some species and the apparent ten- to eleven-year cycle among others. On certain occasions still other controlling factors may play the chief role, tending to upset the rhythm temporarily. This explanation accounts for the occurrence of severe fluctuations primarily in the north, where more rigorous climates exist, with a greater range of variability,

than in the tropics or temperate zones. It suggests that fluctuations are less violent on islands than on continents because of the greater uniformity of the insular environment, tempered as it is on all sides by water and isolated more or less against invasion by diseases, parasites, or terrestrial predators. This explanation further indicates how migratory species, able to escape the effects of unfavorable environment, to a certain extent at least, are less subject to fluctuations in numbers. The idea of a more or less fixed breeding potential in each species of an area, with the net results of the breeding affected favorably or adversely by one or more environmental factors (variable both in nature, in time, and in extent), may help to explain fluctuations in animal numbers which are sometimes general, sometimes local, in extent and which are sometimes cyclic, sometimes irregular, in occurrence.

APPENDIX

LIST OF PLANTS

In the following list of Huron Mountain plants mentioned in this study, the nomenclature of the ferns and fern allies is after Tryon (1940); that of orchids follows Bingham (1939); and the nomenclature of other flowering plants is that adopted by Robinson and Fernald (1908). A more complete list of the flora of the region may be found in Dodge (1918).

Reindeer moss	*Cladonia* sp.
Liverwort	*Marchantia* sp.
Sphagnum moss	*Sphagnum* sp.
Shining clubmoss	*Lycopodium lucidulum* Michx.
Flatbranch groundpine	*Lycopodium obscurum* Linn.
Running clubmoss	*Lycopodium clavatum* Linn.
Groundpine	*Lycopodium complanatum* Linn.
Common polypody	*Polypodium virginianum* Linn.
Bracken	*Pteridium aquilinum* (Linn.) Kuhn
Wood fern	*Dryopteris spinulosa* (Müll.) Watt
Long beech fern	*Dryopteris Phegopteris* (Linn.) Chr.
Oak fern	*Dryopteris Linnaeana* Chr.
Rattlesnake fern	*Botrychium virginianum* (Linn.) Sw.
White pine	*Pinus Strobus* Linn.
Jack pine	*Pinus Banksiana* Lamb.
Norway pine	*Pinus resinosa* Ait.
Tamarack	*Larix laricina* (DuRoi) Koch
White spruce	*Picea canadensis* (Mill.) BSP
Black spruce	*Picea mariana* (Mill.) BSP
Balsam fir	*Abies balsamea* (Linn.) Mill.
Hemlock	*Tsuga canadensis* (Linn.) Carr.
Northern white cedar	*Thuja occidentalis* Linn.
Common cat-tail	*Typha latifolia* Linn.
Club rush	*Scirpus* spp.
Cotton grass	*Eriophorum callitrix* Cham.
Sedge	*Carex* spp.
Jack-in-the-pulpit	*Arisaema triphyllum* (Linn.) Schott
Bog rush	*Juncus* spp.
Yellow clintonia	*Clintonia borealis* (Ait.) Raf.
Canada mayflower	*Maianthemum canadense* Desf.
Twisted-stalk	*Streptopus amplexifolius* (Linn.) DC

Hairy Solomon's seal	*Polygonatum biflorum* (Walt.) Ell.
Iris, blue flag	*Iris versicolor* Linn.
Moccasin flower	*Cypripedium acaule* Ait.
Hooker's orchis	*Habenaria Hookeri* Torrey
Round-leaved orchis	*Habenaria orbiculata* (Pursh) Torrey
Lesser rattlesnake plantain	*Epipactis repens* (Fernald) Eaton
Menzies' rattlesnake plantain	*Epipactis decipiens* (Hooker) Ames
Heart-leaved twayblade	*Listera cordata* (Linn.) Brown
Large coral root	*Corallorrhiza maculata* Raf.
Striped coral root	*Corallorrhiza striata* Lindley
Calypso	*Calypso bulbosa* (Linn.) Oakes
Poplar, aspen	*Populus tremuloides* Michx.
Balm of Gilead	*Populus balsamifera* Linn.
Sweet gale	*Myrica Gale* Linn.
Ironwood	*Ostrya virginiana* (Mill.) Koch
Yellow birch	*Betula lutea* Michx.
White birch	*Betula alba* Linn.
Tag alder	*Alnus incana* (Linn.) Moench.
Red oak	*Quercus rubra* Linn.
Slender nettle	*Urtica gracilis* Ait.
Hepatica	*Hepatica triloba* Chaix
Goldthread	*Coptis trifolia* (Linn.) Salisb.
Red baneberry	*Actaea rubra* (Ait.) Willd.
White baneberry	*Actaea alba* (Linn.) Mill.
Mandrake	*Podophyllum peltatum* Linn.
Pitcher plant	*Sarracenia purpurea* Linn.
Early saxifrage	*Saxifraga virginiensis* Michx.
Mountain ash	*Pyrus americana* (Marsh.) DC
Wood strawberry	*Fragaria vesca* Linn.
Cinquefoil	*Potentilla canadensis* Linn.
Red raspberry	*Rubus idaeus* Linn.
Thimbleberry	*Rubus parviflorus* Nutt.
Dewdrop	*Dalibarda repens* Linn.
Pin cherry	*Prunus pennsylvanica* Linn.
White clover	*Trifolium repens* Linn.
Wood sorrel	*Oxalis Acetosella* Linn.
Striped maple	*Acer pennsylvanicum* Linn.
Mountain maple	*Acer spicatum* Lam.
Sugar or hard maple	*Acer saccharum* Marsh.
Red maple	*Acer rubrum* Linn.
Jewelweed	*Impatiens biflora* Walt.
Basswood	*Tilia americana* Linn.
Blue violet	*Viola* sp.
Sundrops	*Oenothera fruticosa* Linn.
Wild sarsaparilla	*Aralia nudicaulis* Linn.
Sweet cicely	*Osmorhiza Claytoni* (Michx.) Clarke
Bunchberry	*Cornus canadensis* Linn.
Pipsissewa	*Chimaphila umbellata* (Linn.) Nutt.
One-flowered pyrola	*Moneses uniflora* (Linn.) Gray
Indian pipe	*Monotropa uniflora* Linn.
Labrador tea	*Ledum groenlandicum* Oeder
Pale laurel	*Kalmia polifolia* Wang.
Bog rosemary	*Andromeda glaucophylla* Link
Leatherleaf	*Chamaedaphne calyculata* (Linn.) Moench.
Trailing arbutus	*Epigaea repens* Linn.
Wintergreen	*Gaultheria procumbens* Linn.
Bearberry	*Arctostaphylos Uva-ursi* (Linn.) Spreng.
Creeping snowberry	*Chiogenes hispidula* (Linn.) T. & G.
Huckleberry	*Gaylussacia baccata* (Wang.) Koch
Blueberry	*Vaccinium pennsylvanicum* Lam.
Cranberry	*Vaccinium Oxycoccos* Linn.
Starflower	*Trientalis americana* (Pers.) Pursh
Black ash	*Fraxinus nigra* Marsh.

Self-heal	*Prunella vulgaris* Linn.
Bedstraw	*Galium* sp.
Partridge berry	*Mitchella repens* Linn.
Bush honeysuckle	*Diervilla Lonicera* Mill.
Fly honeysuckle	*Lonicera canadensis* Marsh.
Twinflower	*Linnaea borealis* Linn.
Goldenrod	*Solidago* spp.
Large-leaved aster	*Aster macrophyllus* Linn.
Cat's foot	*Antennaria fallax* Greene
Pearly everlasting	*Anaphalis margaritacea* (Linn.) B. & H.
Thistle	*Cirsium* sp.
Dandelion	*Taraxacum officinale* Weber

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PLATE I

FIG. 1. View of Plot 1, September 26, 1941. Area of jack pines.

FIG. 2. View of Plot 2, September 17, 1941. Stand of virgin hardwoods, predominantly sugar maple.

PLATE II

FIG. 1. View of Plot 3, September 2, 1941. Grove of virgin hemlocks.

FIG. 2. View of Plot 4, September 11, 1941. Area burned about 1900, now covered chiefly with white birch and poplar.

PLATE III

FIG. 1. View of Plot 5, May 27, 1942. Area clean-cut about 1930, now a tangle of hardwood saplings, chiefly sugar maple.

FIG. 2. View of Plot 6, September 29, 1941. Part of a dense white cedar swamp.

PLATE IV

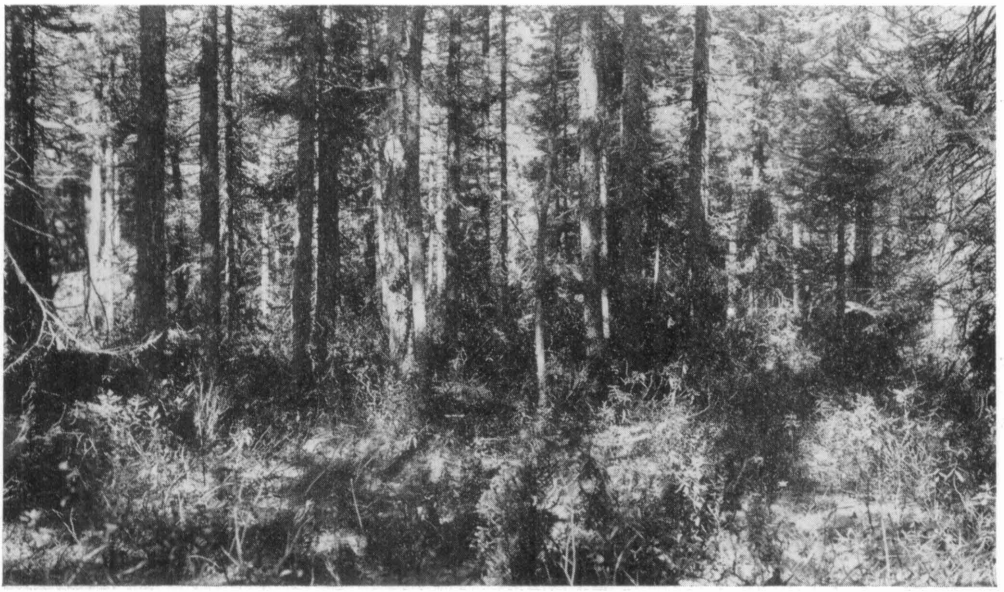

FIG. 1. View of Plot 7, September 17, 1941. Swamp with a nearly pure stand of black spruce.

FIG. 2. View of Plot 8, October 12, 1941. Area of virgin hemlock with a few mixed hardwoods.

(*Continued from inside front cover*)

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