THE QUADRAT METHOD OF STUDYING SMALL MAMMAL POPULATIONS

By

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INTRODUCTION

In 1932 The Cleveland Museum of Natural History began a series of intensive ecological studies of different habitats in the Cleveland region. In each of these, the problem of small mammal abundances immediately presented itself. Williams (1936) and Aldrich (MS.) attacked the problem by using trapping quadrats of small size. In the following year, 1933, the writer and his co-worker, Mr. P. N. Moulthrop, took over the quadrat trapping portions of their investigations and started a comparative study of the yields and value of different sizes of quadrats. The study has been carried on exhaustively since that time. Conclusions have been carefully checked through several years of experience and the results are now ready for publication.

The writer is deeply indebted to Dr. S. Charles Kendeigh, of the University of Illinois, for his guidance and advice during the course of this work, which was partially completed while Dr. Kendeigh was a member of the faculty of Western Reserve University; and to Drs. Arthur B. Williams and John W. Aldrich, of The Cleveland Museum of Natural History, for their advice and generous permission to incorporate some of their data in the present paper; and lastly, to the unflagging interest and zeal of the writer's co-worker, Mr. Philip N. Moulthrop, and his several field assistants, especially Mr. Scott R. Inkley and Mr. Winston Jesseman. This paper would have taken many more years to attain even its present preliminary status had it not been for their co-operation and industry in the field. Further acknowledgments are certainly due the host of property owners who have permitted repeated invasions of their lands by field workers from The Cleveland Museum of Natural History. In this connection, our especial thanks go to the Cleveland Metropolitan Park Board, to the Little Mountain Club, to the Baldwin Bird Research Laboratory, and to Messrs. Woods and Charles King, Trustees of the Cleveland Museum.

LITERATURE

The need for some method of estimating mammal populations has long been recognized. Various workers have in recent years emphasized the lack of standardized quantitative methods; others have gone farther and have suggested different ways in which counts may be made. The first concrete suggestion for a basic unit for population estimates was that of Grinnell (1914, p. 92) who advocated the use of "trap-nights". The total number of traps set in each locality is multiplied by the number of nights the trapline functions. The yield for each species per trap-night is then figured out, or the yield for all trap-nights. This method is admirably adapted to the needs of the field collector of small mammals. It has been frequently followed by various writers in subsequent years in determining the relative abundance of species in given districts; but there are several difficulties connected with its use, as suggested by Dice (1931, p. 377), to wit: the skill of the individuals setting the traps varies considerably; the yield decreases after the first night in most cases; the weather, make of traps, age of traps, and the species of animal, all afford factors tending to affect the significance of the total yields. Another difficulty might be noted from the ecologist's point of view: trap-nights give no indication of the actual abundance in numbers per unit area unless combined with other methods. Dice (loc. cit.) himself used "first trap-nights" only in some of his work, but concludes that, owing to the fact that certain species come to traps earlier and more readily than others, they do not give fair estimate of the relative abundance of the various species in the area trapped.

Besides using trap-nights per unit area, Taylor (1930, pp. 523-542) made counts of different species along lines of specified lengths and also made counts of the animals killed around standard amounts of poisoned grain. In addition, he used quadrats in making counts of hares and rabbits. These quadrats were designed to prevent ingress and egress of only the larger rodents. He also counted fecal pellets in given areas, and the numbers of used burrows and runways, a method also advocated by Phillips (1931, pp. 633-649), who suggested the basing of population estimates on the average number of animals in certain sample lairs or burrows, the average number per sample lair being multiplied by the total number of lairs per unit area. Recently MacLulich (1937, pp. 25-39) has shown that counts of droppings in a series of small quadrats can give a reliable index of the relative abundance of certain species. Grinnell and Storer (1924, p. 22), suggested using time units in place of space units, the species or individuals captured or seen per day or hour being substituted for areal units. The writer has found this useful in obtaining figures on the abundance of diurnal species, but the method is obviously under limitations when used at night, and is subject to the full brunt of varying conditions and possible interpretations, due to the weather and other factors above mentioned. Dice (1931) suggested that the use of indices affords the best method of expressing the relative abundance of species. He would list the number of individuals of each species observed or taken in each ecological habitat, and would base his indices on the frequency of each species in any one habitat. He stresses that the indices must be specific for each habitat and that the different techniques necessary for the capture of different size-groups of mammals must be taken into account. Subsequently, he has abandoned the use of indices in favor of population estimates based on the computation of home-ranges from the data yielded by large-size quadrats (1938, pp. 119-130). Hamilton (1937, p. 780) secured figures on the populations of *Microtus pennsylvanicus* about Ithaca, New York, by trapping all the mice out of areas "more or less defined by natural boundaries", varying from one-half to twelve acres.

Quadrats have long been used as a means of determining the abundance of plants in ecological studies. For an account of the development of the quadrat method, the reader is referred to Kenoyer (1927). Thus Pound and Clements (1898) developed a scale of seven degrees of frequence, based on quadrats five meters on a side. Jaccard (1912) used adjacent quadrats as bases for a frequence index. Using much of the early work in addition to his own, which involved the use of circular units instead of quadrats, Raunkaier (1918) developed his "Law of Frequence". Briefly, this is explicable as follows: Given a number of quadrats, perhaps ten; and a number of species, ten for instance; if one species occurs on all ten quadrats, its *percentage of frequence* is 100; if on but one, 10. There will be a higher number of species occupying a small proportion of the quadrats than of species occupying most or all of them. The ratio of these frequences will be 5:2:1:0:1, where each number refers to the frequency for each of five classes of abundance (classes A, B, C, D, E, referring to the occurrences of a single species in 1-20, 21-40, 41-60, 61-80, 81-100 per cent of the quadrats, respectively). As Kenoyer (1927, p. 343) points out, this may be expressed by a graph, wherein the curve representing the numbers of frequences has two crests, one much lower than the other. The first crest represents the number of least frequences and the second the number of the greatest. Raunkaier himself based this concept on over 8000 percentages of frequence, which arranged themselves according to the above formula. Kenoyer found that his surveys of vegetation in the Lake Michigan region supported the Raunkaier formula. From the point of view of the developmental history of the subject of this paper, it is of importance that he (1927, p. 236) suggested the use of this formula and, by inference, the quadrat method, with regard to birds and mammals. He found that the formula held very well for sweeps of the insect-net over known grass-land areas, and for micro-organisms in hay infusions. The applicability of the formula to small mammals will be discussed shortly.

A number of other workers, in addition to Taylor (loc. cit.), have used quadrats in studying small mammal populations, among them Elton, Middleton and their co-workers (several papers), Townsend (1935), Chitty (1937), Williams (1936), and Hatfield (1938). Townsend's paper appeared after the initiation of this work. In it is presented a somewhat novel method of obtaining actual figures for small mammals per acre of ground. The method devised was that of the "moving quadrat" that consisted of three parallel trap-lines one rod apart. Each trap-line consisted of a row of triads of traps three feet apart. Thus the trap-lines were in all 33 feet long and about of the same depth, forming a quadrat of a size intermediate between the 10-meter and 50-foot sizes, later to be considered in this report, but much nearer the 10-meter unit. The trap-lines were "cascaded" by shifting the rearmost row to a new position one rod in front of the first row. This was done every day for fourteen days, during which time a stationary trap-line was run in the same habitat. The idea was evidently suggested by the work of Elton (1925). Populations per acre were estimated on the basis of the yield over a three-day period.

Chitty (1937) used blocks of traps (Tring live traps) spaced so as to form a quadrat 90 feet on a side. He concluded that there was a large amount of drift into units of this size from adjacent terrain, and later used areas "9 or 10 times as large", concluding that even these larger units are subject to considerable drift. Hatfield (1938) used small quadrats (24 feet on a side) in studying the habitat preferences of certain small mammal species in Minnesota. Williams (1936) made estimates of population per acre on the basis of the yields during several days from quadrats 10 meters on a side. It was his four-year study of the North Chagrin forest near Cleveland that stimulated the present investigation. His original population studies were made with but one size of quadrat. As the writer took over the quadrat portion of Dr. Williams' researches in 1933, all of the quadrat trapping data secured by workers from the Cleveland Museum is incorporated in this paper, including that which has already been published by Williams (1936).

Dice (1938, pp. 119-130) used quadrats in the course of studying small mammal home-ranges. His quadrats were of single chains on a side (1 chain = 66 feet) and of multiples thereof. From the data obtained through the use of live traps and the marking of his animals, he was able to derive an interesting formula for the rough calculation of an individual home range: $NX^2 = (A + X)(B + X)$, where N is the number of adults of the sex or age group being considered, known to be living on the quadrat, X the mean width of an individual home range, A the width of the quadrat from outside trap to outside trap, and B the length of the quadrat. The difficulty arising from this method is that the quadrat must approximate the actual home range or the results are subject to considerable error.

QUADRAT WORK OF INVESTIGATORS FROM THE CLEVELAND MUSEUM

Dr. Williams (loc. cit.) was primarily interested in the ecology of sixty-five acres of virgin beech-maple forest situated in the northeastern corner of Cuyahoga County, Ohio at the North Chagrin Reservation of the Metropolitan Park System of Cleveland. His trapping of small mammals there constituted but a small part of his investigations. He used five quadrats of small size — ten meters on a side, apparently following the suggestion of Shelford (1929, p. 55). These are referred to hereafter as 10-meter quadrats.

Aldrich (MS) also used the 10-meter quadrats, singly and in blocks of nine (thus forming a quadrat 30 meters on a side), in studying the small mammal populations of various communities of the hydrosere at Aurora Pond, Portage County, Ohio. His work began during the summer of 1933 and continued through 1934. No trapping was done at Aurora Pond during 1935, but since that year further studies, with larger quadrats, have been made annually by the writer and Dr. Aldrich.

Believing that the use of units as small as the 10-meter quadrats greatly increased the probability of error when they were used as bases for the estimation of actual numbers, the writer tried a number of different methods. In 1933 fifty-foot and 150-foot quadrats were operated synchronously at a number of stations and the results carefully compared. In 1934 the 50-foot and 10-meter sizes were compared, and in 1935, the 150-foot and 10-meter sizes. In 1936 the conclusions arrived at were carefully re-checked by another exhaustive comparison of the 10-meter and 150-foot sizes, on a far wider scale than heretofore. The smaller sizes were discarded thereafter, and work was continued with the 150-foot units. In 1938 the desirability of a "one-man quadrat" was fully recognized and trial was made of 100-foot units. In this year, and 1939, circular units of approximately the same area (½ acre) as the 150-foot sizes were tried, upon the recommendation of Dr. S. C. Kendeigh.

Various other modifications were also attempted: protective "shelter-belts" of traps and quadrats, insulated from the in-wanderings (drift) of small mammals by sheet-iron sunk into the ground to a depth of several inches. Full study was made of the yields of central quadrats in blocks of nine. A similar system was used by Elton, Davis, and Findlay in estimating the population of voles in Scotland (1935, p. 284). All these studies were made in many different habitats, and the quadrat-behavior of thirty species of small mammals was noted. The scientific names of the various species concerned are given in Table X. Elsewhere they appear as binomials. For the sake of uniformity and brevity the subspecific names are omitted. In a few cases, as in the daily yield tables, more than one subspecies of the same animal are concerned in the averages, and in several others, the actual identity of the subspecies in question is still in doubt.

The population estimates as derived from each quadrat are given to the nearest whole animal; thus, a yield of 1 *Blarina* from a 150-foot quadrat is interpreted as 2 animals per acre instead of 1.94 animals. The average figures are given, however, to the nearest tenth or hundredth of a point.

FIELD METHODS

The method of quadrat trapping followed by workers from the Cleveland Museum of Natural History is as follows: a square of land of known area is marked off. Traps are set over the entire square, the number varying according to the needs of the terrain. They are placed in such a way that they will as quickly as possible drain the area of its resident and transient small mammal population. The traps are kept in operation for three days or until there is no further yield, or until the daily yield has reached a minimum. A field map of the quadrat is made, showing trap-sites, rocks, logs, etc. The record of each trap is kept on the map, while the daily catch is added up and tabulated on the back of map or on a separate sheet. When specimens are saved, the quadrats they came from are reported on the field tags along with the date and other data. Many different sizes and groupings of quadrats may be used, and the relative efficiency of the different methods varies. From the yield obtained per quadrat the number of animals per acre, per square mile, or any other large area, may be computed, providing the ecological conditions of the large area are uniform and similar to those in the quadrat.

In forest quadrats, ninety-five percent of the traps are set in underground runways which may be found by rapid probing or tapping with one's forefinger, and which can often be detected by an experienced field worker simply by walking over the terrain of the quadrats.

The number of traps set per quadrat depends entirely upon the terrain, but under all ordinary circumstances at least 12 traps are placed in each 10-meter unit and at least 100 in each 150-foot (half-acre) area. Traps are *never* set at fixed intervals within the quadrat; they are placed where they will catch the mammals. Every effort is made to reduce the bait factor to a minimum by setting the traps in such a way that the mammal will be caught whether the trap is baited or not. Local conditions — that is, the underground runways, in which most traps are set — make bait unessential for the capture of all the insectivores and all the voles considered in this report. Bait (rolled oats or dried fruit) is usually used, however, except in the rainiest weather, in order to attract certain other species, notably the small sciurids and jumping mice, which do not habitually use runways. For the bait preferences of certain small mammals, the reader is referred to Townsend (1935, pp. 22-28).

The specialized technique used when we operated quadrats insulated from drift is considered later on in this report in conjunction with the data yielded by that type of quadrat.

COMPARISON OF THE YIELDS OF 10-METER AND 150-FOOT QUADRATS

The five 10-meter quadrats used at North Chagrin Metropolitan Park were operated for the purpose of studying small mammal populations per acre and population fluctuations from 1932 to 1936 inclusive, by Dr. Williams. Data obtained in all the years except 1936 have been published by that worker (1936, pp. 46-47). That for 1936 appears for the first time in this paper.

North Chagrin Metropolitan Park is very fully described as a Beech-Maple climax community (loc. cit.). Suffice it to say here that two of the five 10-meter quadrats (B and D, see Tables) were situated on points of land overlooking the valley of the Chagrin River, in situations where hemlock was an important member of the plant community. Conditions of soil and cover were typical of the forest as a whole in all but one of the quadrats (A) where there was a deficiency of cover and humus. Quadrat C was encompassed by a grid of nine 50-foot quadrats in 1935 and 1936 in an effort to study the effect on its yield of a shelter-belt of traps designed to exclude non-resident animals that drift into such small units during

TABLE I. Summary of Total Yields from 10-Meter Quadrats, North Chagrin Metropolitan Park, Cuyahoga County, Ohio. [In Part after Williams (1936, p. 46).]

Quadrat	Year	Blarina	Sorex fumeus	Sorex cinereus	Parascalops	Tamias	Sciurus huds.	Peromyscus leuc.	Microtus	Pitymys	Zapus	Napaeozapus	All Species
A.	1932	10	0	0	0	–	–	8	0	0	0	0	18
	1933	4	1	0	0	–	–	1	0	0	0	0	6
	1934	2	0	0	0	–	–	0	0	0	0	0	2
	1935	8	0	0	0	1	1	3	0	0	0	0	13
	1936	2	0	0	0	0	0	0	0	0	0	0	2
B.	1932	12	0	0	0	–	–	3	0	0	0	1	16
	1933	0	0	0	0	–	–	0	0	0	0	0	0
	1934	0	1	0	0	–	–	0	0	0	0	0	1
	1935	2	0	0	0	2	0	5	1	0	0	0	10
	1936	0	1	0	0	1	0	0	0	0	0	0	2
C.	1932	5	0	0	0	–	–	6	0	0	0	0	11
	1933	3	0	0	0	–	–	0	0	0	0	0	3
	1934	1	0	0	0	–	–	0	0	2	0	0	3
	1935*	2	0	0	0	0	1	0	0	1	0	0	4*
	1936*	0	0	0	0	0	0	0	0	0	0	0	0*
	1937*	0	1	0	0	0	0	0	0	0	0	0	1*
	1938*	1	0	0	0	0	0	0	0	0	0	0	1*
	1939*	0	0	0	0	0	0	0	0	0	0	0	0*
D.	1932	6	0	0	0	–	–	5	0	0	1	0	12
	1933	2	0	0	0	–	–	3	0	0	0	0	5
	1934	1	0	0	0	–	–	1	0	0	0	0	2
	1935	5	0	0	0	0	0	7	0	0	0	0	12
	1936	4	0	0	1	0	0	1	0	0	0	0	6
E.	1932	4	0	0	0	–	–	6	0	0	0	0	10
	1933	3	0	0	0	–	–	1	0	0	0	0	4
	1934	2	0	0	0	–	–	3	0	0	0	0	5
	1935	4	0	0	0	0	0	8	0	2	0	0	14
	1936	3	0	0	0	0	0	0	0	0	0	0	3
All Quadrats													
	1932	37	0	0	0	–	–	28	0	0	1	1	67
	1933	12	1	0	0	–	–	5	0	0	0	0	18
	1934	6	1	0	0	–	–	4	0	2	0	0	13
	1935	21	0	0	0	3	2	23	1	3	0	0	53
	1936	11	1	0	1	1	0	1	0	0	0	0	13

* See p. 26-28. – : no rat traps used.

trapping operations. Hence, its yields are not strictly comparable to those of the others during these two years, but are of interest nevertheless.

Table I gives a summary of the total yields during approximately twelve days time from these 10-meter quadrats. Total yields are here given instead of the yields during a shorter period because the table is an enlargement of one used by Dr. Williams (1936, No. 12, p. 46), who based his population estimates on the sum and total of all specimens taken during the period of trapping. Evidence is given subsequently in this paper that estimates should be based on the yields during only the first three days of trapping. It will be noted that the lack of humus and cover characteristic of quadrat A had no apparent effect on its yields, probably for the reason that it was well within the normal wandering range of numerous small mammals whose incursions into the area were of temporary nature. It will also be noted that the yields of quadrat C from 1935 on are much lower than the yields for the corresponding years from the other units, because of the "shelter-belt" surrounding it.

In these figures summarizing the results of all the quadrats it may be seen that small mammal populations were great in 1932 and 1935, indicating that these years probably marked peaks of small mammal abundances. Closer inspection of the data, however, reveals that the character of the peaks was determined almost entirely by two species, the short-tailed shrew, and the deer mouse. The more unusual species do not seem to follow the same curve.

In Table II are found population-estimates per acre for each species, based in part on the figures in Table I. There the numerical changes may be more easily visualized. It will be shown subsequently that these figures are in all probability far higher than they should be, but as the sources of error are common to all, the figures are comparable to each other with the possible exception of those of quadrat C from 1935 to 1939. They show two definite peaks in the populations of at least two species, and provide the first evidence of a short-wave cycle of about three years among the woodland small mammals of our latitudes in North America. Subsequently, as is shown in Table II, evidence was gathered that seems to show that *Blarina* is either non-cyclical or has a cycle of a length as yet not definitely determined. The figures of Townsend (1935, p. 48) give population-estimates per acre for the years 1931-1934, but do not entirely bear out the existence of such a cycle in all communities. The increased populations in certain habitats during the years 1931 and 1932 he ascribes to factors influencing the moisture and hence humidity of the community, and cites figures showing that in certain habitats, such as very moist woods, there is a remarkable constancy of populations from year to year. He believes that certain small mammals may migrate into the moister areas during dry periods, a feature noted by numerous other workers, including the writer. It is to be expected, however, that cyclical changes in small mammal populations are more likely to be noted in areas not permanently suited to small-mammal occupancy; and the writer believes that Townsend's figures lend considerable support to the fast-accruing evidence of the existence of cycles for certain species.

In 1935 a grid of 50-foot quadrats, numbering nine in all, actually constituting a quadrat 150-feet on a side, was operated at the site of 10-meter quadrat C, which formed the center of the central unit of the grid. Such grids had been used as early as 1933 by the writer, but it was not until two years later that grids were operated at the same station with 10-meter units. The purpose of the grid was to study the yield from the center quadrat, which it was hoped would provide accurate figures on small mammal populations from an area protected from drift (by the outside quadrats). However, it was soon discovered that it was virtually impossible to get a fair cross-section of a given population from such central quadrats, while the entire grid usually gave a very complete picture. The data obtained in 1935 from the North Chagrin grid are given in Tables II, IV, and V.

The yield for the 10-meter quadrats (Table III) and the 150-foot grid (Table IV) are compared in Table V. In all such grids treated in this report, No. 5 is the central 50-foot unit and Nos. 1, 3, 7, and 9 are corner quadrats. It will be seen that the five 10-meter quadrats (Table III) captured nearly two-thirds as many animals within three days as the grid (Table IV), although their combined areas amounted to less than one-quarter of the grid's area. Consequently, the figures per acre for each species are very much greater when based on the smaller units. Since drift into the grid has not been completely stopped by any means, the figures obtained from it are

TABLE II. Populations-per-acre based on Total Yields from Five 10-Meter Quadrats and the 3-day Yields from 150-foot Quadrats in Beech-Maple Forest at North Chagrin Metropolitan Park.

Quadrat and Year	Blarina	Sorex fumeus	Sorex cinereus	Parascalops	Condylura	Tamias	Glaucomys	Sciurus huds.	Peromyscus leuc.	Microtus	Pitymys	Zapus	Napaeozapus
10-Meter.													
1932	296	..	..	P	..	P	P	P	224	..	..	8	8
1933	96	8	..	P	P	P	P	P	40	..	..	..	..
1934	48	8	..	P	..	P	P	P	32	..	16	..	..
1935	184	..	..	P	..	24	P	16	216	8	24	..	..
1936	89	8	P	8	..	8	P	P	8	..	16	..	..
150-Foot.													
1932*	42	..	..	?	..	?	?	?	32	..	..	P	P
1933*	17	2	..	?	..	?	?	?	6	..	..	..	..
1934*	7	2	..	?	..	?	?	?	5	..	3	..	..
1935	29	..	..	2	..	4	P	P	27	..	17	..	..
1936	18	6	2	P	..	2	2	P	2	..	2	..	..
1937	40	10	4	10	..	P	P	P	8	..	..	..	4
1938**	29	3	..	P	..	1	1	?	20	..	4	..	..
1939**	12	7	..	5	..	1	P	..	2	..	4	..	..

* Figures from corrections made on 10-Meter yields, the proper corrections determined from the relative yields of 10-Meter and 150-Foot quadrats in 1935 and 1936 at this station.

** 2 quadrats in average.

Blank : no records for year. P : population below 8 per acre (10-Meter) or 1 or 2 (150-Ft.).

? : present, but reliable figures lacking.

certainly not too low, even taking into account the fact that a small number of animals escape, or drag traps into places from which they cannot be recovered. Such occurrences are rare and are usually omitted in compiling the data here given, although in the case of moles, these are carefully taken into account. Elton (1935) and co-workers, Hamilton (1937) and other workers have overcome this difficulty by the use of traps that captured their animals alive, a method preferable from many points of view, but too time-consuming for the worker who wishes to cover large sections of the country in a short space of time. The grids, as was mentioned above, were set up with the idea that the central quadrat would have the drift eliminated and that an accurate picture of the inhabitants of the quadrat could thus be obtained. This is undoubtedly true, at least as compared to quadrats unprotected from drift; but an attempt to base the total population of a large area on only one such unit gives the anomalous results indicated in Table V. It happened, in the case of quadrat C-5, that an infestation of *Pitymys* was centered in that locality, and that the population of *Blarina* was somewhat denser than usual. But in the first three days, no *Peromyscus* was taken, indicating a total lack, in that small unit, of one of the most abundant and characteristic mammals of the North Chagrin woods. However, if many such central quadrats are averaged (See Table VI), from similar woods in different localities with the same general

TABLE III. 1935 3-Day and Total Yields from the five 10-Meter Quadrats at North Chagrin Metropolitan Park, Cuyahoga County, Ohio. Total Yields in Parentheses. For the distribution of these quadrats, see p. 26.

Species	A	B	C	D	E	Totals
Blarina brevicauda.....	3 (8)	2 (2)	1 (2)	3 (5)	3 (4)	12 (21)
Peromyscus leucopus...	0 (3)	2 (5)	0 (0)	2 (7)	2 (8)	6 (24)
Pitymys pinetorum.....	0 (0)	0 (0)	1 (1)	0 (0)	2 (2)	3 (3)
Sciurus hudsonicus.....	1 (1)	0 (0)	0 (1)	0 (0)	0 (0)	1 (2)
Tamias striatus........	0 (0)	1 (2)	0 (0)	0 (0)	0 (0)	1 (2)
Microtus pennsylvanicus	0 (0)	0 (1)	0 (0)	0 (0)	0 (0)	0 (1)
Totals, All Species.....	4 (12)	5 (10)	2 (4)	5 (12)	7 (14)	23 (52)

Quadrat C was situated at the center of the 150-foot grid (See Table IV and pp. 26-28). The drift it would normally have captured was collected by the outer portions of the grid; hence, the yields for this particular quadrat were much lower than those of the others. There is evidence to show that some of its residents drifted *outwards* and were taken in the grid.

The area of the five 10-meter quadrats is 0.123 acre. The total trapping time for each of the five quadrats was nine days in 1935.

TABLE IV. 1935 Record of the North Chagrin Park 150-Foot Quadrat (Grid of nine 50-Foot Units); the 3-Day and Total (9-Day) Yields, the latter in parentheses. Area of Grid, 0.516 acre.

Species	C-1	C-2	C-3	C-4	C-5*	C-6	C-7	C-8	C-9	Totals
Blarina brevicauda....	4 (6)	0 (0)	1 (3)	1 (1)	3 (4)	1 (1)	1 (1)	3 (4)	1 (1)	15 (21)
Peromyscus leucopus..	3 (4)	0 (0)	3 (5)	1 (2)	0 (4)	1 (2)	3 (4)	0 (1)	3 (4)	14 (26)
Pitymys pinetorum...	1 (1)	0 (0)	0 (0)	1 (3)	5 (5)	2 (3)	0 (0)	0 (0)	0 (0)	9 (12)
Sciurus hudsonicus....	0 (0)	0 (0)	0 (0)	0 (0)	0 (1)	0 (0)	0 (0)	0 (0)	0 (1)	0 (2)
Tamias striatus.......	0 (0)	2 (2)**	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (2)
Glaucomys volans....	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (1)	0 (1)
Totals, All Species....	8 (11)	1 (2)	4 (8)	3 (6)	8 (14)	4 (6)	4 (5)	3 (5)	4 (7)	40 (64)

*Center quadrat of grid. This quadrat includes the 10-Meter quadrat C (See p. 26 and Table III). The figures here given include those for 10-Meter quadrat C as given in Table III. It is a matter of chance, however, that the yields from C-5 are the largest of any of the grid quadrats.

**Quadrat C-2 contained the only chipmunk citadel (using this word in the sense of Grinnell). It is noteworthy that no other species was taken in its immediate vicinity.

TABLE V. Comparison of Population Estimates based on Yields of the North Chagrin 10-Meter and 150-Foot Quadrats in August, 1935.

	Blarina	*Peromyscus*	*Pitymys*	*Tamias*	*Sciurus huds.*
Population per acre, based on the 10-Meter 3-day Yields.	97	49	24	8	8
Population per acre, based on the 10-Meter Total Yields.	184	216	24	24	16
Population per acre, based on the 150-Foot 3-day Yields.	29	27	17	4	2
Population per acre, based on the 3-day Yield of C-5 only (the center quadrat of grid)	53	....	85	....	....
Population of the 65-acre area, based on the 10-Meter 3-day Yields............	6341	3171	1585	538	538
Population of the 65-acre area, based on the 10-Meter Total Yields............	11097	12602	1585	1076	1076
Population of the 65-acre area, based on the 150-Foot 3-day Yields............	1890	1754	1224	254	....
Population of the 65-acre area, based on the 150-Foot Total Yields............	2856	3536	1632	254	254

population figures, the picture becomes more normal, and, as is to be expected, the estimates per acre run on the average below those obtained from 150-foot quadrat data; in fact, for several species in Table VI there are no records at all for the center quadrats, a situation which may be partially duplicated if any other quadrat of the grid is taken in place of the central one. However, the fact that the outside quadrats always show a *slightly* better picture than the centers indicates that drift is at work, and is an argument for a very short trapping period. Thus, the number of grids necessary to provide good average data for the center quadrats is very great. Most workers using quadrats have indicated the necessity of obtaining figures from a large number of quadrats when working on the relative abundance of organisms, as were Raunkaier (1918), Gleason (1920), Kenoyer (1927), and Dice (1931 and 1938). This holds equally true for workers interested in actual abundance. A difficulty arises in the fact that in order to obtain sufficient records of central quadrats from one and the same tract of woodland or field, which is to be preferred over quadrats in different districts, a great deal of time must be spent and the resultant depopulation arising from the use of many grids would be considerable and conceivably might seriously alter the ecological picture. Furthermore, as Dice points out (1938, p. 125) it seems wasteful of time and data not to use the information accruing from the sheltering tier of quadrats themselves. The utility of a central quadrat might be greatly increased if enlarged from 50, to let us say, 150 feet or more, but modifications in the shelter-belt must then be made or the usefulness of the method will speedily collapse. Some further observations on shelter belts will be made later on in this report.

TABLE VI. Population Estimates based on the Yields of fourteen 150-Foot Grids, each of nine 50-Foot Quadrats, and on the Yields of the Central Quadrats of these Grids. All Data secured in 1938 in Climax Forests.

QUADRAT	Blarina brevicauda	Sorex fumeus	Sorex cinereus	Parascalops breweri	Condylura cristata	Tamias striatus	Glaucomys volans	Sciurus hudsonicus	Peromyscus leucopus	Microtus pennsylvanicus	Pitymys pinetorum	Zapus hudsonius	Napaeozapus insignis
Centers..	12.6	10.9	0	1.2	0	0	0	0	18.2	1.2	1.2	0	3.8
Grids....	34.2	9.7	0.14	1.1	0.28	1.1	1.6	0.14	22.2	0.28	2.9	0.14	1.6

THE YIELDS OF 50-FOOT AND 10-METER QUADRATS

In 1933 the writer believed that the accuracy of a quadrat could be greatly increased if the size of the unit used were increased by using 50-foot instead of 10-meter units. The area of a 10-meter quadrat is but 1/41 of an acre, while that of one 50-feet on a side is approximately 1/17. The increase seemed quite important and a great deal of data was secured during 1933 and 1934 with the use of the new size of quadrat. It seems unnecessary to compare in detail the yields of the two sizes; it will suffice to report that in any given year the yields from the 50-foot units were in general slightly the greater, the yield of the larger units being to those of the smaller as 6 to 5, instead of 2.5 to 1, as one might expect from the relative areas of the two units. The average daily yield from the two sizes is compared in Fig. 2. The fact that the 50-foot line is usually below the 10-meter line is due to the fact that the 10-meter line covers two "mouse years", 1932 and 1935, while the 50-foot data was almost all gathered in 1933 and 1934, years of low small mammal populations. The point to be gained from this may be much better emphasized by comparing the 50-foot yields with those of the 150-foot quadrats, the contrast in which is of similar order as that between the 10-meter and 150-foot units. At Little Mountain, Geauga County, Ohio, a series of 50-foot quadrats and 150-foot grids were operated synchronously. As a check on the North Chagrin data, let us consider that obtained at Little Mountain.

THE YIELDS OF 50-FOOT AND 150-FOOT QUADRATS COMPARED

Trapping was carried on at Little Mountain with these two units in 1933, an ebb-cycle year further characterized by great drought. Since 1935 only the larger units have been used. The actual field technique was the same as was used at North Chagrin and elsewhere. The presence of Mr. Philip N. Moulthrop as field assistant, who had done the bulk of the trapping at North Chagrin, tended to standardize the trapping technique and eliminate error due to the varying experience of different workers. This error is chronically brought up as an objection or a difficulty to be encountered in assembling quadrat and other trapping data, vide Dice (1931) and Ruhl (1932). In this connection, it might be well to mention that any differences in trapping technique speedily manifest themselves in the yields of the quadrats. In the course of this work, every field assistant is given a rigid course of training before being allowed to trap inside quadrats, and the yields of each trapper are carefully and continuously examined. The most efficient trapper is he who gets the most small mammals of *all* species in a given area in the shortest time. No great deviation below this can be tolerated, and it has been found that well-trained workers do not deviate in their outputs to any appreciable extent.

The numbers of the different sizes of quadrats used at Little Mountain were: in 1933, eight isolated 50-foot units and three 150-foot grids; and in 1935, four 150-foot grids only, and three grids only from 1936 to 1939 inclusive. In 1933 and 1935 trapping was done for comparable lengths of time in the early summer. From 1936 on the quadrats were worked for but little longer than three days.

Grids of quadrats were maintained as follows: one in a nearly pure hemlock community, the "hemlock block" hereinafter mentioned; one in white pine woods, the "pine ridge" block; one in a second-growth oak-chestnut area on the central "saddle" of the mountain where pines are invading, the "pine seedling" block; and one in a beech-cucumber area, the "beech-cucumber" block. Except for the lattermost, all were worked in both 1933 and 1935. The beech-cucumber block was completely worked only from 1935 on, although two of its corner quadrats were worked in 1933 as isolated 50-foot units. During 1936 and 1937 the hemlock and pine-seedling grids were discontinued, and in their place there was substituted the "Daley's Field" grid in a woods-edge community of sumacs, aspens, young red maples, pine, and Kentucky coffee trees. The hemlock quadrat was revived in 1938 and 1939 in place of this unit.

A chart summarizing the results obtained in 1933 and contrasting the yields of 50-foot and 150-foot units constitutes Table VII. It will be seen that the average per 50-foot solitary quadrat is higher in all cases than the averages for the grids, for the two species that appeared in the three-day totals in both the grids and the solitary units. This also raises the estimate per acre and hence the estimate for the population of the seventy-five acre area under consideration, as indicated. Thus further evidence is provided that the estimates based on small units are always larger than those based on larger ones.

Remembering that the estimates per acre given in Table VII are based on a three-day, and not on a total yield, the population per acre of *Blarina* and *Peromyscus* on Little Mountain in 1933, as furnished by the data in this table, may be compared to the figures given by Williams, for 10-meter quadrats as recorded in Table II, for those species at North Chagrin in the same year. It will be noted that the divergence in figures per acre between North Chagrin and Little Mountain is tremendous. At that time the writer felt that the North Chagrin woodland naturally had a much higher number of resident small mammals than did Little Mountain, even taking into account the sources of error already mentioned. However, the results of our 1935 and subsequent work with large grids indicate no actual fundamental differences (see Tables V and IX) between the two communities.

Table VIII gives the actual yield from each of the three grids used in both 1933 and 1935 on Little Mountain. They help to give an idea of the size of the series of specimens on which the total population is based. This total (Table VII) is obtained from the average figures for the three grids, here considered as three large quadrats.

Corroborating the North Chagrin records insofar as relative abundances and increase are concerned is the fact that the populations of *Blarina* and *Peromyscus* underwent an increase of roughly 400 percent between 1933 and 1935. The appearance of many more species in the three-day totals for 1935 than for 1933 is another indication of a general increase not confined to any one species. The fact that chipmunks and flying squirrels were not taken in 1933 is due, however, to our not having used rat-traps regularly in that year.

The writer feels that the estimate for *Pitymys* is approximately correct, but that the one for this vole obtained by the grid-census at North Chagrin in 1935 is somewhat too large owing to the fact that the grid apparently encompassed a colony. The 10-meter quadrats (Table I) at North Chagrin tend to show that *Pitymys* is less generally distributed than either *Blarina* or *Peromyscus* and that the population is not generally as dense as in the 150-foot quadrat, further indication of the fact that more than one quadrat, of any given size, should be used if population estimates for a larger area are to be made. In this connection, attention is called to Table IX (pp. 41-42), wherein the summarized estimates for all the 150-foot quadrats on Little Mountain are recorded. It will be noticed that in certain cases, notably those of *Blarina* in the pine ridge and beech-cucumber grids, the yearly records from a single 150-foot quadrat do not indicate the same cyclical tendency that the averages from several quadrats do. Similarly, it will be seen that the estimates based on the center quadrats are irregular and hopelessly out of step with those based on the grids. The figures, to the writer's mind, entirely remove the central-quadrat method from the field of reliability except under certain conditions already enumerated. A 50-foot quadrat, even if sheltered from drift, can give no picture with any degree of completeness of the small mammal population of a large area, and if sheltered from drift from the outside has nothing to prevent drift out of itself. The estimates tend to be inflexible and either too high or too low as compared to the estimates based on the large units. Thus, the smallest possible figure obtainable from a single 50-foot unit is 17 per acre, on the basis of one animal captured. The averages from a very large number of centers give a better picture, but the difficulties accruing to this method have already been pointed out. From the central quadrat of the hemlock block it would appear that the *Peromyscus* population diminished by half from 1933 to 1935, the exact reverse of the situation as recorded in all other quadrats, protected and unprotected. Another conclusion that might be pointed out from the above and that has already been indicated is that the population of the more generally distributed species seems to be more or less constant in northeastern Ohio, during a "mouse year", or increase of the cycle, from woodlot to woodland and from one climax forest type to another (See Table IX, pp. 41-42).

TABLE VII. Summary of the Quadrat-Trapping Work on Little Mountain in 1933.

Species	3-Day and (Total) Yields from 8 isolated 50-foot quadrats	Ave. per quadrat of the 8 isolated units (based on 3-day yield)	Ave. number per quadrat of Pine-Ridge grid of nine 50-foot quadrats	Ave. number per 50-foot quadrat of Pine-Seedling grid	Ave. number per 50-foot quadrat of Hemlock grid	Population of 75-acre area, based on 3-day yields of isolated 50-foot units	Population of area based on 3-day yield from grids (150-ft.)	Population of area based on center quadrats of the three grids	Population per acre based on 3-day yields from isolated units (left) and from grids (right)	
Blarina brevicauda........	3 (15)	0.375	0.22	0.22	0.33	490	324	....	6.4	4.3
Sorex fumeus fumeus......	0 (1)	....	....	0.22	0.44	....	279	444	...	4.0
Peromyscus leucopus......	8 (16)	1.00	0.67	0.33	0.67	1308	693	1333	17.2	9.3
Napaeozapus insignis.....	1 (3)	0.125	....	....	....	163*	....	....	2.2**	...
Tamias striatus...........	0 (1)	....	....	....	....	....	....	....	...	...
Sciurus hudsonicus........	0 (1)	....	....	....	....	....	....	....	...	...

*Too high an estimate, as the Woodland Jumping Mouse is limited to wet ground.

**For wet, cool areas only.

Attention is called to the estimates based on the center-quadrats and the isolated 50-foot units as compared to those based on the 150-foot grids taken as units.

Table VIII. The Yields of Three 150-Foot Quadrats on Little Mountain for the Years 1933 and 1935.

Species	Pine-Ridge		Pine-Seedling		Hemlock		Totals	
	1933	1935	1933	1935	1933	1935	1933	1935
Blarina brevicauda	2 (13)	7 (44)	2 (8)	15 (30)	3 (6)	10 (30)	7 (27)	32 (104)
Sorex fumeus fumeus	0 (2)	1 (5)	2 (2)	2 (5)	4 (10)	4 (14)	6 (14)	7 (24)
Parascalops breweri	0 (0)	1 (3)	0 (0)	0 (1)	0 (0)	0 (0)	0 (0)	1 (4)
Peromyscus leucopus	6 (9)	17 (41)	3 (7)	10 (22)	6 (11)	21 (49)	15 (27)	48 (112)
Pitymys pinetorum	0 (0)	1 (5)	0 (0)	4 (8)	0 (0)	0 (1)	0 (0)	5 (14)
Mus musculus	0 (0)	0 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (1)
Tamias striatus	0 (0)	8 (23)	0 (0)	2 (6)	0 (0)	4 (8)	0 (0)	14 (37)
Sciurus hudsonicus	0 (0)	0 (2)	0 (0)	0 (0)	0 (0)	1 (1)	0 (0)	1 (3)
Glaucomys volans	0 (0)	2 (4)	0 (0)	2 (5)	0 (0)	2 (5)	0 (0)	6 (14)

Trapping-times: Pine-Ridge, 22 days in 1933, 18 in 1935; Pine-Seedling, 17 days in 1933, 16 in 1935; Hemlock, 11 days in 1933, 17 in 1935. Average for all quadrats: 16⅔ days in 1933, 17 in 1935.

TABLE IX. Populations-per-acre in different Forest Communities on Little Mountain, Geauga and Lake Counties, Ohio. Figures Based on the 3-Day Yields of 150-Foot Grids and their Central 50-Foot Quadrats.

QUADRAT and YEAR	Blarina	Sorex fumeus	Parascalops	Tamias	Glaucomys	Sciurus huds.	Peromyscus leuc.	Microtus	Pitymys	Synaptomys	Mus	Napaeozapus
PINE RIDGE												
Grid												
1933	4	..	..	..	..	..	12	..	..	..	..	..
1935	14	2	2	16	4	..	34	..	..	..	..	..
1936	18	4	4	2	..	..	..	..	4	..	..	..
1937	20	16	..	..	..	..	10	..	..	..	..	..
1938	22	12	..	2	4	..	10	..	4	..	..	..
1939	26	18	4	2	..	..	..	..	..	..	..	..
Center												
1933	..	..	..	..	..	..	..	..	..	..	..	..
1935	17	..	..	..	..	..	17	..	..	..	..	..
1936	..	..	..	..	..	..	..	..	..	..	..	..
1937	17	..	..	..	..	..	17	..	..	..	..	..
1938	..	17	..	..	..	..	..	..	..	..	..	..
1939	..	..	..	..	..	..	..	..	..	..	..	..
PINE SEEDLING												
Grid												
1933	4	4	..	..	..	..	6	..	..	..	..	..
1935	28	4	..	4	4	..	20	..	8	..	..	..
Center												
1933	..	..	..	..	..	..	..	..	..	..	..	..
1935	17	..	..	..	..	..	..	..	..	..	..	..
HEMLOCK												
Grid												
1933	6	8	..	..	..	..	12	..	..	..	..	..
1935	20	8	..	8	4	2	42	..	..	..	..	..
1938	8	12	..	4	..	2	16	..	..	..	..	..
1939	12	18	..	2	..	..	4	..	..	..	2	..
Center												
1933	..	..	..	..	..	..	34	..	..	..	..	..
1935	..	..	..	..	..	..	17	..	..	..	..	..
1938	17	..	..	..	..	..	..	..	..	..	..	..
1939	17	17	..	..	..	..	..	..	..	..	..	..
DALEY'S FIELD												
Grid												
1935	24	2	4	8	2	2	34	4	6	4	..	..
1936	12	..	24	10	..	..	..	..	..	..	..	..
1937	34	..	12	2	4	..	18	..	..	..	..	2
Center												
1936	17	..	..	..	..	..	..	..	..	..	..	..
1937	..	..	..	..	..	..	51	..	..	..	..	..

Quadrat and Year	Blarina	Sorex fumeus	Parascalops	Tamias	Glaucomys	Sciurus huds.	Peromyscus leuc.	Microtus	Pitymys	Synaptomys	Mus	Napaeozapus
Beech-Cucumber												
Grid												
1935	38	8	2	6	4	4	22	..	4	..	..	..
1936	32	16	6	4	..	..	4	..	..	..	..	..
1937	24	24	4	2	..	..	16	..	..	..	..	..
1938	30	58	8	4	4	..	22	..	..	..	..	..
1939	22	32	4	..	..	..	2	..	..	..	..	..
Center												
1935	..	..	17	..	..	..	17	..	..	..	..	..
1936	..	..	..	..	..	..	..	..	..	..	..	..
1937	..	17	..	..	..	..	34	..	..	..	..	..
1938	..	85	..	..	..	..	17	..	..	..	..	..
1939	..	..	..	..	..	..	..	..	..	..	..	..
Averages, All Quadrats												
Grid												
1933	4.7	4.0	P	0.4	P	P	9.7	..	P	..	P	P
(1934)*	(10.0)	(4.5)	(3)	1.9	(P)	0.5	(15)	..	(1.5)	..	(P)	..
1935	24.8	4.8	2.6	8.4	3.6	3.6	30.4	0.8	4.5	0.8	P	..
1936	15.2	6.3	4.7	P	P	P	3.3	P	1.3	..	..	..
1937	25.0	12.7	4.7	P	P	P	14.7	..	P	..	..	0.6
1938	20.0	27.3**	2.7	3.3	2.7	0.7	16.0***	..	1.3	P	P	..
1939	20.0	22.7	2.7	1.3	..	P	2.0	..	P	..	0.7	..
Center												
1933	5.6	5.6	..	..	..	..	17.0	..	..	..	..	..
1935	****8.5	..	..	..	..	..	12.7	..	..	..	..	..
1936	17.0	..	..	..	..	..	5.6	..	..	..	..	..
1937	5.6	5.6	..	..	..	..	34.0	..	..	..	..	..
1938	5.6	34.0	..	..	..	..	5.6	..	..	..	..	..
1939	5.6	5.6	..	..	..	..	..	..	..	..	..	..

*Figures for 1934 are hypothetical when parenthesized, and are based on yields at other stations. Otherwise the 1934 figures are based on spot censi.

**Peak Population not duplicated at other stations than Little Mountain. Elsewhere, 1937 was peak year for *Sorex fumeus*.

***Peak much lower than elsewhere, due to failure of key food crop in 1937 (acorns). At other forest stations, Beech and Sugar Maple predominate; they are rare on Little Mountain.

****Does not include figures for Daley's Field, which was not a grid in this year.

P Present, but in populations too low to be measured by only three or four quadrats.

Key to Forest Communities: Pine Ridge, *Pinus-Acer* Facies of *Pinus-Tsuga* Association; Pine Seedling, *Quercus-Castanea* Association with understory of young white pines; Daley's Field, a Woods-Edge Community (*Acer-Populus Associes*); Beech-Cucumber, *Fagus-Magnolia* Facies of *Acer-Fagus* Association. See p. 36.

TABLE X. Check-list of the Mammals Mentioned in This Report. Names for the most part are taken from "List of the Mammals of Ohio," Ohio State Mus. Mimeographed Bull. No. 1, by E. S. Thomas and B. P. Bole, Jr., February, 1938.

Common or Virginia Opossum	*Didelphis virginiana virginiana* Kerr
Smoky Shrew	*Sorex fumeus fumeus* Miller
Canada or Masked Shrew	*Sorex cinereus cinereus* Kerr
Thompson Pigmy Shrew	*Microsorex hoyi thompsoni* (Baird)
Common Short-tailed Shrew	*Blarina brevicauda brevicauda* (Say)
Old-field Shrew or Little Short-tailed Shrew	*Cryptotis parva* (Say)
Prairie Mole	*Scalopus aquaticus machrinus* (Rafinesque)
Hairy-tailed Mole	*Parascalops breweri* (Bachman)
Star-nosed Mole	*Condylura cristata* (Linnaeus)
Eastern or Common Raccoon	*Procyon lotor lotor* (Linnaeus)
Eastern Skunk	*Mephitis mephitis nigra* (Peale and Beauvois)
Allegheny Least Weasel	*Mustela rixosa allegheniensis* (Rhoads)
New York Weasel	*Mustela frenata noveboracensis* (Emmons)
Eastern Red Fox	*Vulpes fulva fulva* (Desmarest)
	(This species and the next are not distinguished in the text)
Eastern Gray Fox	*Urocyon cinereoargenteus cinereogenteus* (Schreber)
Middle-Eastern Chipmunk	*Tamias striatus fisheri* Howell
	(In a few cases the form *lysteri* is also included under *Tamias*)
Middle-Eastern Red Squirrel	*Sciurus hudsonicus loquax* Bangs
	(Unless otherwise specified, all records of *Sciurus* refer to this form)
Northern Gray Squirrel	*Sciurus carolinensis leucotis* (Gapper)
Middle-Western Fox Squirrel	*Sciurus niger rufiventer* Geoffroy
Middle-Eastern Flying Squirrel	*Glaucomys volans volans* (Linnaeus)
Prairie White-footed Mouse	*Peromyscus maniculatus bairdi* (Hoy and Kennicott)
Northern Deer Mouse	*Peromyscus leucopus noveboracensis* (Fischer)
Stone's Lemming or Lemming-Vole	*Synaptomys cooperi stonei* Rhoads
Eastern Meadow-Mouse or Field-Vole	*Microtus pennsylvanicus pennsylvanicus* (Ord)
Mole Pine-Mouse or Pine-Vole	*Pitymys pinetorum scalopsoides* (Audubon and Bachman)
Common House Mouse	*Mus musculus musculus* Linnaeus
Norway or Barn Rat	*Rattus norvegicus* (Erxleben)
Hudson Bay Jumping Mouse	*Zapus hudsonius hudsonius* (Zimmerman)
Woodland Jumping Mouse	*Napaeozapus insignis insignis* (Miller)
Eastern Cottontail Rabbit	*Sylvilagus floridanus mearnsi* Allen

EXPERIMENTS WITH QUADRATS INSULATED BY SHEET-IRON

The method of enclosing quadrats with galvanized iron sheeting to exclude drift was first attempted with the aid of Dr. S. C. Kendeigh at the Baldwin Bird Research Laboratory in August, 1934. A 50-foot quadrat was selected, and a trench dug completely around its borders to a depth of from six to ten inches. Galvanized iron sheeting three feet in height was set in these trenches, which were purposely dug below the level of mole and pine-mouse runways. The sheeting was supported by being nailed to small posts that did not reach the top of the sheeting. The sheeting was nailed to inward side of the posts so that any mammal desiring to leave the quadrat could not jump up to the tops of them or climb them. Previously Dr. Kendeigh had determined the height to which deer mice (*Peromyscus leucopus*) could jump. This he accomplished by placing live mice in garbage pails whose sides were one foot high and two feet high respectively. Two placed in a one-foot container escaped at once. Of ten animals, both adults and young, placed in a two-foot container, only one succeeded in escaping and apparently did so by running centrifugally around the rusty walls of the can until the top was reached. The highest jump made by excited mice did not exceed eighteen inches. Thus it was believed that the additional nine or ten inches afforded by the iron sheeting constituted defense against drift.

After the sheeting was installed, the trenches were refilled and the ground about the sheeting was tamped down hard, to make excavation as difficult as possible. Finally collars of tin sheeting were placed about every tree inside the quadrat and all those immediately outside, to prevent species of arboreal tendencies, such as *Tamias* and *Peromyscus*, from entering or leaving by this route. Traps were then set throughout the quadrat and about the bases of each post supporting the sheet-iron, while a few were placed about the bases of nearby trees unprotected by sheeting.

The result of all this elaborate preparation was exactly zero in 1934. It seemed quite possible to the writer that no small mammals would stay in a 50-foot area while posts were being pounded and sheet-iron rattled for the better part of a day. However, the experiment seemed well worth trying, and it must be said that there was virtually no recent small mammal sign whatever in the quadrat.

The attempt was resumed in a different place next year, complete in every detail. It should be remembered that the purpose of the sheet-iron was to exclude drift and that therefore, if the sheeting shut off all runways, the total yield should give the exact population of the 50-foot unit. The traps placed outside the quadrat along the bases of the posts and trees might be expected to catch the drift animals that would otherwise have been taken in the quadrat in the absence of the sheeting. Some idea of the proportion of drift to inhabitants should thus be obtained, realizing that any animal happening to be in the quadrats at the time they are set up is considered "resident".

From Table XI, it will be seen that just one *Blarina* was taken inside the sheeting, on the third day of trapping. During the five days that the traps were kept working, four *Blarina*, four *Peromyscus*, and one *Pitymys* approached the quadrat and were captured outside the sheeting and in its immediate vicinity, all these exterior traps being less than ten feet from it. Of these nine animals, six were taken in the first three days and two on the last two. It is possible that some of these were animals dispossessed during the installation of the metal.

One *Blarina* per 50-foot quadrat indicates a density of 16 or 17 individuals per acre, rather lower than the average of figures obtained from other sources. The fact that no other species whatever were taken in the quadrat seemed to suggest again that the animals might have left due to the disturbance attendant upon the installation of the sheeting. It was therefore decided to leave the quadrat as it was except for removing four eight-foot sections of iron, one on each side, to permit animals to go in and out. It was decided to allow the quadrat to become "naturalized" in this way for a few months, and then to return and quickly install the few remaining sections which would entail a minimum of disturbance.

Accordingly, in November, 1935, Mr. Moulthrop returned to the quadrat and installed the four missing sections. There had been a fall of leaves since the summer work, and conditions in general were more favorable for small mammals. The trapping was complicated by several falls of snow, which covered the traps to a depth of six inches on one occasion. The traps were run from November 27th to December 5th, inclusive. During this time no less than 13 *Blarina* were taken inside the quadrat; 2 *Parascalops* and 2 *Pitymys* also were captured before all signs of activity ceased. In the peripheral traps on the outside of the sheeting, the "drift" consisted of 8 *Peromyscus* in the same length of time. The astonishing yield of shrews came almost entirely in the first five days, the trapping on the second, third, and fourth days having been almost entirely stopped by snow and hard rains. Ten of the *Blarina* and 2 *Pitymys* were taken within three days of actual trapping. Both moles eluded capture until the seventh and ninth days of trapping, and Mr. Moulthrop believes that a third animal was left uncaught.

These results are not surprising, in consideration of the inability of 50-foot quadrats to give a fair sample of the population of a large tract of woodland or field. The *Blarina* yield would give a population of 217 animals to the acre, a concentration highly unlikely in view of the summer's trapping records. Furthermore, no *Blarina* were taken outside the quadrat in November. This seemed to mean that the number of shrews within the quadrat was for some reason unusually high, perhaps because of the insect concentration, which was very conspicuous as compared to the ground outside the quadrat.

It may be suspected that the sheeting insulation "leaked," and that the *Blarina* were really drifting in under it. All that can be said in answer to this is that not a sign of tunneling under the sheeting was discovered either in 1934 or in 1935. By 1936, however, there was definite evidence that considerable tunneling had taken place under the sheeting, and it was reset. In addition to the animals captured inside the quadrat (see Table XI), several *Peromyscus* were captured outside the iron sheeting, as was the case in 1935. In 1937 further evidence of leakage was found and the tunnels were plugged. The results obtained in these two years in general seem to corroborate a deduction that was obvious as early as the fall of 1935 — that the metal quadrats acted as a trap of sorts for insectivores, especially for *Blarina*. It is difficult to see just why a shrew should be less able to find its way out of one of these quadrats (open in four small sections) than into it, but such seemed to be the case, to judge from the records. The explanation lies in the fact that moles plough up

TABLE XI. Yields of Control and Insulated Quadrats Compared (50-Foot Size). Estimates-per-acre, based on 3-Day Yields in the Controls and on Total Yields in the Insulated Units.

	1935						1936						1937*					
	Control			Insulated			Control			Insulated			Control			Insulated		
Species	3-Day Yield	Total Yield	Est. per Acre	3-Day Yield	Total Yield	Est. per Acre	3-Day Yield	Total Yield	Est. per Acre	3-Day Yield	Total Yield	Est. per Acre	3-Day Yield	Total Yield	Est. per Acre	3-Day Yield	Total Yield	Est. per Acre
Blarina	1	3	17	10	13	227	2	3	34	6	9	152	1	1	17	2	8	170
Peromyscus	1	1	17	0	0	0	2	2	34	0	0	0	3	5	51	1	2	34
Pitymys	0	1	0	2	2	34	0	0	0	0	0	0	0	2	0	0	0	0
Parascalops	0	0	0	0	3	51	0	0	0	1	2	34	0	1**	17**	0	0	0
Sorex fumeus	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0

*1937 trapping done by Drs. S. C. Kendeigh and R. A. Huggins.

**Based on the record of workings of one animal.

the ground inside the metal units to an extent unapproached outside the quadrat, form networks of runways three or four layers deep, and thereby greatly increase the foraging terrain not only for *Blarina*, but for soil invertebrates as well.

I believe that what was said about center-quadrats will also apply to the metal quadrats — namely, that estimates for a large area should certainly be based on several of them and not on just one. In this case the expense of the metal, the manual labor involved, and the length of time it takes for the quadrat to become repopulated after the initial installation of the sheeting, renders the method impracticable. If, as seems to be the case, the insulated quadrats trap certain species and thereby create unusually favorable soil conditions for still others, the insulated quadrat method would appear to be the most inaccurate source of information on populations, giving a faulty picture of not only the actual, but also the relative abundance of the species of any given small mammal fauna.

THE 100-FOOT QUADRAT, 0.229 ACRE

By the end of the summer of 1938 a total of seventy-eight 150-foot quadrats had been operated since the beginning of the work. In the course of all this a fundamental practical weakness in this size of quadrat was made clearly evident: the 150-foot quadrat must be set by at least two men. One man cannot properly set one of these quadrats in the eastern United States in less than a full day's time; and a serious error appears in the data if he takes this long. If he sets half of a quadrat in the morning and the other half in the afternoon, he will have caught several animals, under normal circumstances, before the quadrat is completely set. If, as is customary, the first day's yield is considered to be that of the first night following trap-setting, he is "padding" his results with the yield of part of an extra day. If he counts his trap-setting day as his first, he is obviously getting little service from the part of the quadrat that he last set. In short, all of his quadrat does not work for a comparable length of time, which is not to be desired. It is impractical to try to end the trapping of the two halves of the quadrat at different times, i. e. as they were set. Consequently, no less than two men should be used to set a 150-foot unit. They can finish it in half a day. They also tend to keep the movement of the small mammals at a minimum during trap-setting. There is usually very little activity around the trapper for a radius of 50 feet during trap-setting, and two workers virtually cover a 150-foot quadrat in this way. But even when two or three men are used, some captures will often be made during the trap-setting period.

In view of the fact that two workers are not always available, there is a definite need for a "one-man" quadrat. The 100-foot quadrat largely supplies this need. During 1938 the writer instructed one of the Museum's field-workers, Mr. Winston Jesseman, in the use of these units. Mr. Jesseman operated six of them in 1938, and two in 1939. The writer operated one in 1936 and two in 1938, all three in New England.

As might be expected, the population estimates based on the yields from these quadrats (which have to be multiplied by a factor of 4.35 in order to give figures per acre) run noticeably higher than the 150-foot estimates, and much lower than the estimates based on yields from smaller quadrats. These facts, as expressed by the line representing the average daily yield, may be observed in Fig. 2. The yields after the third day in this series of quadrats are undoubtedly lower than they would have been if a series of length comparable to that of the 150-foot units had been used.

During 1938 most of the open-field 100-foot quadrats yielded population figures for *Microtus* of over 50 per acre, which is considerably higher than the average for the year for the same species as deduced from a large series of 150-foot units. Only three times since 1933 have the larger units yielded figures higher than 50 per acre for this species. Similarly, *Peromyscus leucopus* populations appeared to be about 40 per acre in 1938 on the basis of three-day 100-foot yields as opposed to the 150-foot figures, in the same ecological environment (climax forests), of 22.2.

While the error would thus appear to be considerable, it is far smaller than that incorporated in the data of smaller quadrats, and under certain circumstances this may be compensated for by the greater ease in operation that this quadrat affords in comparison to the 150-foot unit. One man *can* operate it, but wherever it is possible, two or three men should operate a 150-foot quadrat instead. The relative efficiency of the 100-foot quadrat may be visualized in Fig. 1.

CIRCULAR UNITS

Dr. S. C. Kendeigh and his students at the University of Illinois have used half-acre units of circular outline, corresponding to the 150-foot units used by the writer. A circular area with a radius of 83.2 feet that he trapped in an Illinois oak-hickory woods in November 1938, gave populations for *Peromyscus leucopus* of 16 per acre (40 per hectare), 6 per acre for *Pitymys*, 2 for *Blarina*, and 4 for *Glaucomys*. These figures are far lower than the averages for the same species in the same year in Ohio, but well in line with some other Illinois figures at hand. Unfortunately, the writer has no data that is strictly comparable to this, but a 100-foot quadrat operated by Mr. Jesseman in a swamp forest community at Bloomington, Illinois, in the same year, gave figures of 17 per acre for *Peromyscus* and 26 per acre for *Blarina*. These are well below the Ohio figures for the same habitat as furnished by 100-foot quadrats.

Dr. Kendeigh prefers the half-acre circular unit to the 150-foot quadrat because its perimeter, and hence its edge-exposure to drift, is 67 feet less and its area exactly a half-acre. The fact that this museum's youthful assistants invariably prefer to trap in the corner 50-foot quadrats of each grid, and that the corner quadrats show consistently higher yields than the others after the second day of trapping, indicates that Dr. Kendeigh's preference is very well founded. However, the difference in the yield-behavior of the various parts of a 150-foot quadrat only becomes evident after the initial three-day period is nearly over. If the three-day limit is adopted, there is no apparent difference in the yields of the two types of trapping areas in the comparative data so far accumulated by the writer (in 1939, three circular units operated, two at Aurora Pond, Ohio, one at the Holden Arboretum). However, there is no doubt that the half-acre circular unit is preferable, where it can be practically operated.

In open fields the laying out of a circular unit is an easy matter — far easier than laying out a grid or an unsubdivided 150-foot quadrat. In thorn scrub it may take ten times as long as to run the grid. The writer believes that the circular unit should be used wherever a worker can describe a perfect circle about a central point and at the same time lay a trail of string behind him. Where this cannot be done, the circular unit can still be established by running at least four cross-lines outwards from the center, but the inaccuracy of the circle thus described vitiates wholly or in part the advantages of the circle over the 150-foot square unit. As the latter is almost always easier to run in forested country or in heavy brush, it should be used in most such cases.

GENERAL CONSIDERATIONS

An attempt to apply Raunkaier's Law of Frequence to the small mammal populations of northeastern Ohio upland forests appears in Table XII. The average percentage of frequence given for each species is that over a five-year period beginning in 1935. In compiling the data it was noted that the cyclical species usually changed their group classification from year to year, and that the Raunkaier formula failed to hold for each season. It will be seen, however, that the averaged figures closely approximate the Raunkaier formula, and seem to indicate that the law holds good among mammals as well as plants and invertebrates. Close inspection of the data reveals that the one species falling in Group D (60-80%) is *Blarina brevicauda* and that a gain of but 2/10 of a point would cause its classification in Group E. This would make the figures even more similar to the Raunkaier formula. Similarly, a gain of one point would take *Tamias* from Group A into Group B. It will also be seen that at least four of the species in Group A (*Synaptomys*, *Microtus*, *Mus*, and *Zapus*) are not strictly animals of the upland forest and are not represented by any more than one or two specimens per season; if these are deleted, the forest frequences conform still more strictly.

Fifty-foot quadrats (in all cases components of grids) are used here instead of the larger units, as the problem at hand is the relative rather than the actual abundance, and small quadrats seem to be as useful as the large. Actually, a 150-foot unit almost invariably is large enough to include most if not all of the small mammal species of an Ohio woodland. Thus, the smaller quadrat seems actually preferable to the larger for the purpose of testing the Raunkaier formula.

It is of interest to note that in Table XII we see a recapitulation of the periodic population maxima that we found in the other tables. In this case, however, we are dealing with the distribution of the species rather than population density. In general, it would seem that widespread dispersal goes hand in hand with high density of population. That the former may sometimes occur before the attainment of the latter is indicated by the figures for *Peromyscus leucopus*. Thus, the frequence of this species was almost as high in 1937 as in the ensuing peak year 1938; but if we turn to Table XIV, we find that the 1937 populations were not nearly so great as those of 1938.

It is often asked whether the use of quadrats in counting motile organisms is justifiable. The method was originally devised for counting stationary living things like plants. The only way in which an animal such as a small mammal may be considered stationary is to think of it in terms of its "home range" in the sense suggested by Seton (1909). Insofar as its home range is concerned small mammals may be considered as fixed organisms, at least during the breeding period, if not during most of the year. If a quadrat is used that is large enough to include several home ranges, we are obviously removing "units", in a sense fixed units, in the course of trapping, and we can get a close approximation to the actual number of individuals in the area. It is equally obvious that if a small enough quadrat is used we are dealing with a part of one or more-home ranges. Eventually the animal, whose home-range includes the small quadrat, is captured, and forms part of the basis for estimating the population of a larger area than the quadrat. This population is based, however, on the yield for the small quadrat, and five animals for each 100 square meters gives a very much larger population figure per acre or hectare than one based on five animals per area ten times as great, although the larger area may more nearly approximate the actual home-ranges of the five animals than the smaller area. The accompanying graph, Fig. 1, shows quadrats of different sizes yielding the same number of animals apiece, and how the estimate per large area, based on this yield, increases as the size of the quadrat decreases. The time element is here considered constant for all sizes of quadrats.

From the above, it is evident that the smaller the quadrat, the larger is its yield in proportion to its area. Figures obtained in the

TABLE XII. Climax Forest Percentages of Frequence of Small Mammals in the Cleveland Region, 1935-1939, and their Distribution into Groups according to Raunkaier's Law. Figures give Frequences derived from Records of Approximately one hundred 50-Foot Quadrats (Components of Grids) in Each Year.

YEAR	Blarina	Sorex fumeus	Sorex cinereus	Parascalops	Condylura	Tamias	Glaucomys	Sciurus huds.	Sciurus car.	Peromyscus leuc.	Pitymys	Synaptomys	Microtus	Mus	Zapus	Napaeozapus	Sylvilagus
1935	92.6	25.9	....	11.1	....	46.4	31.4	22.2	1.8	90.7	31.4	....	....	1.8	....	....	....
1936	77.7	24.0	1.8	35.1	5.6	27.8	3.7	11.1	....	16.6	3.7	....	1.8	....	....	3.7	1.8
1937	82.2	33.3	4.4	28.8	6.7	6.7	6.7	....	....	64.4	2.2	....	....	2.2	2.2	11.0	....
1938	81.8	28.6	0.7	5.6	1.4	7.7	9.1	0.7	....	70.6	14.0	0.7	1.4	1.4	....	....	....
1939	64.8	42.5	0.9	31.4	1.8	7.3	0.9	....	....	20.3	6.4	....	....	1.8	0.9	2.7	0.9
Average, All Years	79.8	30.8	1.5	22.4	3.1	19.1	10.3	6.8	0.3	52.5	11.5	0.1	0.6	1.4	0.6	3.4	0.5

Frequence	A	B	C	D	E
Percentage Groups	0–20%	20–40%	40–60%	60–80%	80–100%
Number of Climax Forest Frequences, per group	13	2	1	1	0
Ratio of Frequence Dispersion, According to Raunkaier's Law	5	2	1	0	1

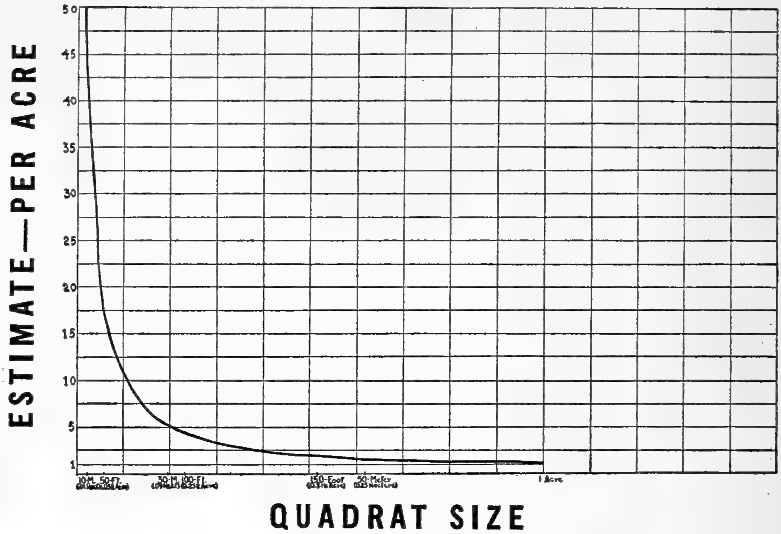

Fig. 1. Estimate-per-acre Plotted Against Quadrat Size, Yield Constant (1 animal per quadrat).

field bear out this theorem, particularly when estimates are based on total yield rather than on a limited yield after two or three days. Figure 1 indicates that there is an enormous error in estimates based on the yield from single 50-foot quadrats as compared to the "large" quadrats of 150 feet. For instance, a yield of five animals for a 50-foot quadrat gives a population of 87 per acre; for a 150-foot unit, between 9 and 10; while a yield of five per 10-meter unit gives over 200 per acre! Actually, however, it is not meant to imply that other things being equal a small quadrat will give the same yield as a large area. Over a long period of trapping, the yield of a small quadrat is to the yield of a large one more nearly as the sum of the lengths of the sides of the small one are to the sides of the large, rather than as the area of the small is to the area of the large (Table XIII). The longer the traps are kept in operation the truer this becomes, as indrifting animals which enter by the four sides of the quadrat, become a larger and larger percentage of the total. Drift is never entirely eliminated in an open quadrat unprotected by a shelter-belt of some sort, but in proportion to the "resident" population, it becomes larger and larger as the area of the quadrat is made smaller, since the length of the perimeter of the quadrat decreases more slowly than the area enclosed. In using "total yields" with small quadrats, we are therefore confronted with two errors, the one arising from drift which cannot be legitimately considered part of the resident population, and the other from the fact that this error is greatly enlarged when it is a component of the figure per quadrat area used in estimating the population of a much larger unit.

The full import of drift in a small quadrat, even when the yield for a single night is considered, may be made obvious by the concept of a stump in the central quadrat of a grid of nine 50-foot units. Let this be theoretically the home of five deer mice (*Peromyscus*

Table XIII. Drift Rates of 10-Meter and 150-Foot Quadrats Compared to Each Other and to Certain Basic Quadrat Relationships.

A.	Sum of the Length of the Sides of a 10-Meter Quadrat	131.4 Ft.
B.	Sum of the Lengths of the Sides of a 150-Foot Quadrat	600.0 Ft.
C.	Ratio of A to B	1:4.565
D.	Ratio of the Area of a 10-Meter Quadrat (1076.3 Sq. Ft.) to that of a 150-Foot Quadrat (22,500 Sq. Ft.)	1:20.905
E.	Average Daily Yield per Quadrat from four 10-Meter Quadrats from the 4th to the 9th Day of trapping in 1935	1.2
F.	Average Daily Yield per Quadrat from six 150-Foot Quadrats from the 4th to the 9th Day of Trapping in 1935	5.8
G.	Ratio of E to F	1:4.83
H.	Average Daily Yield per Quadrat from four 10-Meter Quadrats from the 4th to the 7th Day of Trapping in 1936	0.25
I.	Average Daily Yield per Quadrat from twenty-three 150-Foot Quadrats from the 4th to the 7th Day of Trapping in 1936	2.19
J.	Ratio of H to I	1:8.76
K.	Ratio if the Yields During the First Six Days instead of the Last Six are used in Computing the Daily Average per Quadrat of the 10-Meter Series, 1935	1:404
L.	Ratio if the Yields During the First Four Days are used instead of Those During the last Four in Computing the Daily Average per Quadrat of the 10-Meter Series, 1936	1:4.38

leucopus noveboracensis). Let us consider that traps are set in only one 50-foot corner quadrat, and that the large quadrat constitutes the major part of the home range of the colony.* Eventually all five will wander into the corner quadrat and will be captured. This may happen in the first night and experience has shown that this is usually the case with this species in favorable weather. If, on the other hand, traps are spread over all of the nine quadrats, the chances are greatly in favor of the five being caught elsewhere in the large quadrat, perhaps one animal in each of five of the nine. Whatever the arrangement, we now have five animals caught in approximately half an acre, while in the case of the corner quadrat we have five animals caught in only 1/17 of an acre. If there are two flying squirrels (*Glaucomys volans volans*) in the district, they are as apt to be caught in the 50-foot unit, if it alone is trapped, as in the larger one if traps are set over the whole area. But the interpretation of the yield would be quite different.

Chitty (1937, pp. 50-52) emphasizes the fact that not all small mammal species are equally wide-ranging or sedentary in their habits, and that a trapline or quadrat may draw some species from a much larger area than it does others in the same length of time. It is all the more important, therefore, to use large quadrats from which the resident population can be removed at once through the medium of a large number of traps. Unless the traps are numerous enough to cut all channels of movement within the area trapped, the resident population may not be removed before the yields become seriously enlarged through drift, and this drift may consist largely of active, widely-ranging species. The impression is then made that these species are relatively more numerous in the habitat than is actually the case. Obviously, population estimates based on total yields are subject to an error from this source in addition to the others already mentioned.

The determination of the exact time after which the yield from a quadrat can be said to be of drift only is still a matter of some conjecture, but evidence is presented on the following pages in support of an arbitrary three-day limit. Until the entire small mammal

* Murie and Murie (1931, pp. 207-8) indicate that the home-range of *Peromyscus maniculatus artemisiae*, a related form, is in the vicinity of 100-yards in diameter.

fauna of a given area is rounded up with live-traps, marked, set free, and then recaptured and the details of their movements carefully noted, the problem is not likely to be satisfactorily solved. A host of American, English and Russian workers are at present engaged in research that has already added much to our knowledge of the problem. Certain species, however, are difficult to capture in live-traps, notably, among the species considered in this report, the insectivores and the lemming *Synaptomys cooperi stonei*.

It is the consensus of opinion among most mammalogists that for most cases the great majority of mammals on a trapline are removed in three nights. Townsend (1935), Hamilton (1937), and Dice (1938), used three-day limits. Elton, et al. (1935) based the estimates for their quadrats on a four-day yield. The writer feels that if large quadrats and a sufficiently large number of traps are used, the four-day limit is much too long.

The accompanying figures (Nos. 2 and 3) are indicative of the fact that there is usually a sharp decline in the daily total of captures until the third day of trapping, after which the rate of decline is much more gradual. It will also be seen that the general level of the line for any given year as compared to those of other years is an indication of the "population pressure" during that year, as evidenced by the rate of drift. A similarity in the rate of decline from year to year may also be noted, although the rate for 1933 (Fig. 3) is irregular and resembles that of the smaller quadrats (Fig. 2). Had a larger number of quadrats been used there is every likelihood that the irregularities would have disappeared. The peak occurrence on the fourth day of the 1938 trapping is an irregularity that must for the moment remain unexplained, as a large number of the 1938 quadrats contributed to the peak, and it cannot be explained on the basis of too few quadrats having been used or on any single atmospheric condition. In the average line for all five years such peaks vanish. The similarity of decline, emphasized in the average line, indicates a more or less constantly decreasing rate of drift, although the zero rate is probably never attained if a sufficient number of units are used. We may call this rate of decline after the third day "drift curve" and we note at once that in the absence of a well marked initial peak in the case of the 10-meter units (Fig. 2), the entire series of early yields seem to resemble a

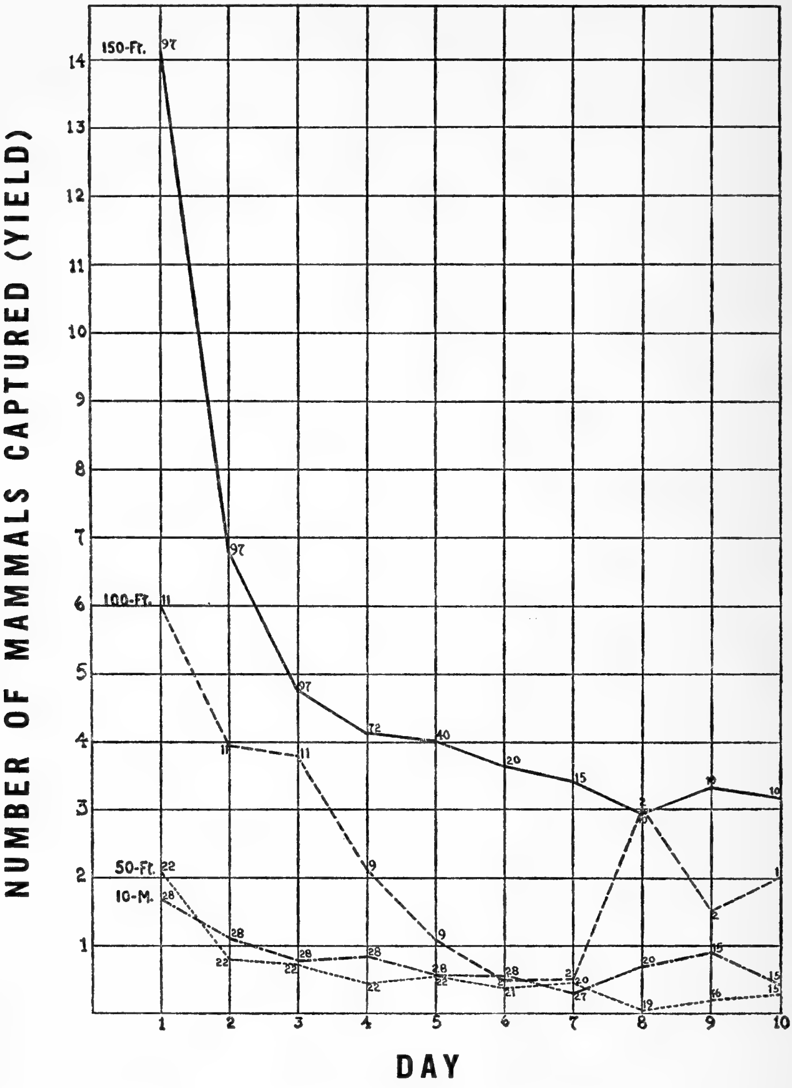

Fig. 2. Average Daily Yields of Small Mammals from Four Different Sizes of Quadrats Operated from 1932-39, Inclusive. At each point are figures giving the number of quadrats in the Average.

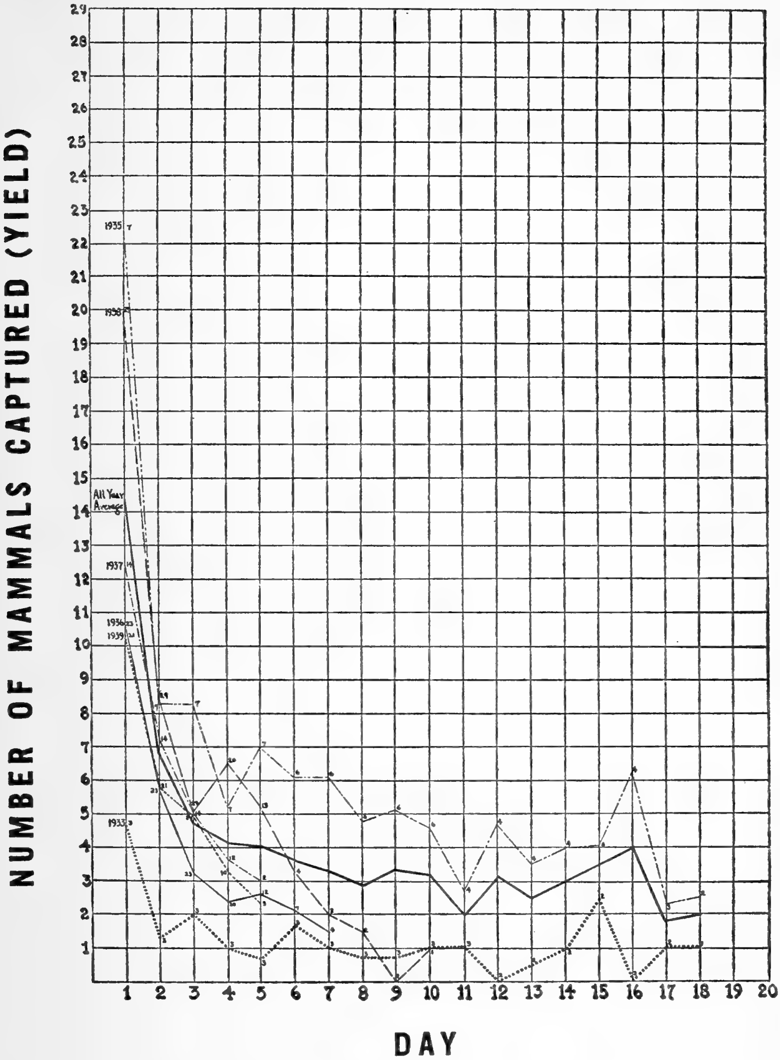

Fig. 3. Average Daily Yields from 150-Foot Quadrats in Six Different Years, with the Average Daily Yield per Quadrat for All Years. At each Point are numbers giving the number of quadrats in the Average at that point.

drift curve. On theoretical grounds, it is legitimate to assume that a 10-meter quadrat's yield would consist largely of drift owing to its small area, and the nature of the drift curves seems to support this. Further support is provided by the last item of Table XIII, where a substitution of data obtained on the first six days of trapping with 10-meter quadrats, for the data obtained from the fourth to ninth days (last six days) actually makes the ratio of the small and large quadrat yields more nearly as 1:4.5. This ratio, mentioned in Table XIII, can obviously hold only if there is some drift, i. e., a regular rate of influx. If populations are so low in any given locality that there is virtually no drift, as was the case at North Chagrin in ebb-cycle years (1933, 1936, 1939), the ratio breaks down. The weakness of the data given in Table XIII lies in the fact that all of the 10-meter quadrats were operated at but one place, whereas the 150-foot series covered a large number of localities and hence more nearly represent an average set of data. Had more 10-meter units been used, it would doubtless have become apparent that even with this size of quadrat the drift figure of zero would never be reached, and the ratio would hold.

While it may seem possible that all the residents of a quadrat might not be captured until after a three-day period, it must be remembered that some drift is occurring from the onset of trapping, and that in all probability this more than compensates for the residents uncaptured at the close of the three-day period (cf the data obtained from insulated quadrats, p. 53, Table XII). Whether this is true or not depends largely upon the thoroughness with which the quadrat is trapped.

In compiling the averages from the daily yields of the various quadrats, it became quite apparent that weather conditions greatly influence the wandering of insectivores, particularly shrews, and that a cool, humid night preceding or following rainy weather caused a marked increase in the rate of drift of these animals, while unusually hot and dry nights caused a sharp decline. Since *Blarina* is the most abundant of Ohio's mammals in nearly all habitats, it is obvious that for any one quadrat rather spectacular peaks may occur in the daily records far beyond the three-day limit, although in normal years these do not usually reach the proportions of the third or second-day yields. The sixth day peak in the 1933 record was caused by a cool humid night preceding a light rain in the case of two of the three quadrats comprising the record, and was made up of a sudden yield of *Blarina* and *Sorex fumeus*. Where large numbers of quadrats are used, however, these peaks are usually leveled off and become lost, although in 1938 a well-marked peak occurred on the fourth day (See Fig. 3). Even here, however, the "peak" figures are inconsequential in comparison to the enormous first-day yield, and the peak disappears in the line representing the average daily yields over a six-year period.

Admittedly the selection of a three-day limit as a standard, as is done in this paper, is somewhat arbitrary. All that can be said is that the characteristic drift curve becomes pronounced either at or before the third-day, and rarely if ever after it, and that for this reason even a two-day limit seems to be more accurate than the four-day one used by Elton, at least for all the districts in which the writer has trapped. It might be added that 150-foot quadrats used in California in 1934 and in Maine in 1936 supported the data here to be given. The western quadrats will be treated in another paper.

Truly accurate data on the length of time necessary to trap the entire resident population of an area can admittedly be obtained only by the long use of quadrats thoroughly insulated from drift. The anomalous character of the results of preliminary experiments with insulated quadrats has already been indicated.

Dice (1938, p. 126) states that it is unnecessary to kill the animals taken in the course of quadrat research. The writer will be unable to agree with this statement until some satisfactory method is devised for the taking alive of shrews and moles, which often comprise nearly two-thirds of the small mammal population in Ohio. Live-trapping for *Blarina*, *Parascalops*, and *Condylura* is as yet an unfathomed problem, to the writer's knowledge, and if accurate data are required on a small mammal fauna these species must be taken.

How close together may two quadrats be placed? The answer is that in open fields they may be placed at least as close as their own diameters. Three quadrats were operated on the Holden Arboretum in 1938 along the hawthorn-covered banks of a shallow ravine. These were placed in a row up the draw, the second but 50 feet from the first, and the third about 150 feet from the second. All three gave yields of all species normal for the habitat. There was not the slightest evidence of there having been any drainage of mammals from one to another; in fact, the first quadrat, somewhat less favorable for mammals, gave smaller initial figures than the second and third. *Synaptomys* appeared in the second but not the first or third. *Sorex cinereus* and *Mus* appeared in the third only, and *S. fumeus* in the first and third, but not the second. *Peromyscus leucopus*, *Microtus*, *Zapus*, *Condylura*, *Parascalops*, and *Blarina* were taken in all three. It might be added that in these quadrats trapping was initiated in sequence, and that the first was operated throughout the trapping period of the second and third, and the second through that of the third, which was run for four days only.

In forest habitats quadrats should undoubtedly be placed farther apart than this. A 50-foot quadrat placed about 200 feet from a grid operated at the Baldwin Bird Research Laboratory in 1935 gave every evidence of having been seriously affected. However, trapping in the smaller unit was not initiated until the grid had been trapped for six days. Three hundred yards is a safe distance; no disturbances in the yields have been noted where the quadrats have been this far apart.

The simplicity of operating break-back traps, as compared to live-traps, and the simplification of the resultant record-keeping are points in favor of the present method. There are also a number of other practical points that recommend the quadrat system. For one, a 150-foot quadrat is an excellent de-mouser for areas somewhat larger than itself, and is a useful instrument for rodent-control under certain conditions. Furthermore, there is no other way in which examples of rare species in a fauna may be so readily secured. In ordinary trapping, long trap-lines, no matter how long, usually exhaust the more abundant species before the more desirable forms are taken. This often takes several days. A 150-foot quadrat, if properly set, yields its *Napaeozapus*, *Synaptomys*, and rarer shrews on the first night, along with the usual flood of *Blarina* or *Microtus*. The taxonomist who is trying to build up a collection or who needs series of certain rare species would do well to use the quadrat method to the exclusion of ordinary trap-lines. For many years Ohio naturalists have pronounced the species of *Sorex*, *Pitymys*, and *Synaptomys*, rare and local; the quadrat method reveals that these forms are generally distributed and locally abundant.

The reader has already been referred to the work of Townsend (1935) with regard to the bait preferences of certain small mammals. On theoretical grounds it would seem that the use of bait should very definitely increase the rate of drift at least for certain species. With this in mind, two quadrats were operated in 1939 without any bait whatever. No differences could be noted in the yields of baited and unbaited quadrats, although the test was scarcely a fair one for *Peromyscus leucopus*, which in 1939 was very low in numbers anyway. During the last six years very few of the quadrats were baited during wet weather. Another objection has been noted in the course of baiting: it attracts insects to the traps, and hence shrews; and attracts larger mammals also, — foxes, raccoons, opossums, and fox squirrels, which snap the traps and break into covered mole sets. This was found to be a serious source of trouble in 1932 when meat baits were regularly used. Since that time rolled oats have been the standard bait used by the writer and his assistants for all mouse traps; and dried fruits for the rat traps used for chipmunks, red squirrels, and flying squirrels.

Nearly all of the work heretofore reported was carried on in climax forests of different types. During 1936, 1937, 1938, and 1939, a large amount of data was obtained on the populations of many species of small mammals in a large number of different habitats. It seems unnecessary to record in detail the support given to the conclusions deduced from the work in earlier years. Suffice it to say that the following facts remain clear: (1) that the 150-foot quadrat is far better to use than any smaller size, unless but one trapper is available, in which case the 100-foot unit should be used; (2) that the basing of estimates on center quadrats of grids is faulty due to the difficulty of getting figures from a sufficiently large number of units, and that in consequence it is both unnecessary and undesirable to subdivide acre or half-acre quadrats into grids of smaller ones except as it may facilitate mapping or trap-setting; (3) that estimates of populations for any habitat should be based on more than one half-acre quadrat wherever possible; (4) that *all* parts of the quadrat must be of similar ecological constitution; (5) that the three-day limit is under most conditions the proper time allowance and (6) that violent rain storms and severe drought may alter conditions sufficiently to make a longer time allowance desirable. In general, census-taking should be avoided during excessively dry weather. If a heavy thunder-storm snaps most of a quadrat's traps before the third day, the work should be done over in a new place.

POPULATIONS

From time to time in recent years there have appeared figures on the populations of small mammals indicating that certain species. may run as high as 100 individuals to the acre, or very much higher. Williams (1936) published figures on *Blarina brevicauda* and *Peromyscus leucopus* of over 200 per acre at North Chagrin Metropolitan Park in Ohio, as previously discussed in this report. Townsend (1935, p. 49) records 104 per acre for *Blarina;* Hamilton (1937) reports that *Microtus pennsylvanicus* attained figures of from 160 to 230 per acre during the 1935-36 mouse year in New York State; Elton, Davis, and Findlay (1935) estimate densities of over 100 and less than 200 per acre for *M. agrestis* in Scotland. These figures are minimal indeed compared to some others. Hall (1927) estimates 4,000 per acre for *Microtus californicus* during a mouse plague in California, while *Mus musculus* was estimated at the colossal figure of 78,000, an all-time high for such studies. Piper (1909) gives figures of 8,000 to 11,000 per acre for *Microtus montanus* in Nevada. That such figures are not reported solely by American workers is indicated by an estimate of 6,000 per hectare for *Microtus pelliceus* in the Soviet Union [Pidoplichka, reported by Vinogradov, (1934)]. A population of mice such as 10,000 per acre means one mouse for every four square feet of ground, and it is obvious that no habitat could stand such a population except during the passing of a great migrating horde. The writer has never encountered any such populations while using 150-foot quadrats in Ohio, Maine, Massachusetts, and California. Only once during seven years of quadrat work have we found populations greater than 100 per acre for any one species. At Aurora Pond, Ohio, in 1938 *Microtus pennsylvanicus* registered a total of 118 per acre in a rich, wet meadow. This density the writer believes to have been artificial, caused by a flooding of part of the normal habitat through the raising of the pond's water-level. In the quadrat in question a *Microtus* was captured in every other trap of the 150-foot quadrat during the three-day trapping period. It is frankly not conceivable to the writer how populations could be much denser, but this nevertheless made him more tolerant than he previously had been of some of the published figures.

A summary of the populations per acre of some Ohio small mammals follows. All the figures are based on the three-day yields of 150-foot (45-meter) quadrats (See Table XIV). The species may be treated individually. The cyclical aspects of the figures will be treated in greater detail in a forthcoming paper.

Blarina brevicauda. Short-Tailed Shrew

Blarina, the short-tailed shrew, is the most widely distributed and most abundant mammal in Ohio. Although it is locally outnumbered in hayfields by *Microtus*, and in forests by *Peromyscus leucopus* or *Sorex fumeus*, its general average is higher than for any other species. Preliminary records seem to indicate that *Blarina* is non-cyclical, although severe drought may curtail the population sharply over a period of years. Populations have run from 0 to 30 per acre in grassland habitats, with an average of 18; in forests, the average is 26 per acre, with the highest population recorded 48 per acre. During the 1933-34 drought period figures sank as low as 4 and 10 per acre in habitats that since 1935 have yielded from 20 to 40. Nothing approaching Townsend's 104 per acre (1935, p. 49) has been recorded under natural conditions.

Cryptotis parva. Old-Field Shrew

This tiny shrew is a very rare animal in northeastern Ohio, and has been taken just once inside a quadrat, in a fallow field habitat at North Chagrin Park.

Sorex fumeus. Smoky Shrew

Smoky shrew populations are very susceptible to drought, and apparently are affected by cycles as well. During the 1937-38 *Sorex* peak their numbers reached 15 per acre in upland forests, while in one instance at Little Mountain, a population of 58 per acre was recorded, one of the highest ever discovered for any species in the course of this work. In habitats other than climax forests *Sorex fumeus* is distinctly uncommon, the average being less than 1 per acre.

Sorex cinereus. CANADA SHREW

The transitory characteristics of Ohio *Sorex cinereus* populations afford special problems in determining peaks and population figures. 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. Such migrations may occur several times in one year. Where suitable dry-weather habitats are lacking, *Sorex cinereus* does not occur in Ohio. Figures available indicate that the species was at peak in 1937 with populations of from 1 to 11 per acre. High figures (5 per acre) in fields during 1938 were caused by excessively high water-levels in bogs and marshes generally. During other years the population is usually much lower than 1 per acre.

Parascalops breweri. HAIRY-TAILED MOLE

The hairy-tailed mole is one of the most important forest mammals in Ohio from an ecological standpoint. Its numbers were at a great peak in 1936 during which populations of as high as 24 per acre were noted. The average for climax forests was 7.6, as opposed to figures of 1, 2, or 3, per acre in other years. In other habitats the population has usually been in the vicinity of 1 or 2 per acre. The species avoids most communities of the hydrosere except during drought years. Trapping *Parascalops* with mouse-traps, the only practicable means in quadrat work, requires a special technique of setting which is only learned through experience. The writer's limited experience with *Scalopus*, which no longer occurs in the region under consideration, indicates that the same methods will not always work with that form.

Condylura cristata. STAR-NOSED MOLE

Star-nosed moles offer few special problems in trapping, and a population may be easily removed with mouse traps. Although climax forests are not this species' favorite habitat, they constitute the best areas for cyclical studies. It is evident that they were at peak in 1936, and the highest population noted, 6 per acre, was recorded in a sedge meadow during that year. Ordinarily this mole is more abundant in swamp forests than elsewhere. Its concentrations there are dependent upon water levels. During very wet years it freely invades hayfields and fallow land.

Tamias striatus. Chipmunk

The cyclical nature of seed production of beech and sugar maple seems to be the basic factor regulating the changes in chipmunk population densities. In 1935, following a year of great seed production by these trees, chipmunk populations reached a figure of 8.7 per acre in upland forests, a density that is undoubtedly exceptionally high, as similarly favorable conditions in 1937 resulted in but a very slightly higher figure (1.14 per acre) for 1938 than the lowpoint of the previous year (0.8 per acre).

Sciurus hudsonicus. Red Squirrel

Red squirrel populations in Ohio were at their highest in 1935 (1.7 per acre), since which time they have steadily dwindled to a point where they no longer figure in quadrat records, a truly remarkable decline. Careful counts made at Little Mountain over a period of years corroborate the results obtained with the quadrats.

Glaucomys volans. Flying Squirrel

Like the other herbivorous species treated in this paper, flying squirrels were at peak in 1935, when populations were generally in the vicinity of 3 per acre in woodland habitats. A sharp drop to 0.4 occurred in 1936, since which time there has been a slow recovery. The largest population ever noted was one of 6 per acre during the late summer of 1938, in a beech-maple forest. During this year a low peak was registered. In 1939 the species suffered a virtual eclipse, the writer's field assistants having been unable to supply the Cleveland Museum's Preparation Department with enough specimens for a small habitat group.

Peromyscus leucopus. Deer Mouse

Great cyclical disturbances occur in the deer mouse populations of any Ohio woodland, but the numbers of this ordinarily abundant mammal apparently do not approach the figures reported by other workers for other localities. A density of 46 per acre, recorded in 1938 in an isolated beech-maple woodland, was the greatest noted. Average figures for all upland forest habitats were 29 per acre during the 1935 peak. In 1936, during the ebb of the cycle, *Peromyscus* became positively uncommon, 5.2 per acre, a figure below that of *Sorex fumeus* and *Parascalops breweri* for the same year. Recovery progressed steadily after 1936 and an average figure of 22.2 per acre was attained by the summer of 1938. Staple food crop failures during this year curtailed the trend, however, and the figure of 22.2 in 1938 marks another maximum which completes a second three-year interval between peaks. During 1939 *Peromyscus* virtually vanished from Ohio's forests.

In other habitats deer mice come and go, depending on conditions within the upland forests. Populations are rarely as great as they are there. In general thorn-apple scrub and fallow fields are not inhabited unless populations are nearly at peak in the forests. Swamps and bogs show fluctuations corresponding to changing water-levels, and in open country, far from scrub or woodland, this species is replaced by the next, *P. maniculatus bairdi*.

A curious population of 38 per acre was noted in a flood-plain woodland along the Rocky River west of Cleveland in 1936. This was more than twice as great a population as was noted in any other habitat during that year, was more than six times as great as any population at any other station, and was all the more remarkable in that the habitat is periodically under from one to three feet of fast-moving water each winter. In general it may be said that the herbivorous species of small mammals were all at figures reminiscent of the 1935 peak at Rocky River, where for some reason, to date undiscovered, the factors tending to liquidate the 1935 peak were not effective.

Peromyscus maniculatus. White-Footed Mouse

Prairie white-footed mice are rare and local in northeastern Ohio, except on the beaches and sand-dunes along the shore of Lake Erie. Here, in 1935 transect trap-line records used in conjunction with a 50-foot quadrat indicated that a 150-foot quadrat might have yielded very high figures. By 1936, when the first large quadrat was used, populations were still at 22 per acre, although far less numerous than in the previous year. The habitat has not been trapped since. Elsewhere, the highest population noted is 4 per acre, with the average for fallow fields of 1.5 in 1938, 0.7 in 1937, and no records whatever in 1936. These fragmentary records suggest that 1935 and 1938 both marked peak years for this form, as for other herbivorous species.

Microtus pennsylvanicus. FIELD VOLE

As usual elsewhere with most workers, it is a species of *Microtus* that holds our Ohio records for the greatest number of individuals per acre, as noted previously. Figures of 118 per acre in a rich meadow in 1938 constitute an all-time high. A second quadrat nearby reduced the average for that particular habitat to 85 per acre, which is still higher than any recorded elsewhere. The species was at peak in 1929, 1932, 1935, and again in 1938, although there were no factors now apparent that should have tended to keep the populations from further increasing in 1939. Actually, sharp decreases were noted in 1939. The 1935 peak was by far the greatest.

Microtus is generally distributed in all habitats in which herbaceous vegetation is continuously abundant throughout the year. Populations often show great numerical variations in any given year, but the general tendency has been strongly cyclical in all habitats save those in which water levels have caused migrations of seasonal character. The 1936 figure of 28.3 per acre in fallow fields is far higher than it should be as it includes in its record but three quadrats and one was in a field at Rocky River, already alluded to, in which a single quadrat yielded a figure of 76 per acre.

Pitymys pinetorum. PINE VOLE

Pine voles are forest-edge animals in Northern Ohio. During cyclical maxima they spread inwards into the forests and are then to be found throughout the larger woodlands in the Cleveland region. The North Chagrin Park figure of 18 per acre (1935) is by far the highest ever recorded by means of quadrats, and brought the average figure for that year to 6.4 as compared to the ebb-cycle figure of 0.5 per acre in 1937. The 1938 record shows that *Pitymys* was again at peak.

Synaptomys cooperi. Lemming Vole

Ohio's only lemming is generally distributed but not at all common. The somewhat meager evidence available from small quadrat and trapline sources indicates that a very high peak occurred in 1935, when the species was first reported for the region under consideration. Just how great the populations were at that time is somewhat of a mystery as but one quadrat was operated in a habitat suitable to this species. This gave a figure of 4 per acre. The highest figure obtained since 1935 is one of 6 per acre at the Holden Arboretum in July, 1938. The average for this year, 1.5, is no higher than that for 1937. That the species was at peak seems to be indicated by the fact that it appeared in a greater variety of habitats in 1938 than in earlier years, although the figures in every case are very low.

Zapus hudsonius. Hudson-Bay Jumping Mouse

Up to the present time (1939) the figures obtained through the use of quadrats have failed to indicate the existence of a well-marked cycle in the population-changes of this jumping mouse. The highest figures recorded for this species are 18 per acre in a rich meadow and 12 per acre in a swamp shrub (*Alnus-Cephalanthus* associes) community. Both figures were obtained in 1936. In fallow fields the maximum figure of 3.5 per acre was recorded in 1939, while in brushy scrub (*Rhus-Crataegus* associes) the maximum was obtained in 1938. Such figures indicate plainly that *Zapus*, like *Sorex cinereus* and *Microtus*, is greatly influenced by local and seasonal variations of water levels, relative humidity and general precipitation as reflected by lushness of herbaceous vegetation. *Zapus* is not a regular inhabitant of upland forests, the most stable of Ohio habitats, and in consequence cyclical records will be difficult to secure. That cyclical maxima do occur is very probable, in view of the periodic outbreaks of this species in Ohio hayfields. It has not yet been the fortune of the writer to be able to work in such a locality.

Napaeozapus insignis. Woodland Jumping Mouse

Trapping has been continued long enough in the case of the woodland jumping mouse to establish the existence of a cycle, but the length of it has not been determined. The records are very much less numerous than for *Zapus*, but as this species inhabits upland forests, they are relatively little affected by water-table and climatic factors. A peak occurred in 1937, when populations reached a figure of 2.8 per acre, while an ebb apparently occurred in 1934 and 1935, when the species was not taken in any quadrat. The highest figure noted is one of 10 per acre at Shady Lake, Ohio, in a bog forest (*Acer-Betula* associes) in 1938. This is the first and only time the species has been taken in this habitat.

Mus musculus. House Mouse

House mouse records are scattered and irregular and show no convincing evidence of peaks or other manifestations of cyclical phenomena. A population of 4 per acre in a sedge meadow habitat is the largest yet on record for their species in Ohio.

Other species

Besides the forms listed above, other species are occasionally taken inside quadrats. In all cases these are larger mammals, and the irregularity of their capture is in line with their very apparent low density of population as compared to the smaller forms. The Northern gray squirrel (*Sciurus carolinensis leucotis*) and the cottontail rabbit (*Sylvilagus floridanus mearnsi*) are occasionally captured in the rat-traps set for chipmunks and flying squirrels, and at least once during our work with quadrats of different sizes each of the following have been taken: the skunk (*Mephitis nigra*), Virginia opossum (*Didelphis virginiana*), least weasel (*Mustela rixosa*) and Norway rat (*Rattus norvegicus*). The quadrat method is not effective with these larger species, since there is a great disparity in size between the quadrat and the home range of the animal.

Only four of the terrestrial small mammals known to occur in northeastern Ohio have so far eluded capture in the quadrats. One of these is the New York weasel (*Mustela frenata noveboracensis*) and two, the Red-backed vole (*Clethrionomys gapperi*) and Common mole (*Scalopus aquaticus*) are probably extinct today; the last is a very rare shrew (*Microsorex hoyi thompsoni*). The fact that these species have not been taken is evidence of their relatively great rarity.

TABLE XIV. Small Mammal Populations in the Cleveland, Ohio Region, 1935-39. Figures give the number per acre and are the averages of estimates based on the yields of single 150-foot quadrats.

HABITAT and YEAR	Blarina brevicauda	Sorex fumeus	Sorex cinereus	Cryptotis parva	Parascalops breweri	Condylura cristata	Tamias striatus	Glaucomys volans	Sciurus hudsonicus	Peromyscus leucopus	Peromyscus maniculatus	Microtus pennsylvanicus	Pitymys pinetorum	Synaptomys cooperi	Zapus hudsonius	Napaeozapus insignis	Mus musculus	Sylvilagus floridanus	Number of Quadrats in Average
CLIMAX FORESTS																			
1935	25.7	3.7	....	....	2.0	....	8.7	3.3	1.7	29.0	....	....	6.3	....	....	....	....	....	6
1936	23.6	8.0	0.4	....	7.6	0.8	2.8	0.4	0.8	5.2	....	....	1.2	....	....	0.4	....	....	5
1937	29.7	15.5	1.0	....	3.5	0.5	0.8	1.2	0.5	14.0	....	....	0.5	....	....	2.8	....	....	4
1938	34.2	9.7	0.1	....	1.1	0.3	1.1	1.6	0.1	22.2	....	0.3	2.9	....	0.1	1.6	....	....	14
1939	22.9	13.1	0.2	....	5.5	0.4	1.5	0.2	....	3.6	....	....	1.5	....	....	0.7	0.4	0.2	11
BOG FORESTS																			
1936	5.0	0.5	3.0	....	1.5	1.5	0.5	0.5	1.0	4.0	....	3.5	....	....	1.5	....	....	....	4
1937	6.0	3.0	7.0	....	....	4.0	....	3.0	1.0	24.0	....	6.0	....	....	....	....	....	....	2
1938	14.0	3.0	2.0	....	1.0	....	....	....	....	7.0	....	3.0	....	....	....	5.0	....	....	2
1939	24.0	4.0	2.0	....	....	6.0	2.0	....	....	6.0	....	26.0	....	....	....	....	....	....	1
BOG MEADOWS																			
1936	5.0	....	3.0	....	....	4.5	....	....	....	....	....	12.0	....	....	....	....	1.0	....	4
1937	12.0	1.0	2.0	....	2.0	3.0	....	....	....	1.0	....	13.0	....	....	7.0	....	4.0	....	2
1938	4.0	....	1.0	....	....	1.0	....	....	....	2.0	....	35.0	....	....	2.0	....	1.0	....	2
1939	5.0	1.0	2.0	....	....	2.0	....	....	....	....	....	36.0	....	....	....	....	1.0	....	2

TABLE XIV Cont.

Habitat and Year	Blarina brevicauda	Sorex fumeus	Sorex cinereus	Cryptotis parva	Parascalops breweri	Condylura cristata	Tamias striatus	Glaucomys volans	Sciurus hudsonicus	Peromyscus leucopus	Peromyscus maniculatus	Microtus pennsylvanicus	Pitymys pinetorum	Synaptomys cooperi	Zapus hudsonius	Napaeozapus insignis	Mus musculus	Sylvilagus floridanus	Number of Quadrats in Average
FALLOW FIELDS																			
1936	9.3	....	....	....	0.7	....	....	....	....	....	....	29.0	....	0.7	1.3	....	0.7	....	3
1937	11.3	....	0.7	0.7	1.3	....	....	....	....	2.7	0.7	3.3	....	2.0	2.7	....	0.7	....	3
1938	28.5	....	5.0	....	2.0	1.0	....	....	....	2.5	1.5	26.5	....	1.5	0.5	....	....	....	4
1939	8.5	0.5	0.5	....	1.0	....	....	....	....	0.5	0.5	14.5	....	....	3.5	....	1.0	....	4
RICH MEADOWS																			
1936	30.0	....	....	....	2.0	....	....	....	....	2.0	....	16.0	....	....	18.0	....	....	....	1
1937	24.0	....	....	....	....	....	....	....	....	....	....	14.0	....	....	6.0	....	....	....	1
1938	13.0	....	5.0	....	....	1.0	....	....	....	3.0	....	85.0	....	1.0	2.0	....	3.0	....	2
1939	26.0	....	4.0	....	....	....	....	....	....	....	....	18.0	....	....	2.0	....	....	....	1
WOODS EDGE																			
1935	24.0	....	....	....	4.0	....	8.0	2.0	2.0	34.0	....	4.0	6.0	4.0	....	....	....	....	1
1936	16.0	....	....	....	13.0	....	3.0	....	....	....	....	3.0	....	1.0	1.0	....	....	....	2
1937	28.0	....	....	....	7.0	....	1.0	2.0	....	14.0	....	5.0	....	3.0	3.0	1.0	....	....	2
1938	24.0	....	2.0	....	4.0	....	....	....	....	10.0	....	12.0	....	....	4.0	....	4.0	....	1
1939	20.0	14.0	....	....	....	....	....	....	....	....	....	6.0	....	2.0	....	....	....	....	1
THORN SCRUB																			
1938	20.0	0.4	0.4	....	1.2	2.4	2.0	....	0.8	7.2	....	15.6	....	1.2	4.8	....	1.2	....	5
1939	6.0	....	....	....	....	....	....	....	....	2.0	....	....	....	....	2.0	....	....	....	1
FLOOD PLAIN FOREST																			
1936	22.0	....	....	....	2.0	....	....	....	2.0	38.0	....	16.0	....	....	....	....	2.0	....	1
COASTAL SAND DUNES																			
1936	....	....	....	....	....	....	....	....	....	....	22.0	4.0	....	....	....	....	....	....	1

CONCLUSIONS

From a study of the yields of small mammals obtained from several sizes of trapping quadrats over a period of eight years, it is decided that:

(1) The quadrat method provides an accurate means of determining small mammal abundances;

(2) In general, the larger the quadrat the more accurate the results, and that quadrats 150 feet or 50 meters on a side or circular units of corresponding area are still small enough to be easily operated and are large enough to provide a high degree of accuracy, and hence should be considered the standard sizes for population investigations of mammals whose home ranges are of the same size or smaller than that of the quadrat;

(3) The use of shelter-belts or outer tiers of quadrats about a central one is not justifiable because of the tremendous labor involved if the quadrat is maintained at standard size, because the belts themselves cause population disturbances within the quadrat, and because the data the belts yield can be put to better statistical use if the traps that furnished them are part of the quadrat itself;

(4) More than one quadrat should be used in any given community, but should be placed no closer to eachother in forests than 300 yards, and no closer than 100 yards in fields;

(5) All parts of a quadrat must be ecologically uniform and similar to the larger area which it is meant to represent, if figures on populations for one particular habitat are desired;

(6) A three-day trapping limit should be set, as the resident population is practically exhausted in this time;

(7) Trapping within a quadrat must be thorough and executed with the sole purpose in mind of getting all the mammals out of it as swiftly as possible, for which reason traps should be set in underground or surface runways or wherever the mammals are, and should not be set at regular intervals within the quadrat, since the lairs and runways do not so arrange themselves in nature;

(8) The use of insulated quadrats is futile as the metal sheeting used will cause spectacular changes in the ecological picture of the quadrat, particularly if moles are part of the small mammal fauna;

(9) The use of very small quadrats (smaller than 100 feet on a side) is indefensible owing to the relatively high percentage of animals drifting into them from adjacent terrain;

(10) Quadrats are found to be particularly useful in studying cyclical changes in small mammal populations and in collecting the less common species of a given small-mammal fauna.

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