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AN EIGHT AND ONE-HALF YEAR STUDY OF THE RED-BACKED VOLE (Clethrionomys gapperi Vigors) AT CEDAR CREEK FOREST, ANOKA AND ISANTI COUNTIES, MINNESOTA.

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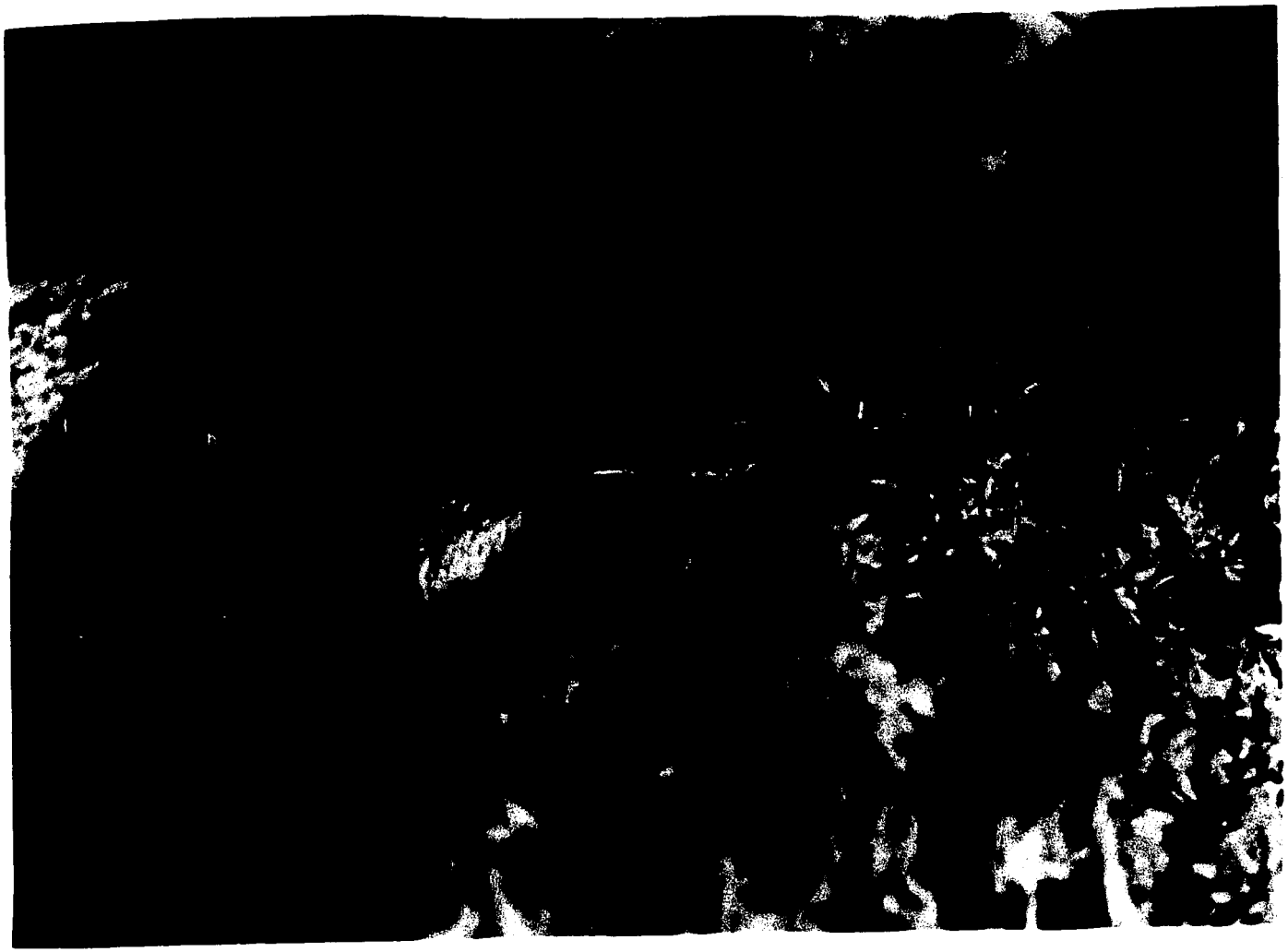
AN EIGHT AND ONE-HALF YEAR STUDY OF THE RED-BACKED VOLE (*Clethrionomys gapperi* Vigors) AT CEDAR CREEK FOREST, ANOKA AND ISANTI COUNTIES, MINNESOTA

by

Harvey L(orraine) Gunderson

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy in the
University of Michigan
1962

Doctoral committee:
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Professor Rogers McVaugh
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Frontispiece. An adult male red-backed vole, Clethrionomys gapperi Vigors (captive).

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TABLE OF CONTENTS

	Page
Acknowledgments	iii
List of Tables	vi
List of Figures	vii
List of Appendices	ix
INTRODUCTION	1
GEOLOGICAL HISTORY OF THE GENERAL AREA, THE ANOKA SAND PLAIN	4
DESCRIPTION OF CEDAR CREEK FOREST AND THE STUDY AREA	9
Cedar Creek Forest	9
Study Area	12
CLIMATE	15
Temperature and rainfall data from Cambridge, Minnesota	15
Minimum-maximum temperatures in the bog	18
OBJECTIVES	18
METHODS	21
Trap spacing and grid pattern	21
Trapping methods and the recording of data	21
GROWTH AND AGE DETERMINATION	27
TRAPPING RESULTS	30
Total number of captures of each species trapped	30
Discussion of trapping results by years	32
1949	32
1950	34
1951	37
1952	39
1953	42
1954	42
1955	43

TABLE OF CONTENTS (Cont'd)

	Page
Discussion of trapping results by years (cont'd)	
1956	44
1957	45
DISCUSSION OF POPULATION DENSITY CHANGES	45
HOME RANGE OF THE RED-BACKED VOLE	63
LONGEVITY	70
THE MAMMALS IN THE BOG	72
WATER AND THE DISTRIBUTION OF THE RED-BACKED VOLE	75
SUMMARY	89
APPENDICES	95
LITERATURE CITED	102

LIST OF TABLES

Table		Page
1.	Mean monthly temperatures (Fahrenheit) from May to October, 1949 to 1956, at Cambridge, Minnesota	17
2.	Monthly rainfall (inches) from May to October, 1949 to 1956, at Cambridge, Minnesota	17
3.	Numbers of captures of small mammals, arranged in descending order	31
4.	Summary of sex ratios by years	59
5.	Home range data in acres, for all individuals by year, sex, and age	66
6.	Home range data in acres, for individuals caught at other than edge stations, by year, sex, and age	67
7.	Home ranges in acres of adults taken at all stations, and at inner stations only	67
8.	History of individuals caught during two seasons	71
9.	Relative abundance for the five most common species, based on number of captures (not individuals) per 100 trap-nights	72
10.	Original weight of vegetation samples	85
11.	Percentage of water in bog and upland vegetation	85
12.	Water consumption in cubic centimeters per gram of body weight in two groups of adult red-backed voles, given rations of different water content	86
13.	Relative humidities four inches below surface and four inches above surface in the bog and in the upland	88

LIST OF FIGURES

Figure		Page
Frontispiece.	An adult male red-backed vole, Clethrionomys gapperi Vigors (captive)	ii
1.	Map of Anoka Sand Plain	5
2.	Vegetational cover map of trapping plot	13
3.	White cedar with sparse undercover	14
4.	White cedar and tamarack mixture with luxurious herbaceous growth	16
5.	Average weekly minimum and average weekly maximum temperatures for each trapping period in the years 1949 to 1952	19
6.	Average weekly minimum and average weekly maximum temperatures for each trapping period in the years 1953 to 1956	20
7.	Sample page of chronological entries of field data	23
8.	Sample page of weekly trapping summaries	24
9.	Sample page of chronological history of one trapping station	25
10.	Sample page of chronological history of one individual	26
11.	Summary of weekly trapping results for 1949	46
12.	Summary of weekly trapping results for 1950	47
13.	Summary of weekly trapping results for 1951	48
14.	Summary of weekly trapping results for 1952	49
15.	Summary of weekly trapping results for 1953	50
16.	Summary of weekly trapping results for 1954	51

LIST OF FIGURES (Cont'd)

Figure		Page
17.	Summary of weekly trapping results for 1955	52
18.	Summary of weekly trapping results for 1956	53
19.	Number of individuals caught in the peak period of each year	60
20.	Annual population of red-backed voles as shown by the number of individuals taken per 100 trap-nights ..	62
21.	Weekly average in cubic centimeters of water per gram of body weight for each individual	81
22.	Weekly averages in cubic centimeters of water per gram of body weight for each species	82

LIST OF APPENDICES

		Page
APPENDIX I	Dates of live-trapping periods	95
APPENDIX II	Summary of trapping results for each period and year	96
APPENDIX III	Data on individuals used in home range calculations	98

INTRODUCTION

Population dynamics of animals have commanded a great deal of attention from biologists, particularly since the time of Gause's publications (1932, 1934). Results of research, especially on vertebrates, appear in nearly every issue of such biological journals as The American Midland Naturalist, Auk, Ecology, Ecological Monographs, Journal of Mammalogy, Journal of Wildlife Management, The Wilson Bulletin, and others. Chapters in books on animal ecology are devoted to discussions of population dynamics. Among these are Allee, Emerson, Park, Park, and Schmidt (1949), Chapman (1931), Dice (1952), Elton (1927), McFadyen (1957), and Odum (1953). Several reviews devoted entirely to the subject have appeared. An entire issue of the Journal of Wildlife Management, edited by Hewitt (1954), was devoted to A Symposium on Cycles in Animal Populations. The most recent review was a Cold Springs Harbor Symposium on Quantitative Biology (1958), Volume XXII, called, Population Studies: Animal Ecology and Demography.

Practical and immediate use of population studies are of great importance in at least three areas. In recreation, several agencies are concerned either with maintaining or increasing a harvestable surplus of fish and game or with maintaining species for esthetic enjoyment. In agriculture and allied fields, methods of effectively controlling "harmful" species of insects, birds, and mammals have

resulted in a vast literature. In medicine, populations whose individuals are reservoirs or vectors of disease organisms are of great significance. More recently, demography has attained prominence, although contributions to this field come not alone from biologists.

Most population studies center around a search for factors that might cause a change in the number of individuals within a species. The ideal situation for a study of a population that is to be manipulated, would be one in which these factors were reduced to the minimum - one. Andrewartha and Birch (1954) effectively argue that weather, not competition, is the most important regulating factor in insect populations. Lack (1954) champions the idea of competition, particularly for food, while Cole (1954) has implied that populations are affected by such a variety of factors that random oscillations are the result.

The regularity of some fluctuations has brought the term "population cycle" into common although ill-defined use. The best documented of these oscillations are those for the Arctic fox, Canada lynx, and snowshoe hare (Elton and Nicholson, 1942), lemmings (Elton, 1942), ruffed grouse (Clarke, 1936), and the meadow vole (Hamilton, 1937).

Aside from those already mentioned, numerous other factors have been suspected of influencing long term fluctuations in vertebrate populations. One factor that was championed earliest was sunspots, advanced by MacLulich (1936) as well as by DeLury and O'Conner (1936).

Green, Larson, and Bell (1939) have given evidence that shock disease (hypoglycemia) was a cause for periodic decimation of the snowshoe hare in central Minnesota. During the decade following these publications a number of parasites and some viruses (notably the one associated with tuleremia) were implicated as causative agents in population declines.

Selye (1950) has carefully documented an endocrinological set of factors, the general-adaptation-syndrome, as a cause for lowered resistance to disease in humans in times of stress. Christian, in several papers (1953, and others), has applied this concept to non-human mammalian populations. Thus, many students have been stimulated to do research on the phenomenon loosely referred to as "stress reactions".

Pitelka (1958) recently approached the problem of population change by choosing a simplified environment, the Arctic. He wrote, "The total cycle is then generalized as a three-year pattern in which the main population growth [of brown lemmings] occurs in the second and third winters, the summers are intervals when the growth trend is reversed or deflected, and the decline occurs in large part if not almost entirely in the third or last summer. Winter cutting of vegetation and the resulting removal of food and cover exposes peak densities of lemmings to predation, which is the usual agent figuring in the inevitable decline of the population."

Errington (1958) has hypothesized that a combination of physiology and psychology associated with quality of food might be important in causing density changes in muskrat populations. Chitty (1958) has tentatively suggested a rather interesting phenomenon, an hereditary hemolytic anemia, as a self-regulating mechanism in Microtus agrestis populations.

This brief resumé is presented not as an historical survey but to emphasize the complexity of the problems associated with the study of population dynamics and the diverse ideas workers have utilized in attempting to solve them.

GEOLOGICAL HISTORY OF THE GENERAL AREA THE ANOKA SAND PLAIN

In east-central Minnesota, between the Mississippi and St. Croix Rivers, there is a distinct physiographic unit which Cooper (1935) named "The Anoka Sand Plain;" its extent is shown in Figure 1. It is a moderately undulating area with a very gradual slope to the south, consisting of about 860 square miles, in four counties (Anoka, Isanti, Sherburne, and Chisago).

The Anoka Sand Plain now differs from the surrounding area because of its mode of origin. Many geologists have spent considerable time investigating the glacial geology of this region. Two of the pioneers were Newton H. Winchell and Warren Upham, whose results appeared mainly in the Final Report of the Minnesota

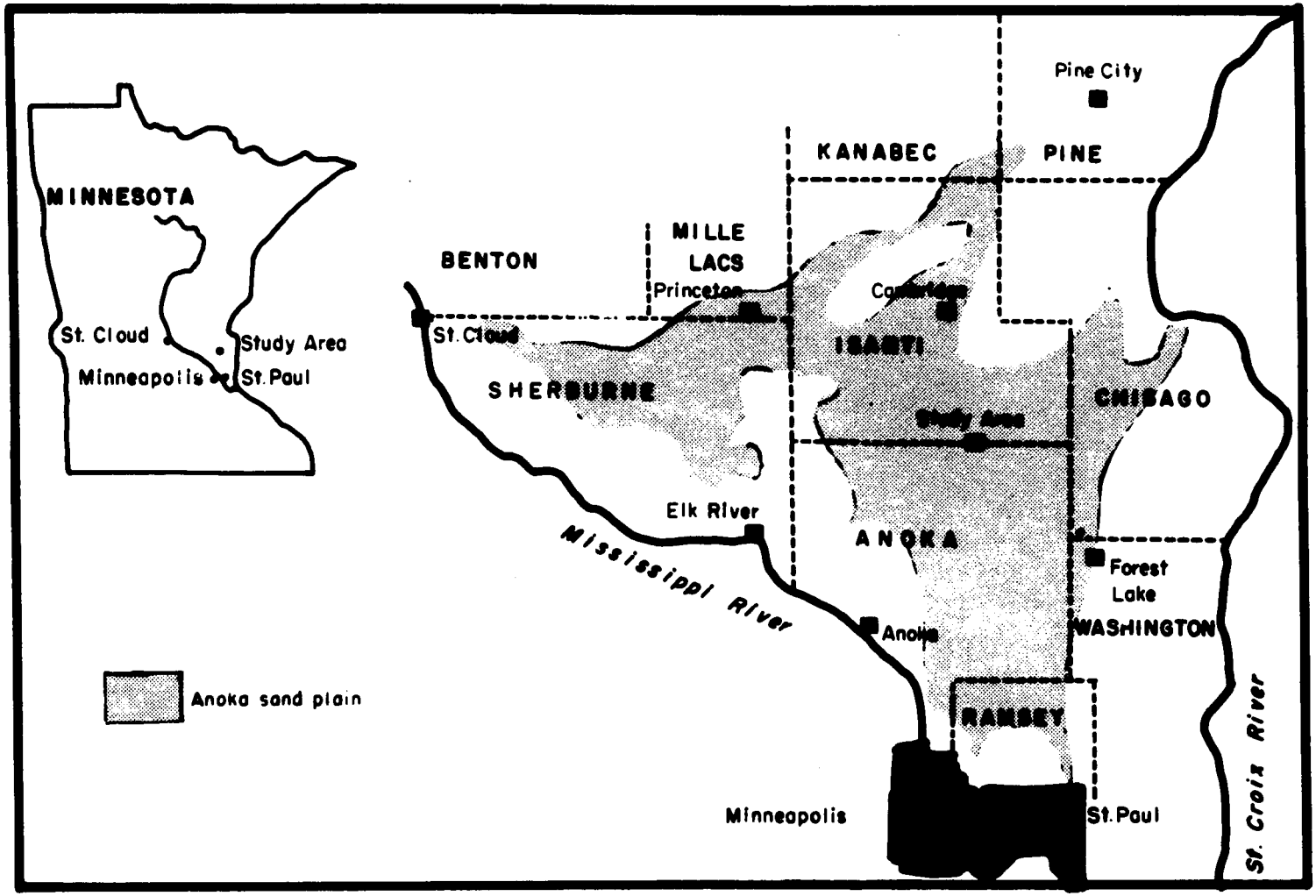


Fig. 1. Map of Anoka Sand Plain. Scale: 1 inch to about 13 miles. After Cooper (1935).

Geological and Natural History Survey (Winchell and Upham, 1899). Later, Frank Leverett and F.W. Sardeson published many papers on the same subject (Leverett, 1912, 1916, 1921; Sardeson, 1897, 1916, 1922, 1923a, 1923b, 1923c, 1933; Leverett and Sardeson, 1917, 1919, 1932).

Upham (in Winchell and Upham, 1888) believed that the blanket of sand which covered the area was "modified drift". Hall, Meinzer and Fuller (1911) seemed to think of the origin of these sand plains in somewhat different terms. They wrote, "Outwash sands and gravels occur in many portions of southern Minnesota. Nearly the whole of Anoka County is covered by them, as well as large portions of many counties to the west."

Sardeson thought the sand in Anoka and surrounding counties was a blanket of dune sand (wind blown) derived from the flood plain of the Mississippi River. He first expressed this view in 1897 (Sardeson, 1897) and last mentioned it in 1932 (Leverett and Sardeson, 1932).

Sardeson's arguments for the eolian origin of the Anoka Sand Plain were briefly summarized by Cooper (1935) as follows:

> The Anoka Sand Plain is a dune area. It lies northeast of the Mississippi, and the sand of which it is composed was derived from outwash and river terraces along the courses of that river and its tributaries, the Elk and the Rum. The sand, blown from these areas by southwest winds, traveled northeastward in the form of dune ridges until held by the wet surfaces of clay moraines or by vegetation. The distances covered by the traveling sand, in various portions of the plain, ranged from 17 to 36 miles, the maximum being in the Anoka-Chisago district, where sand from the Mississippian flood plain actually reached the valley of the St. Croix. The material is relatively coarse near the source of supply and becomes progressively finer northeastward. Stratification is lacking, pebbles are nearly everywhere absent, but small

ones are found close to the source of supply.

Dr. W. S. Cooper, doing botanical work in the area, became convinced that it was of glacio-fluvial and not eolian origin. He took exception to Sardeson's arguments and wrote as follows:

> 'A minute investigation of the plain has shown conclusively that most of these statements are contrary to fact. The plain in general exhibits no evidence of eolian origin; dune forms are found only in certain limited areas, comprising 6 per cent of the whole. There is no general gradation in average size from southwest to northeast. Stratification may be readily seen at points widely spaced over the region, though in the surface layers it has been largely obscured or destroyed. Pebbles, and even cobbles, are present throughout the extent of the plain, though, locally, considerable areas have none. These points will be amplified and evidence will be presented in support of the statements here made.'

Cooper's (1935) reconstruction of the plain is the one now generally accepted and is given here in brief. Of the major ice sheets that covered Minnesota, the last (Wisconsin) naturally has received the most attention. During the Middle Wisconsin phase of glaciation (Cary substage) a lobe of the Laurentide ice sheet from the Patrician center moved southwestward along the Lake Superior trough to form the Minneapolis lobe of this major ice sheet. The front of this lobe remained relatively stationary during the early recession and formed a strong terminal moraine from the northeast to the southwest. Its width was about ten miles. This is the St. Croix Morainic system first described from the Wisconsin portion by Berkey (1897). The Mississippi and St. Croix Rivers formed an intra-morainic drainage system within this drift area.

During the late Wisconsin glaciation, while the ice from the

Patrician center (which came from western Ontario) was receding, two lobes of ice, one originating to the east and one to the west of the Patrician center, were extending into Minnesota and converging upon the upper Mississippi Valley. From the northeast came the Superior lobe which played a minor rôle in the history of the Anoka Sand Plain. The Superior lobe from the Labrador center traversed the basin of Lake Superior but did not extend far beyond.

Of far more importance, in the formation of the plain, was the Des Moines lobe from the Keewatin ice center. It came into Minnesota from the northwest, and extended into Iowa, perhaps not as far as originally thought (Ruhe, 1952). A thin sheet of ice called the Grantsburg sublobe overflowed the St. Crox Moraine between Kimball and Minneapolis and extended in a northeastward direction about eighty miles. This forced the Mississippi River out of its channel. It had been flowing in a southeasterly direction along the edge of the St. Croix Moraine, but now it began flowing in a northeasterly direction along the edge of the Grantsburg sublobe. The meltwaters impounded in the region where Grantsburg, Wisconsin, is now located, have been called Lake Grantsburg.

Lake Grantsburg water came from four sources: (1) the upper Mississippi, (2) drainage from the north, recently vacated by the Patrician ice sheet, (3) drainage from the Superior lobe, and (4) the water melting from the Grantsburg sublobe.

Cooper (1935) wrote,

> The lake came into existence when the Mississippi was first pushed out of its pre-Keewatin course by the ice advancing northeastward between St. Cloud and St. Paul. As the glacial invasion progressed, it grew in size, at the same time constantly shifting northeastward. At firstthere were local pondings of the streams tributary to the Mississippi, the most important of which was the St. Croix, then probably flowing southwestward across Anoka County.

During the shrinking of the Grantsburg sublobe the Mississippi River between St. Cloud and Minneapolis gradually shifted southwestward to it pre-Grantsburg course, which the present course closely approximates.

With the thinning of the ice sheet, the water probably flowed over its surface in some places burying masses of ice beneath a load of sand and gravel. Some of these depressions filled with water and were called "ice-block lakes" by Cooper (1935).

Thus, a great outwash plain covers most of the area which was earlier occupied by the Grantsburg sublobe. This is the Anoka Sand Plain in which Cedar Creek Forest is located.

DESCRIPTION OF CEDAR CREEK FOREST AND THE STUDY AREA

Cedar Creek Forest

Cedar Creek Forest, also called the Cedar Creek Natural History area, is a small portion of the Anoka Sand Plain and was set aside for natural history research. The effort to preserve this unique area was initiated by the Minnesota Academy of Sciences. It is now administered by the University of Minnesota. The forest is located about thirty airline miles north of the University of Minnesota campus, astride the

Anoka-Isanti county line (42° 24' N, 93° 10' W).

The area is unique in at least two ways; firstly, because of its geological history, already discussed, and secondly, because of its vegetation, which has been influenced by the presence of ice-block lakes. The largest of the ice-block lakes is Cedar Creek Bog Lake (also called Lindeman Lake and Cedar Lake) which is almost completely filled with calcium carbonate and organic sediments, including marl and peats of several kinds. Gyttja lying immediately above sand in this lake was dated by Rubin and Alexander (1958) as 11, 830 ± 200 years old.

Except for depressions caused by the ice-block lakes, the Cedar Creek area is almost flat. The western part is drained by a small stream, Cedar Creek. There are some dune areas, mostly in the southeastern part. Within the bog are three upland islands on which mature "maple-basswood climax" is growing. The climax vegetation of these uplands was probably attained because of protection afforded by the surrounding wet bog. These "islands" have been the subject of an ecological study by Chu (1948). The Cedar Creek area can be divided into upland drained sections with sandy soils and lowland poorly-drained sections of muck or peat soils (Bray, Lawrence, and Pearson, 1959). Turnock and Lawrence (1953) found that the ground water was at or near the surface of the muck or peat soils.

The vegetation of the uplands can be divided roughly into three major types according to Bray, Lawrence, and Pearson (1959). These

are: (1) tall grass prairie, including Stipa spartea and Andropogon scoparius; (2) deciduous angiosperm savanna and forest with Quercus ellipsoidalis and Quercus macrocarpa as common species; (3) mixed conifer-angiosperm forest, including Pinus Strobus, Betula papyrifera, and Quercus ellipsoidalis-borealis complex.

The lowland surfaces are covered with four to seven meters of peat (Pierce, 1954) of two kinds: (1) fibrous sedge peat which is compact and has developed from sedge vegetation around the bog lake and along the creek, (2) forest peats which are more spongy because of the sphagnum moss and woody materials incorporated into them. Aside from the bog lakes, the lowlands contain a scattering of marshes, swales, brushlands, and swamp forests. Alnus rugosa, Betula pumila, Populus tremuloides, Larix laricina, and Thuja occidentalis are woody species of the lowlands. Northern plants found in the lowlands are twinflower (Linnaea borealis), goldthread (Coptis groenlandica), and several species of orchids. In Minnesota swamp loose-strife reaches its northern limit at Cedar Lake. Fernald (1950) has been used as a reference for plant names.

According to Pierce (1954), all of the swamp has been selectively cut. First, white pine was removed for timber, then cedar and tamarack were cut for posts and poles. In the lowland, forests seem to have been saved from fire, but wind damage was evident, varying from 10 to 100 per cent. White cedar seemed to suffer most from wind-throw. With the water table so near the surface, the roots spread

laterally rather than downward. In the most recent areas of wind damage cattails (Typha latifolia) were growing.

Study Area

The study plot was adjacent to Cedar Lake. The vegetational succession of Cedar Lake and its immediate area was discussed by Lindeman (1941). Submerged aquatics and floating-leaf aquatics grow in the lake itself. Surrounding the lake is a "sedge mat" composed of Typha latifolia, Phragmites communis, Docodon verticellatus, grasses, sedges, ferns and mosses. The first tree to invade the sedge mat at Cedar Creek Forest is tamarack (Larix laricina). This is followed by white cedar (Thuja occidentalis) rather than black spruce (Picea mariana) which is associated with an acidic bog. It was in this mixture of tamarack and white cedar that the study plot was located; for vegetational map see Figure 2. Associated with the cedar and tamarack were other trees such as paper birch (Betula papyrifera), yellow birch (Betula lutea), white pine (Pinus Strobus), black ash (Fraxinus nigra), green ash (Fraxinus pennsylvanica), and a few black spruce (Picea mariana).

White cedar was the most abundant species of trees; they ranged in size from seedlings to trees 40 feet high. Along the eastern edge and the southern half of the western edge were almost pure stands (Fig. 3); in those areas the herb layer was very sparse. These were also the driest areas. Bordering these, toward the center of the plot

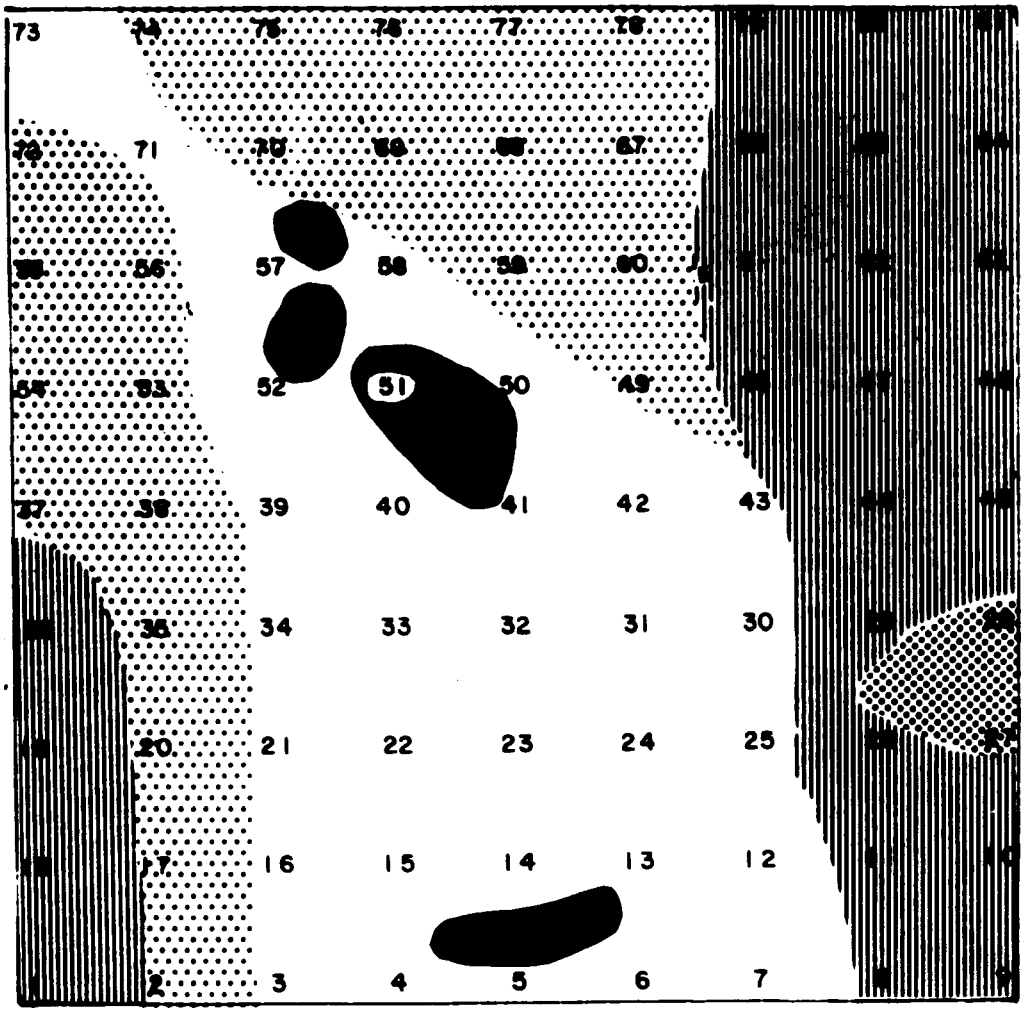


Fig. 2. Vegetational cover map of trapping plot. Scale: 1 inch to about 80 feet. The numbers are trapping station locations which were 52 feet apart.

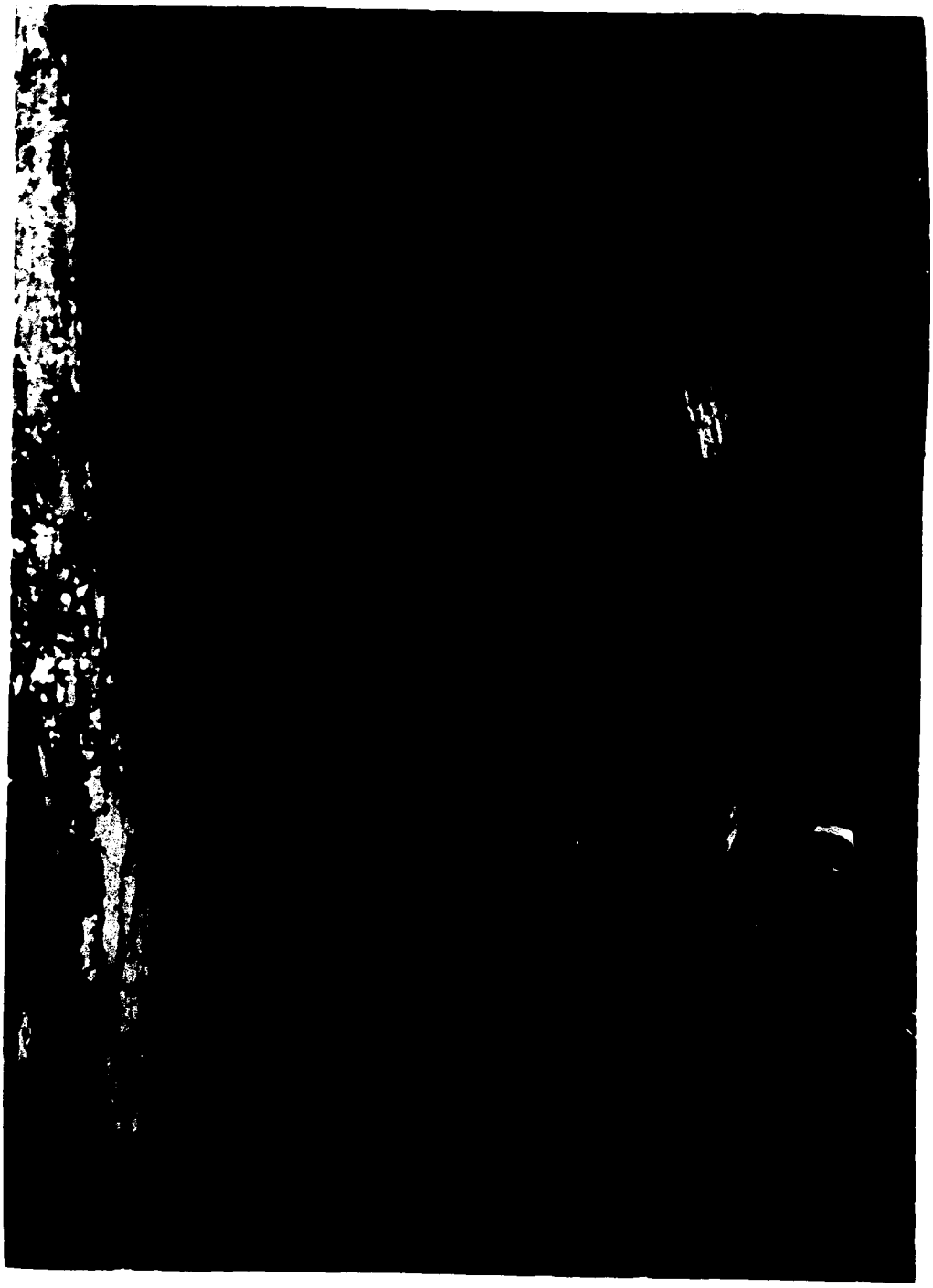


Fig. 3. White cedar with sparse undercover.

was a white cedar area where the ground cover was a mixture of sphagnum, grasses and sedges. This central area (Fig. 4), a mixture of tamarack and white cedar, was also the lowest (wettest) part. There was an understory of shrubs---speckled alder (Alnus rugosa), red-osier dogwood (Cornus stolonifera), poison sumach (Rhus Vernix), beaked hazel (Corylus cornuta), willows of several species, and dwarf birch (Betula pumila). Sphagnum formed the dominant ground cover. Within the area were four wet sites, shown in black in Figure 2, comprised of cattails, sedges and grasses.

CLIMATE

Climatological data are available from Cambridge, Minnesota, ten airline miles from the study area. In addition, I obtained maximum-minimum temperatures both in the bog and in the oak-upland during the trapping periods. The minimum-maximum temperatures in the oak-upland have not been included as they do not apply to this phase of the study.

Temperature and Rainfall Data from Cambridge, Minnesota

A brief summary of temperature and rainfall data are given in Tables 1 and 2. These data were taken from the United States Weather Bureau Climatological Summaries, Minnesota, Monthly and Annual Summaries, 1949 to 1956.



Fig. 4. White cedar and tamarack mixture with luxurious herbaceous growth.

Table 1. Mean monthly temperatures (Fahrenheit) from May to October, 1949 to 1956, at Cambridge, Minnesota

Month	1949	1950	1951	1952	1953	1954	1955	1956
May	57.5	51.2	58.3	56.0	55.5	50.4	60.1	54.5
June	67.9	63.9	61.0	66.5	67.2	67.1	65.2	67.7
July	71.0	67.1	68.1	70.4	69.6	70.0	74.6	65.1
August	69.3	63.9	63.8	66.0	70.4	67.0	72.2	67.6
September	54.6	59.1	55.5	60.4	59.0	56.6	58.5	55.2
October	47.9	49.5	46.4	41.5	54.0	44.5	47.8	53.7
Average	60.1	59.0	58.8	56.7	62.6	59.9	62.0	60.6

Table 2. Monthly rainfall (inches) from May to October, 1949 to 1956, at Cambridge, Minnesota

Month	1949	1950	1951	1952	1953	1954	1955	1956
May	1.16	3.90	2.59	2.03	5.91	3.45	1.04	3.34
June	3.47	0.75	6.53	7.60	5.98	6.75	3.03	4.44
July	4.63	1.49	5.41	5.60	1.68	5.53	4.80	4.07
August	2.84	0.61	4.31	5.96	7.59	3.79	7.66	4.52
September	2.39	3.43	4.09	0.39	2.01	4.12	2.61	1.21
October	2.69	1.51	2.63	0.08	0.37	4.00	1.70	1.80
Average	2.79	1.95	4.26	2.61	3.92	4.61	3.47	3.24

These two tables indicate the weather conditions which prevailed in the general area. During this study the lowest mean monthly temperature was that of May, 1954, with 50.4°; the highest was July, 1955, with 74.6°. The summer of 1952 was the coolest, and 1951 was the next coolest. The summer of 1953 was the warmest. The lowest total precipitation for any month was October, 1952, when only 0.08 inches fell; the highest was 7.66 inches for August, 1955. The trapping season of 1950 was the driest with a monthly mean of 1.95 inches; 1954 was the wettest with a monthly mean of 4.61 inches. The

last four years, 1953 to 1956, were all quite wet. This might have a cumulative effect of raising the water level in the bog considerably.

Minimum-maximum Temperatures in the Bog

Taylor minimum-maximum thermometers containing mercury were used. These were shielded from the sun and were about a foot above the surface. These data are summarized in Figures 5 and 6. The maximum temperatures for each four-day period are averaged and shown by the upper lines. The minimum temperatures for each four-day period are averaged and shown by the lower lines. The highest recorded maximum temperature varied from 77.0° in 1954 to 93.0° in 1950. The lowest recorded minimum temperatures occurred in October of 1952 and 1954. The greatest extremes between minimum and maximum temperatures were in the 1950 season.

OBJECTIVES

This was a study of the population dynamics of a microtine rodent, the red-backed vole (Clethrionomys gapperi Vigors). The objectives were:

1. To evaluate population trends and determine, if possible, any regularity, other than a seasonal one, in their fluctuations.

2. To evaluate the properties of each annual population by sex and age distribution.

3. To determine the home ranges of individuals in this population as revealed by trapping.

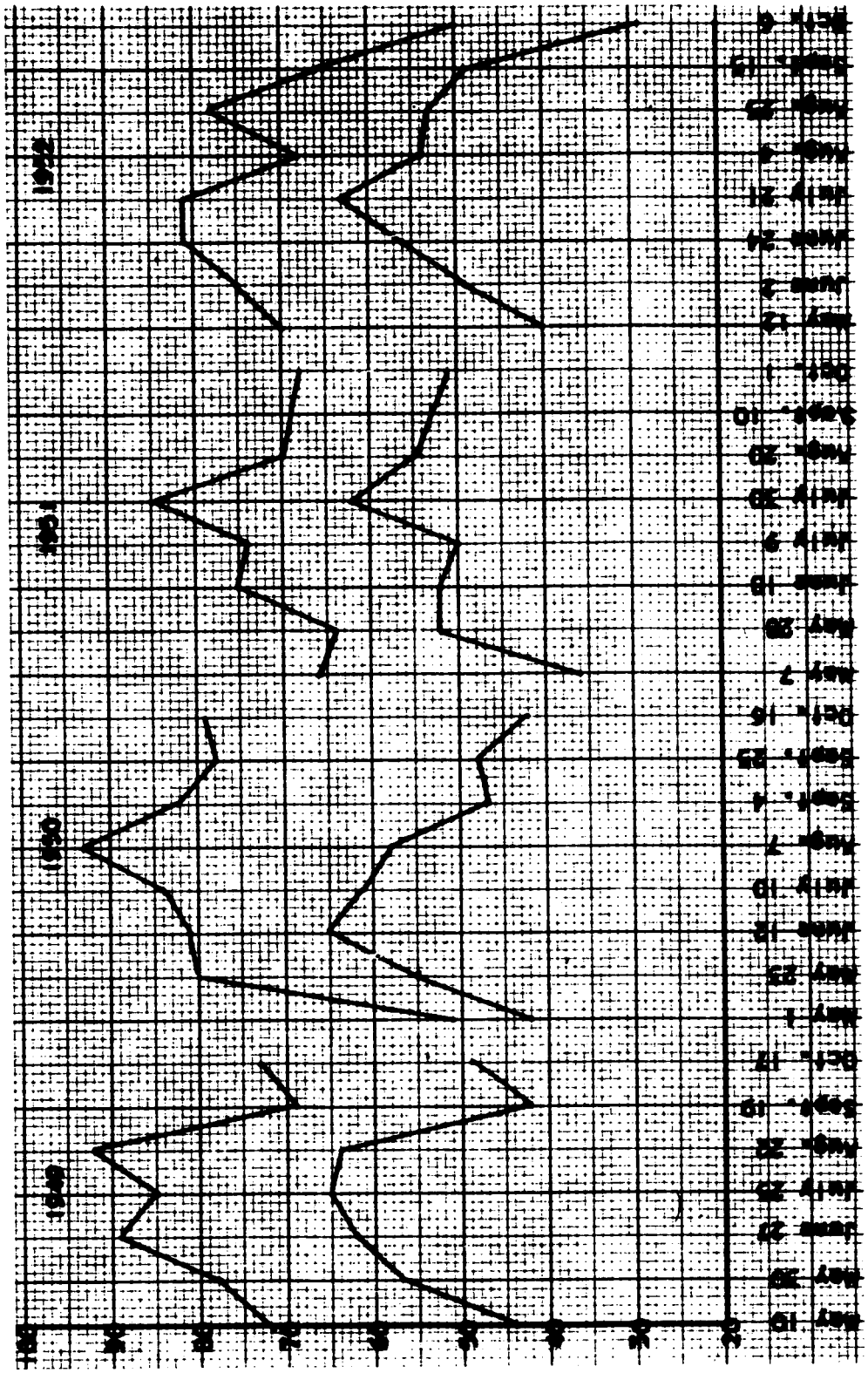


Fig. 5. Average weekly minimum and average weekly maximum temperatures for each trapping period during the years 1949 to 1952. Degrees Fahrenheit on ordinate.

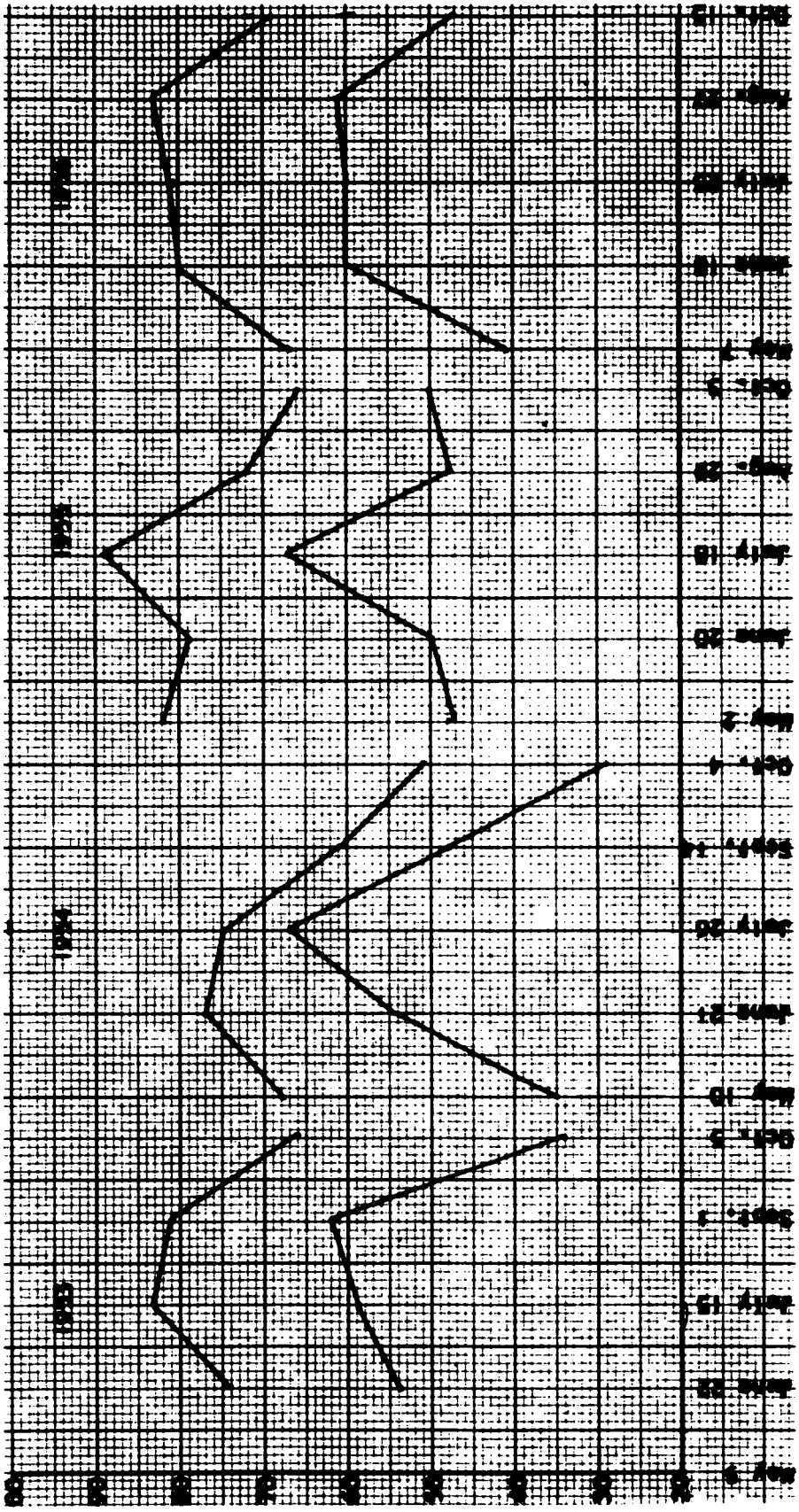


Fig. 6. Average weekly minimum and average weekly maximum temperatures for each trapping period during the years 1953 to 1956. Degrees Fahrenheit on ordinate.

4. To find some factor or factors which might account for the greater abundance of the red-backed vole over other species of small mammals in the bog.

METHODS

Trap Spacing and Grid Pattern

Close spacing of traps seems best for voles of the Subfamily Microtinae, because these animals have small home ranges. Trap spacings of anywhere from 16 to 100 feet have been reported in the literature. I used 81 traps, spaced 52 feet apart in a grid pattern, and the area was nine trap stations square as shown in Figure 2. The base line was in an east-west direction. Five acres were covered with this pattern, if a border strip, its width equal to one-half the distance between the traps, be included.

Trapping Methods and the Recording of Data

The live trap used in this study was a multiple-catch wooden type already described by Gunderson (1950). Traps of this type, made of California redwood, lasted at least four seasons, unless damaged in some way. Deer sometimes stepped on them and rodents damaged them by gnawing. Some voles learned to open these traps. One such was an adult female red-backed vole (no. 224) for which I had this notation, "Is able to lift trap door with teeth and twist its head around underneath the trap door to escape. It does this purposely." I watched this individual leave and enter the trap several times. I

observed another individual (no. 47) which was unable to get out of the trap even though it tried to open the door with its front feet.

Each trapping station was marked by a stake which projected three feet above the ground. A trap was placed within a radius of five feet of each stake. Usually the trap was placed on the highest point available and near or under something which would provide shade. They were baited with rolled oats, and cotton was supplied for nest material. The traps were placed on the stakes between trapping periods, except for winter months, when the traps were taken indoors.

Traps were observed once a day, always in the morning. The only data consistently recorded for species of small mammals other than the red-backed vole were place and date of capture. Traps containing red-backed voles were taken to the University cabin, where each animal was marked (by toe-clipping), weighed, aged, and sexed. These data and any other pertinent information were recorded in chronological order. After each day's trapping these data were copied into a more permanent notebook (Fig. 7). Information on each individual and for each station was further separated and recorded on separate pages (Figures 8 and 9). At the end of each trapping period the results were summarized (Fig. 10).

Usually, traps were set on Monday and "deactivated" on Friday by placing them on the stakes. Trapping was carried on from May to October each year for eight years (1949 to 1956) and in May and June

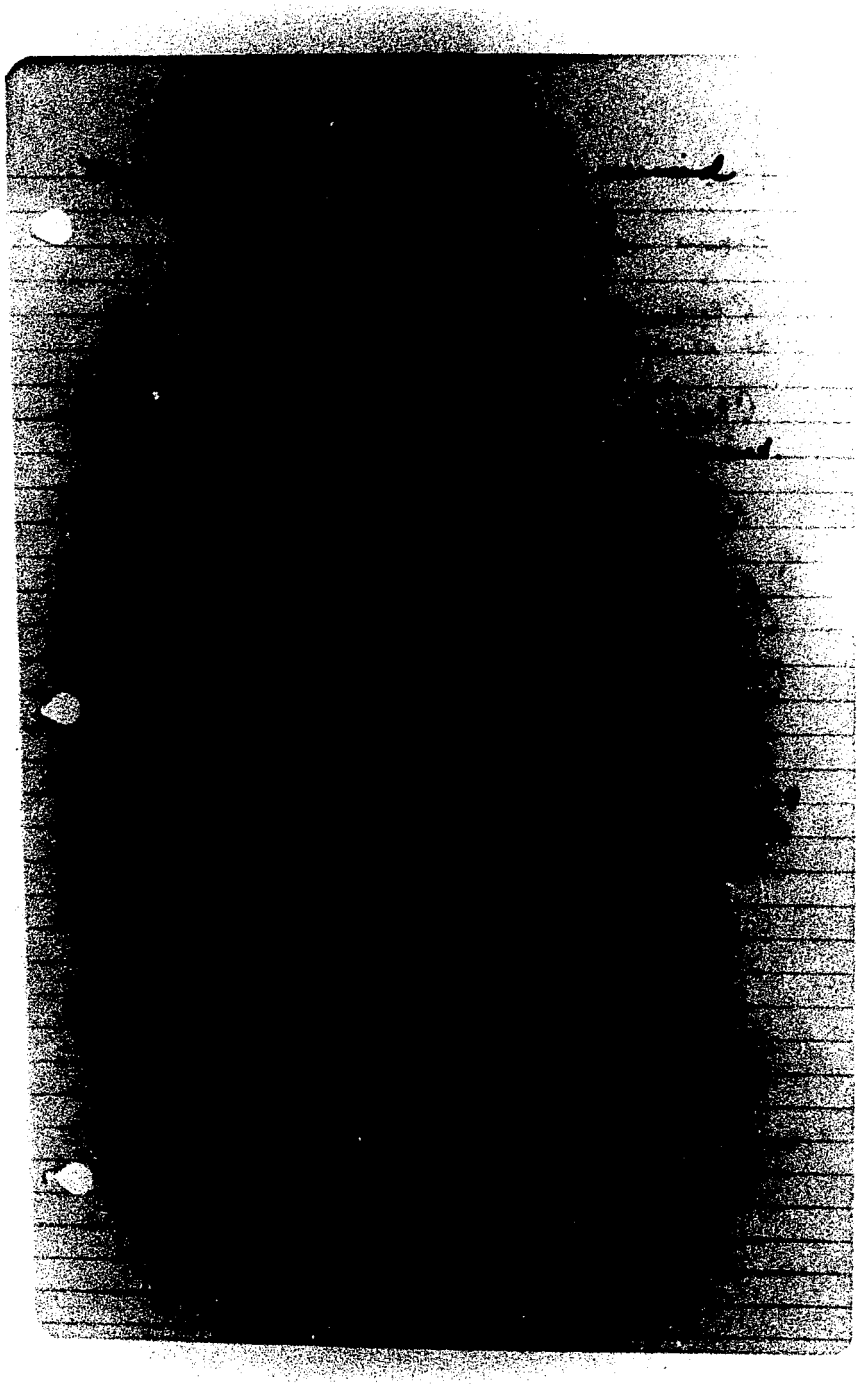


Fig. 7. Sample page of chronological entries of field data.

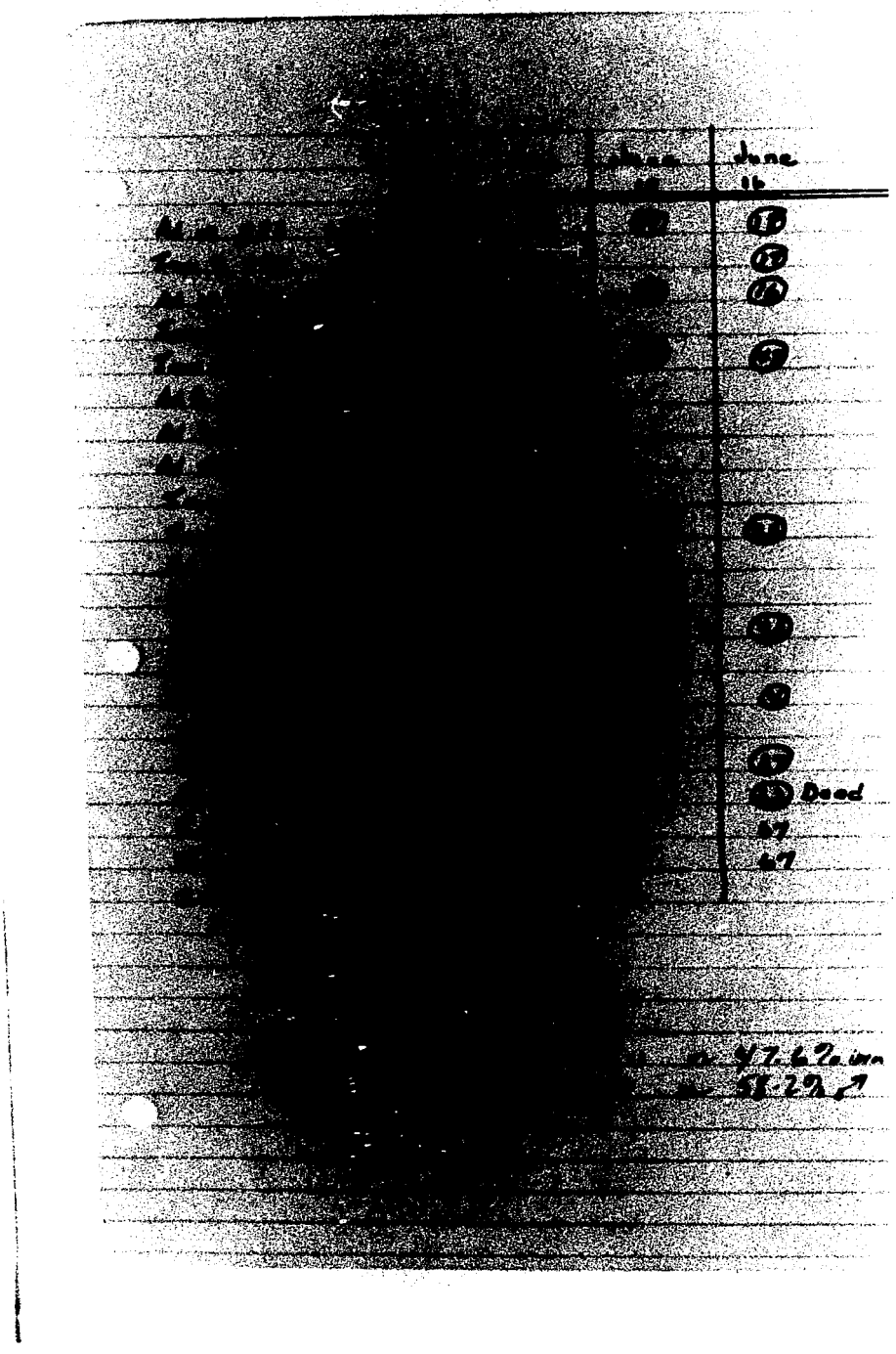


Fig. 8. Sample page of weekly trapping summaries.

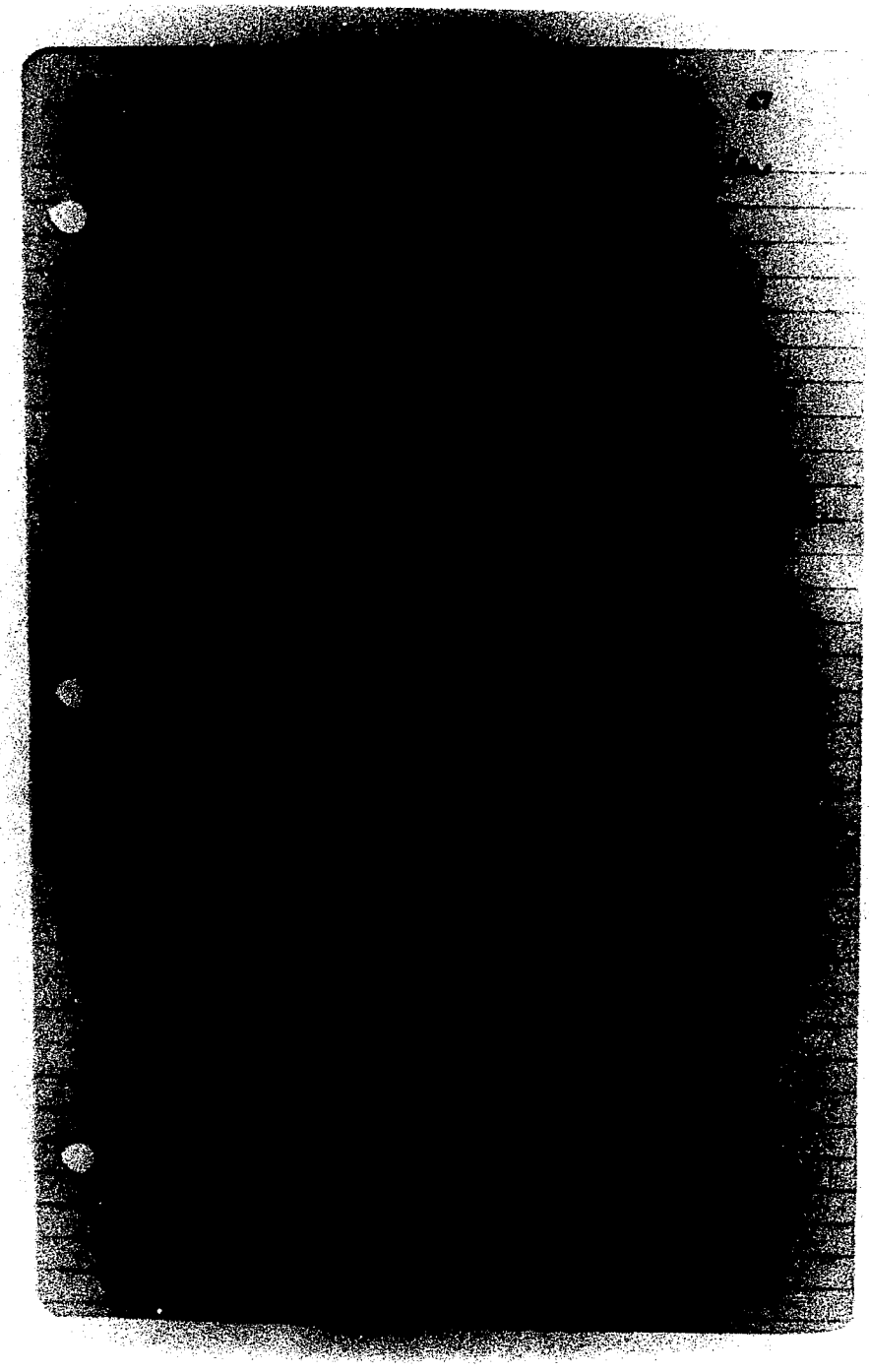


Fig. 9. Sample page of chronological history of one trapping station.

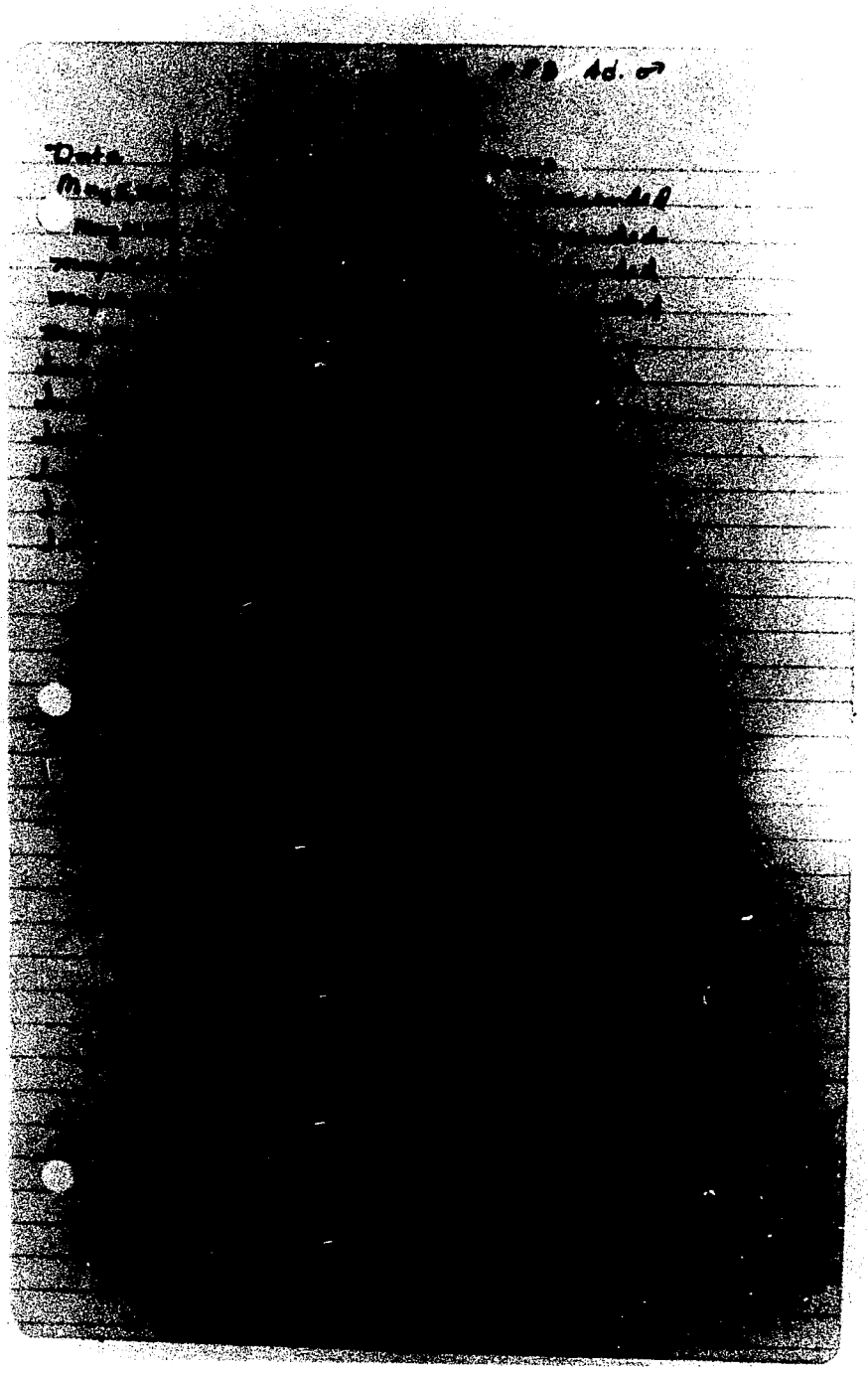


Fig. 10. Sample page of chronological history of one individual.

of 1957. In all, there were 17, 732 trap-nights.

If individual red-backed voles were not released by noon, they quite often showed signs of distress. When such individuals were released near open water they drank copiously. Their signs of distress were attributed to water loss.

GROWTH AND AGE DETERMINATION

In estimating ages of individual voles, two age groups were recognized, adult and immature (young). Individuals capable of breeding were considered adults, all others immatures. Breeding maturity was considered to be attained at between eight and ten weeks. At this age individuals usually weighed between 10 and 12 grams. Those whose weight was at either extreme (less than 10 grams, immature; more than 12 grams, adult) could be assigned easily to an age group.

Evidence for correlating weight with age was afforded by several individuals. One June 29, 1941, four young, still clumsy and poorly coordinated, were caught in the same trap. I estimated their age at about four weeks, for it appeared that they must have recently left their nest. These weighed from 7.0 to 7.9 grams. Svihla (1929) wrote: "The young may be weaned in seventeen days if another litter follows immediately; otherwise, nursing may continue for at least three weeks." Thus, these four young should have been about four weeks old when they weighed approximately seven grams

each.

A female (no. 112), first taken on July 11, 1950, weighed 6.9 grams. The following day she weighed 7.5 grams. To judge from the preceding information, she was probably about a month old at this time. On August 9, thirty days later, she gave birth to young while in the trap. She was presumably between 60 and 70 days old. She would have been less than two months old when she conceived, for according to Svihla (1929) the gestation period is 18 days. She weighed 18.8 grams the day before giving birth and 12.7 grams the day after. At the time of fertilization she probably weighed less than 12.7 grams.

Another female, taken on June 29, 1949, died shortly after she was found in the trap. Her weight was 11.7 grams and she contained six small embryos, one of which measured 2 by 4 millimeters. Although her death could be attributed to lack of water, food, or both (which would decrease her weight), it is safe to assume that she weighed less than 11.7 grams at the time of conception. She was obviously capable of breeding and, therefore, was considered to be adult.

The evidence from these two females is that they were capable of breeding when their weight reached 10 to 11 grams.

This was also believed true of males. On June 30, 1949, a male that weighed 10.1 grams had its testes descended. This was considered a sign of breeding activity. Alan Sargeant (pers. comm.) believes,

from bacular evidence, that male red-backed voles are capable of breeding at slightly over two months of age.

Based on the above evidence, red-backed voles at Cedar Creek Forest weighing less than 11.0 grams were arbitrarily called immature (not capable of breeding) unless there were specific signs of breeding activity. Those weighing 11.0 grams or more were called adults (capable of breeding).

It was more difficult to age individuals in the fall than at any other time. An indication that weight might be gained faster during midsummer than in fall or winter was shown by the following examples. A female (no. 303) caught during midsummer, July 24, 1952, weighed 7.7 grams when first caught, at an assumed age (from the earlier example) of about 30 days. Fifteen days later, at an age of about 42 to 45 days, she had reached a weight of 12.5 grams. In contrast to this, an overwintering adult female had not gained much weight in ten months. She was caught twice in August, 1949 and weighed 14.6 and 13.1 grams. In May, 1950 she weighed 13.6 grams when first taken, but gained about two grams in three days, and weighed 15.8 grams when last taken.

Another criterion used in age determination was pelage color. This was useful for very young animals, or for those older than three months. In the young animal (from one to two months old) the pelage was grayish, particularly on the underside. As the animal grew, the underside gradually became lighter, finally taking on a yellow-gray

appearance. At the same time the tone of the back lost some of its grayness, getting both redder and paler as a result. This change was completed in three months. Any animal that was yellow-gray on the sides and underside and quite reddish on the back was considered an adult.

In summary, the three criteria used to determine whether an individual was immature or adult were: weight, pelage color, and breeding condition.

TRAPPING RESULTS

Total Number of Captures of Each Species

In the eight and one half years of this project (17, 732 trap-nights) four hundred and twenty-six red-backed voles (Clethrionomys gapperi Vigors) were captured and marked; there were 1, 078 captures. Two hundred and thirty-nine died in the traps the first time they were caught.

Few data, except the date and station, were recorded for other species of mammals trapped. The comparative abundance of mammals in the bog as revealed by live-trapping, is shown in Table 3.

Table 3. Number of captures of small mammals, arranged in descending order

Species	Number of Captures
Red-backed vole (Clethrionomys gapperi)	1,078
Meadow vole (Microtus pennsylvanicus)	176
Masked shrew (Sorex cinereus)	101
White-footed mouse (Peromyscus leucopus)	54
Meadow jumping mouse (Zapus hudsonius)	42
Shorttailed weasel (Mustela erminea)	14
Eastern chipmunk (Tamias striatus)	14
Shorttailed shrew (Blarina brevicauda)	6
Pygmy shrew (Microsorex hoyi)	3
Water shrew (Sorex palustris)	2

Masked shrews were caught in five of the years; 1949, 1950, 1951, 1952, and 1955. Sixty-one were caught in 1951. The first of these was taken on July 31, fourteen were trapped on August 23, and the last was caught on October 5, the last day of that trapping season. Shorttailed shrews were caught during only two seasons. One was taken in 1949 and five in 1950. Two water shrews were trapped in 1955. Shorttailed weasels were caught during four years; 1949, 1950, 1952, and 1955. This carnivore was quite cramped when in the trap and represented the upper size of mammals which could be caught in this size trap. Fourteen eastern chipmunks were caught during the first four years; none the last four and one half. White-footed mice (only Peromyscus leucopus was present in the area) were caught each year. Meadow voles were taken in six consecutive years, 1950 to 1955, and in greater numbers but during fewer seasons (six) than white-footed mice. Jumping mice were caught during five

seasons; 1949, 1950, 1951, 1952, and 1955. One pygmy shrew was taken in 1950 and two in 1951. Pygmy and water shrews are rare in Minnesota. No arctic shrews were caught.

Discussion of Trapping Results by Years

The data accumulated by live trapping for each four-night period will be discussed in greater detail for the red-backed vole than for other species. The numbers of individuals (young and adults) of this species taken in each period are indicated in Figures 13 to 20.

1949

In the first four-night period (324 trap-nights), May 11 to 14, only one red-backed vole, a pregnant adult female, was caught; she weighed 23.3 grams. In the next trapping period, May 30 to June 3, one immature and eight adults were captured; five were males and four were females.

From June 27 to July 1, thirty-two individuals were caught, five of which were unmarked dead. Fourteen were immatures and 18 were females. One dead adult female weighed 11.7 grams and contained six embryos. Three males in the trap at station 36 on June 28 probably represented three age groups because of their diverse weights, 6.5, 12.7, and 21.6 grams, respectively. Because only two age groups were used in this work, the individuals that

weighed 12.7 and 21.6 grams were classed as adults. The one that weighed 6.5 grams was apparently just out of the nest. The trap at station 38 contained four young. Because of their poor muscular coordination they were believed to have left the nest very recently. The young weighed 7.0, 7.3, 7.5, and 7.9 grams. The one that weighed 7.0 grams measured 88-22-16 millimeters. The others were not measured. One of these individuals was recaptured the following day, again at station 36, together with an unmarked individual that weighed 7.4 grams. Two were caught at station 53. Two (numbers 20 and 22) were dead in the trap at station 53 on the third day (July 1). Six young that weighed 7.9 grams or less appeared in the traps during this period. These individuals were probably between three and four weeks old, if weaning takes place at three weeks (Svihla, 1929), and, therefore, they were born in the last week of May or the first week of June. Breeding activity would then have started about the second week of May.

In the next period, July 25 to 29, fifteen individuals were caught. Of these, six were young; nine were females. One adult female weighed 27.2 grams and was probably about ready to give birth to young. This was an unusually heavy red-backed vole. The smallest individual taken weighed 7.7 grams.

In the fifth trapping period, August 22 to 26, twelve individuals were captured. Three of these were immature. There were six females and six males.

In the last trapping period, October 17 to 21, of the 1949 season, nineteen individuals were caught. Of these, seven were judged to be immature. Six were females; 13 were males. There was little reproductive activity during this last period. In my field notes I wrote, "During this week's trapping period I found no males with descended testes and no females with open vaginas."

In 1949, ninety-nine red-backed voles were captured 164 times; 48 were females, 51 were males.

1950

Nine adults were caught in the first trapping period, May 1 to 5. Five of these were females. Two individuals had been marked in the previous year. One adult female (No. 59) weighed 14.5 grams when first taken on August 23, 1949. This year she weighed 13.6 grams on May 2, 15.5 grams on May 4, and 15.6 grams on May 6. The other, an adult male (no. 63), weighed 14.2 grams when first taken on October 18, 1949. It weighed 17.2 grams on May 2, 1950. Another adult female (no. 80) taken on May 2 was in "bright" red pelage and was probably also an overwintering individual. Its weight was 13.0 grams. Two masked shrews were caught, the only time during the whole project that these shrews were taken in early May.

In the four nights of May 23 to 27, eleven red-backed voles were captured. Only one of the 11 was immature. It weighed 6.8 grams and measured 83 millimeters, but could not be sexed. None

of the others weighed less than 15.2 grams. Four of the ten adults were females.

The population had increased to 21 individuals, taken in the period June 12 to 16. Twelve, or more than half, were immature. This was the highest ratio of young taken in the 1950 season. Nine of the 21 were females. Another overwintering individual, an adult female, was taken June 13, 1950; weight, 17.4 grams. When first captured, on July 26, 1949, she was immature and weighed 7.7 grams. She was not taken again.

In the period July 10 to 14, forty-two individuals were caught. Of these, 12 were considered immature; 17 were females. This was the peak population for this season, but it did not contain the highest ratio of young. Within this period, on July 12, an adult female with three newly-born young was in the trap at station 26. One of the young weighed 1.6 grams and measured 12 millimeters long. The trap was left open and the following day the young were gone. The first meadow vole taken in the area was on July 13. A dead female pygmy shrew with six embryos was found in the trap at station 49. Two shorttailed shrews were taken; one in a trap with a partly eaten red-backed vole. No markings could be discerned on the uneaten part of the red-backed vole.

The next trapping period, August 7 to 11, was the driest I had experienced in the bog to that time. Twenty-nine individuals were caught, fewer than in the last period. Nine were young; eighteen

were females. An adult female taken on August 8, at station 15, weighed 18.8 grams. The following day at station 21 she and four newly born young were in the trap. Her weight had dropped 6.1 grams, from 18.8 to 12.7. One of the young weighed 1.2 grams. An immature (weight 5.3 grams) taken on August 11 at station 54 had probably left the nest recently. The second peak of young (31.0 per cent of the total) appeared in this period.

In the sixth trapping period of the season, September 4 to 8, twenty-three individuals were taken. Five were young; seventeen were females. It became difficult at this time of year to determine the age of the individuals.

In the seventh trapping period, September 26 to 29, twenty-one individuals were caught; three were young and 15 were females. One female (no. 188) was carrying young and another (no. 175) was lactating. Testes were descended in only one of six males. Reproductive activity was diminishing.

The last trapping period of the season was October 16 to 20, when 19 individuals were caught. Of these, only two were considered immature; thirteen were females. One female weighed 23.4 grams and had enlarged mammaries. None of the males had descended testes. Reproductive activity was at a minimum.

In 1950, one hundred and seventy-five red-backed voles were captured 281 times; 100 were females, and 74 were males. The sex

of one immature could not be determined.

1951

Two adult red-backed voles were taken in the first trapping period, May 7 to 11. One was a female of 13.2 grams and the other a male of 13.0 grams.

From May 28 to June 1, seven adults were trapped; two were females. One of the adult males (no. 94) was first caught in 1950. In that year it was taken twice, on June 13 and on June 16, at stations 14 and 17 in the southwestern corner of the area. On May 29, 1951, it was taken at station 81 in the extreme northeastern corner of the area. It weighed 18.4 grams.

In the trapping period, June 18 to 22, seventeen individuals were caught. Twelve were females; twelve were young. These were the first young to appear in the traps this season.

From July 8 to 13 nine adult males were caught. On July 9, I wrote, "Water level in the bog is very high for this time of the year and much higher than it was during the last trapping period." It was possible the numbers had been reduced by the high water in the bog.

Eleven individuals were caught in the period July 30 to August 3. One of these was considered immature; three were females. The first masked shrew for this season was caught July 31. In all, five masked shrews were taken in this period. It was still extremely wet in the bog, for on August 3 I had written, "Last year at this time

I could go through with tennis shoes and not get wet, but this year I still have to wear hip boots."

During the trapping period of August 20 to 24 the water level in the bog was still very high. Heavy rains on a Monday made it necessary to shift the period to start on a Tuesday. Fourteen red-backed voles were caught. Five of these were young; nine were females. Thirty-six masked shrews were taken in the period. This was the greatest number taken in any period. Of the 36, only two were alive. In one instance two were in the same trap, one alive, the other partly eaten. Because the first shrew of the season was taken on July 31, it would seem that some were moving into the area, rather than all being residents. Twenty-five individuals averaged 3.13 grams (2.3 to 5.1 grams). Only four weighed less than 3 grams. A pygmy shrew caught in this period weighed 2.7 grams.

The trapping period of September 10 to 14 was also extremely wet. It had rained for two nights prior to the beginning and during the second night's trapping, 1.91 inches of rainfall was recorded at the Minneapolis Weather Bureau Station, thirty airline miles away. This rainfall probably adversely affected the trapping results. Seven red-backed voles were caught. Four were young; five were females. Nine masked shrews were taken, a considerable decline from the 36 (34 dead) caught in the previous period.

In the last trapping period, October 1 to 5, seventeen individuals were taken. There were five young; ten were females. There was

little evidence of reproductive activity in the red-backed voles. Eleven masked shrews were caught.

In 1951, eighty-four red-backed voles were captured 151 times; 32 were females, 42 were males.

1952

The greatest number of red-backed voles caught in the first period in any May was during May 12 to 16, 1952, when twelve were trapped. All were adult; four were females. A dead adult female (wt. 25.0 grams) contained five embryos. Another female (wt. 27.8 grams) was judged to be ready to give birth to young. The testes of all the males were scrotal. A female (no. 262) and a male (no. 263) recaptured on May 15, were taken first on October 5, 1951. No individual weighed less than 15.1 grams.

Only eight individuals were caught in the next trapping period, June 2 to 8. One was an immature; three were females. The immature weighed 5.3 grams. On June 5, most of the traps from stations 10 to 49 had been molested, apparently by a raccoon. Some traps had the cotton pulled out (this is why I suspected a raccoon rather than a fox), others were tipped over or had toppled in the water. There were no remains of red-backed voles in any of the molested traps. Probably the traps had been disturbed in the early part of the evening before the red-backed voles had gotten to them. The traps were also disturbed the following night. During this

trapping period the water level in the bog was quite low.

From June 24 to 28, twenty-four red-backed voles were caught. One was immature; thirteen were females. On June 25 a shorttailed weasel was taken in a trap with a partly eaten red-backed vole. The sharp increase in numbers taken in this period, over the last, might be partly accounted for by the disturbance of the traps by raccoon(s) in the last period.

From July 21 to 25, forty-five individuals were caught. This was the greatest number taken in any one trapping period. Six were immatures; twenty-one were females. From this high there was a sharp decline in numbers in each successive trapping period.

From August 4 to 8, thirty-four voles were taken. Three of these were immature; there was one unsexed individual, but of the sexed, 15 were females. Twenty-eight of the 34 were marked prior to this trapping period, an exceedingly high ratio of recaptures.

In the sixth trapping period of the season, August 25 to 29, twenty-four individuals were caught. Three were young; thirteen were females. Twelve of the 24 were marked prior to this trapping period. On August 28 a high-pitched squeaking emanating from a hummock between stations 49 and 60 led me to a red-backed vole nest containing five young. One of the young weighed 4.5 grams; the others were not weighed. The nest was near the top of a sphagnum hummock which projected about four inches above the surface of the immediate vicinity. The diameter of the hummock was between

four and five inches. The nest itself was simple, just a hollow in the sphagnum, without any other nesting material. There was an indistinct entrance (looser sphagnum) from the northwest. The nest was not further disturbed until several days later, when it was again examined. The young were gone. In this trapping period three masked shrews were caught. Only two had been taken previously this year.

Eighteen red-backed voles were caught from September 14 to 18. Five were young; six were females. Eight masked shrews were caught.

In the last trapping period of the year, October 6 to 10, nine individuals were taken. One was judged to be an immature; five were females. There was no indication of reproductive activity.

In 1952, one hundred and seventy-three red-backed voles were taken 286 times; 78 were females, 94 were males. The sex of one immature could not be determined.

In the first four years there were either seven or eight trapping periods each year, from spring to fall. These were spaced approximately three weeks apart. For the last four years, trapping periods were reduced to five each year, from spring to fall. The periods were spaced (in time) to get a sampling from the early spring, breeding, and fall populations.

1953

No red-backed voles were taken in the first period of this year, May 5 to 9. In the next period, June 22 to 26, four adults were caught; two were females. A raccoon had disturbed some of the traps in the northeastern corner of the area.

From July 14 to 18, ten individuals were caught. Of these, one was immature; two were females. A raccoon had again disturbed the traps on the nights of July 17 and 18. The water level was high in the bog during this period.

Only one red-backed vole, an adult male, was caught in the September 1 to 5 period. A meadow vole and a white-footed mouse were taken. Three captures in 324 trap-nights indicated a very low population of small mammals.

From October 5 to 9, four red-backed voles were caught. One was immature; three were females.

In 1953, nineteen red-backed voles were taken 36 times; seven were females, 12 were males.

1954

In the first trapping period this year, May 10 to 14, no small mammals of any species were taken. Some of the traps had been disturbed by some animal on the night of May 11.

From June 21 to 25, nine adult red-backed voles were caught. Four were females. One adult male (no. 372) had four partially

engorged wood ticks on its head.

In the period, July 26 to 30, fifteen red-backed voles were taken. One was immature; eight were females. An adult male (no. 354) taken on July 28 was caught twice in the previous year. In 1953 it weighed 22.4 grams on July 15, and again on July 16. On July 28, 1954, it weighed 18.7 grams. Three hundred and seventy-eight days had elapsed between its first and last capture. Twenty meadow voles were taken in this period; four were dead in the traps. It rained every day of the period, and this may have affected them adversely. One of the red-backed voles was also dead in the trap.

Twenty red-backed voles were taken from September 14 to 18. Seven were young; eleven were females. It rained three of the four nights of the period.

Nine individuals were taken in the last period, October 4 to 8. One was immature; five were females.

In the year 1954, fifty-three red-backed voles were captured 76 times; 28 were females, 25 were males.

1955

No mammals of any species were taken in the first period, May 2 to 6. In the second period, June 20 to 24, seventeen red-backed voles were caught. Two were immature; five were females. There were 23 captures (not individuals) of meadow voles; one masked shrew was caught. Twenty-one adult red-backed voles were caught in the

period July 18 to 22; nine were females. Meadow voles were taken 19 times. From August 29 to September 2, six adult red-backed voles were caught; five were females. Meadow voles were caught 27 times. The meadow vole population was high in the last three periods. I am unable to suggest a reason for this.

In the last trapping period of the season, October 3 to 7, five red-backed voles were taken. All were considered adult, although one was questionable. Four were females. Meadow voles were taken six times. There was as much water in the bog now as in early spring.

In 1955, forty-nine red-backed voles were taken 71 times; 23 were females, 26 were males.

1956

In the period May 6 to 11, one adult female red-backed vole was trapped. Prior to, and during the next period, June 18 to 22, there was a great deal of rain and the water in the bog was extremely high. Only three red-backed voles were caught; one was immature; one was a female.

The water was the "highest I had ever seen it" in the bog during the period of July 22 to 27. Two adults were caught, a male and a female. Only one red-backed vole, an adult female, was taken in the next trapping period, August 27 to 31. There were three white-footed mice, but no meadow voles in the traps. The high water level had

probably left little habitat available for occupancy. In the last period, October 15 to 19, six adult individuals were caught. Three were females.

In 1956, thirteen individuals were taken 14 times, once each except for one taken twice; six were females, seven were males.

1957

In 1957 the water was so high that nothing was caught in the two trapping periods of May 7 to 10 and July 1 to 5. The second period was postponed one week because it was impossible to reach Cedar Creek Forest by automobile because of washed out roads. The information for 1957 is included only to indicate the extreme effect of a high water level on the small mammal populations in a bog at Cedar Creek Forest. The project was terminated.

DISCUSSION OF POPULATION DENSITY CHANGES

The intent of this project was not to obtain an absolute census of red-backed voles on a per acre basis. Rather it was to sample the population periodically in such a manner that changes in density could be detected.

Ideally, the area which such a population occupies should be a large homogeneous habitat of the species studied, so that the sample is from the entire population. Realistically, the limits on the size of the area are usually determined by the number and spacing of traps

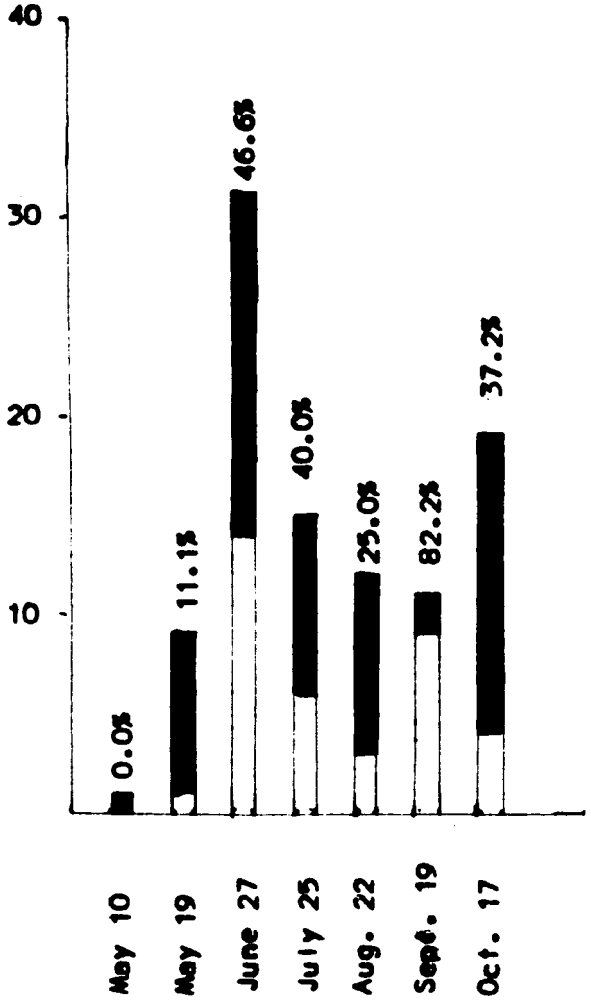


Fig. 11. Summary of weekly trapping results for 1949. Number of individuals along ordinate. Clear areas of bars indicate young, black areas adults. Percentage figures are of young.

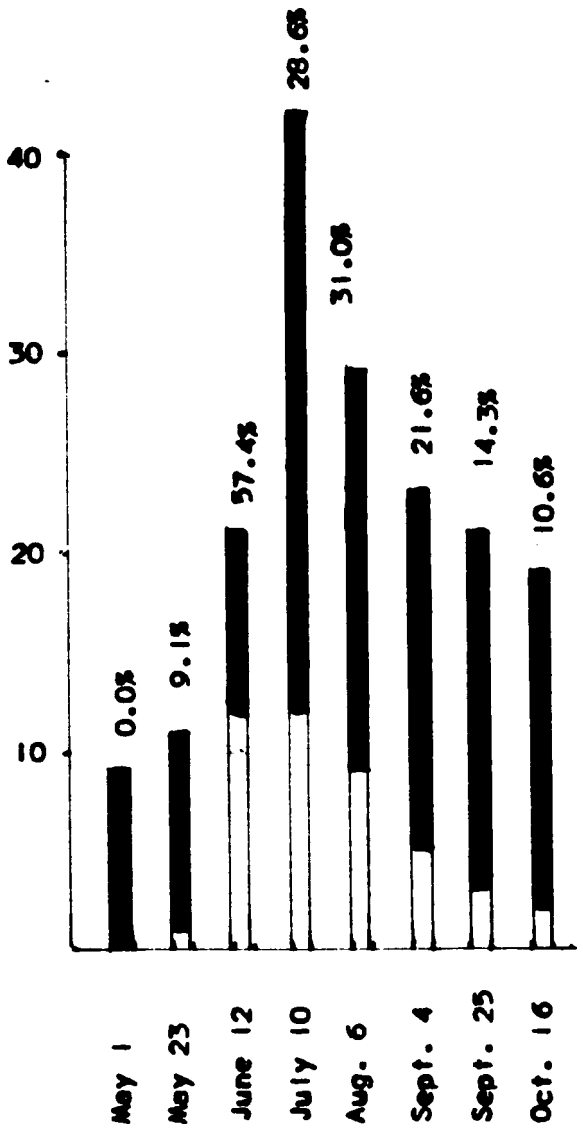


Fig. 12. Summary of weekly trapping results for 1950. Number of individuals along ordinate. Clear areas of bars indicate young, black areas adults. Percentage figures are of young.

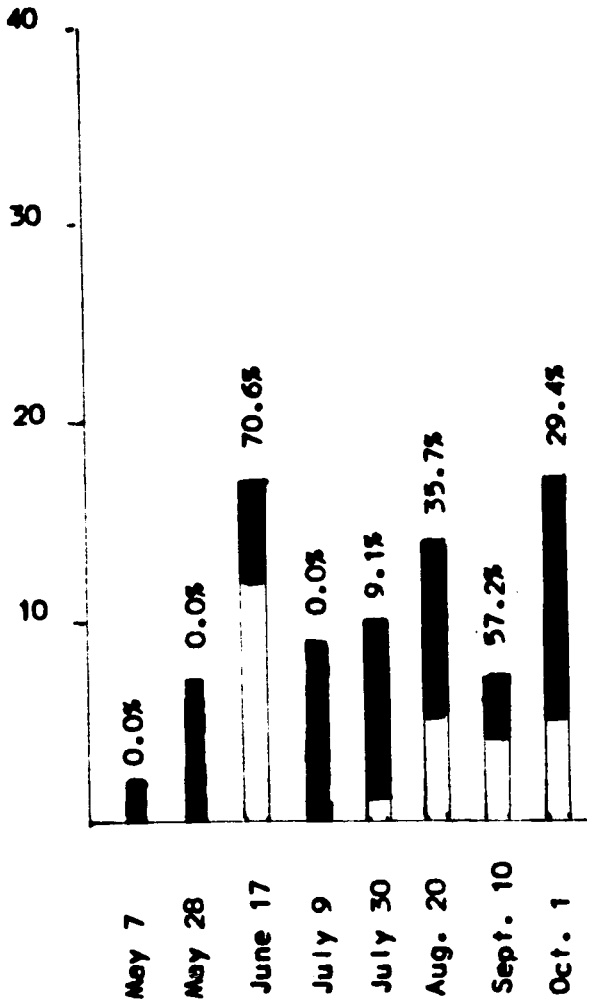


Fig. 13. Summary of weekly trapping results for 1951. Number of individuals along ordinate. Clear areas of bars indicate young, black areas adults. Percentage figures are of young.

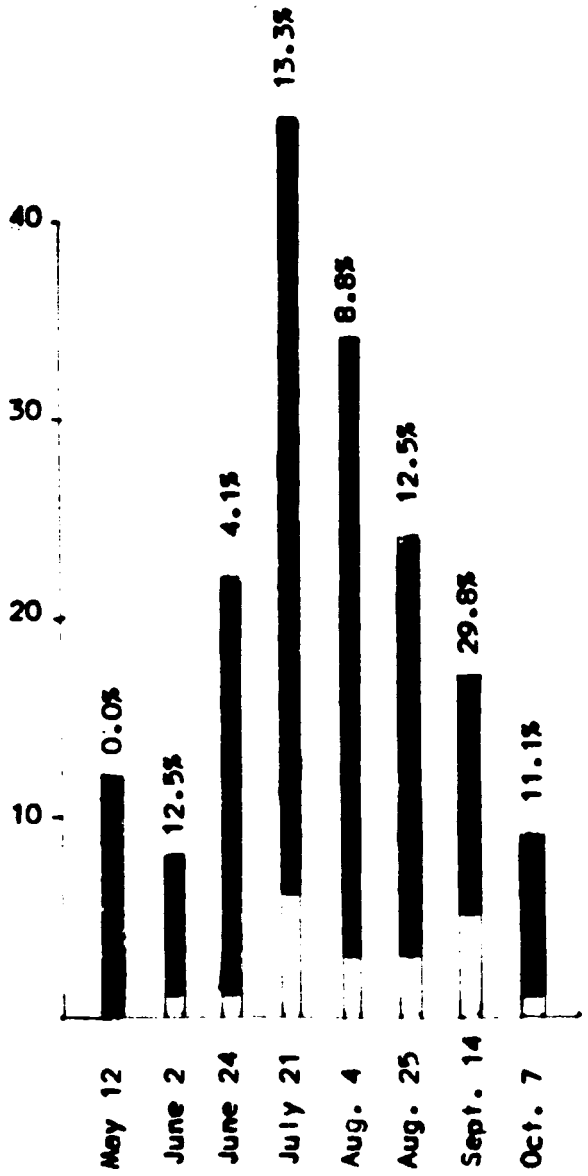


Fig. 14. Summary of weekly trapping results for 1952. Number of individuals along ordinate. Clear areas of bars indicate young, black areas adults. Percentage figures are of young.

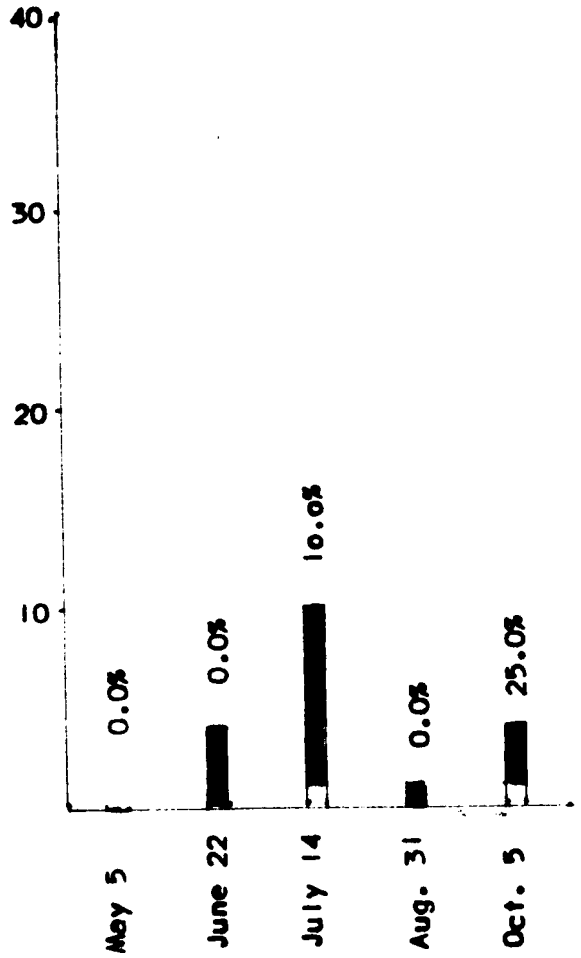


Fig. 15. Summary of weekly trapping results for 1953. Number of individuals along ordinate. Clear areas of bars indicate young, black areas adults. Percentage figures are of young.

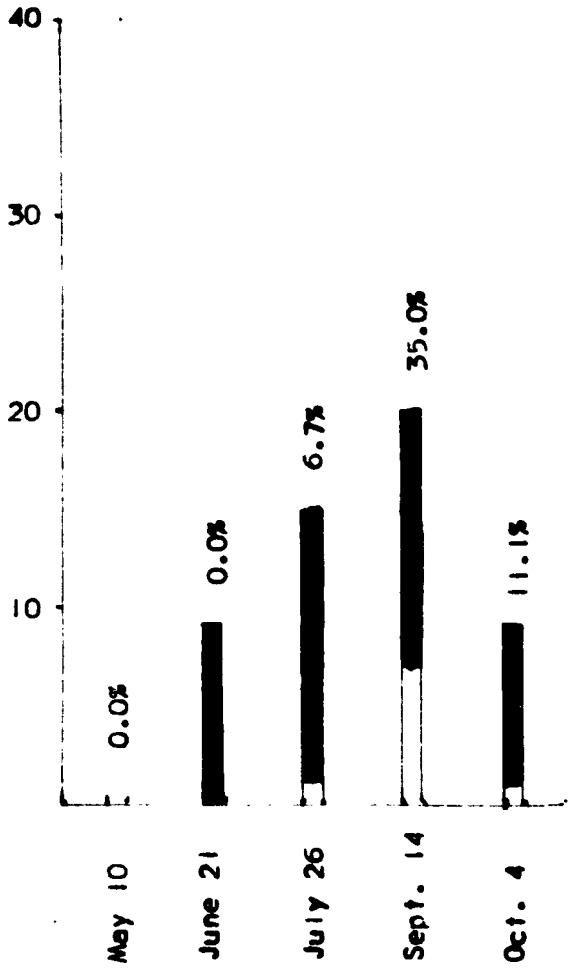


Fig. 16. Summary of weekly trapping results for 1954. Number of individuals along ordinate. Clear areas of bars indicate young, black areas adults. Percentage figures are of young.

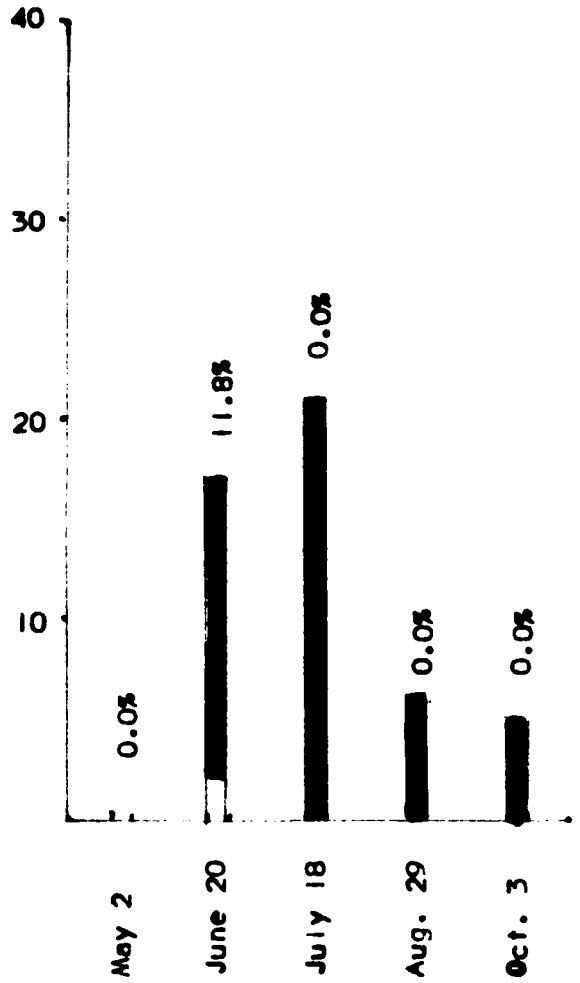


Fig. 17. Summary of weekly trapping results for 1955. Number of individuals along ordinate. Clear areas of bars indicate young, black areas adults. Percentage figures are of young.

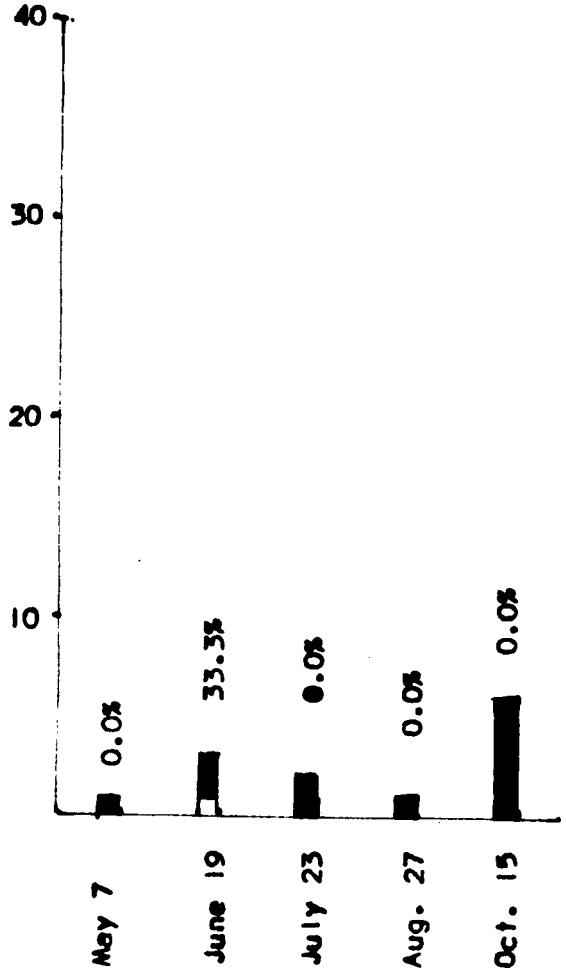


Fig. 18. Summary of weekly trapping results for 1956. Number of individuals along ordinate. Clear areas of bars indicate young, black areas adults. Percentage figures are of young.

that the researcher can handle. In this project 81 live traps, spaced 52 feet apart covered five acres. This acreage figure included a boundary strip on each side of the area, the width of which equalled half the distance between traps.

There was the same number of trap nights (four) in each trapping period, but not the same number of trapping periods in each year. Thus, the number of individuals caught in any four-night trapping period can be compared with the number of individuals caught in any other four-night trapping period, but the number of individuals taken in any given year cannot be compared directly with the number of individuals taken in any other year.

In temperate climates the characteristic seasonal pattern of density changes in small mammal populations contains a peak sometime in midsummer, then a gradual decrease in numbers to a low sometime in the spring. Breeding activity is at a minimum (or stopped) during the winter season. Most workers are of the opinion that very few individuals in a population of small rodents overwinter (Baker and Ranson, 1933; Blair, 1948; Burt, 1940; Hamilton, 1937; Frenzel, 1957, and others)

Although it would seem that in temperate climates a greater mortality occurs in winter than at other seasons, this may not be true for small mammals. Burt (1940) stated that, "The population curve throughout the year reflects the breeding activity of the animals." Blair (1948) wrote about his work in southern Michigan,

"The individual small mammal's chance of surviving are, therefore, roughly equal at all seasons of the year."

With the arrival of spring, reproductive activity either begins or increases (if there has been reproductive activity during the winter). Although there may be some reproductive activity at all seasons, there are usually two major peaks, the second not as great as the first, sometime in summer.

The bog at Cedar Creek Forest, in which this work was done, is surrounded partly by lake, by marsh and by higher land nearby. This high land nearby may serve as a refuge for some animals when the water is high in the bog. The lowest red-backed vole populations for each year (except in 1952) occurred in the first trapping period in the spring. At this time of year there was either much water or ice in the bog, sometimes water on top of the ice. By the time of the second trapping period, which was the last week of May at the earliest, the water usually had receded and the ice was gone. Normally there was an increase in number of individuals taken in the second period, again with the exception of 1952, as shown in Figures 13 to 20.

Contributions to this increase may have come from several sources. The appearance (in traps) of young out of the nest contributed to this increase in the years 1949, 1950, 1955, and 1956. Two other sources are possible: (1) the voles moved to higher ground in the winter or in the spring thaw and were not present in the first

period, but might have moved back into the bog when the water receded; (2) movements of the animals were diminished, thereby making their access to the traps more difficult, in times of high water, such as might occur in the first or second week of May. Buell and Buell (1941) have reported on surface level fluctuations taken along a transect from the upland through the bog to the sedge mat. These measurements were taken semiannually, spring and fall, from 1934 to 1939. The highest surface levels at all stations along the transect were recorded in the spring of 1936. The lowest levels were recorded in the fall of 1936 at stations A and B, and in the fall of 1934 at stations C, D, E, and F. They wrote, "The extent of this fluctuation in bog level varies from a small but appreciable change (about 4 inches) in mature bog underlain by rather solid peat, to a foot and one half and more in marginal bog forest of tamarack underlain by less compact peat."

In the four years, 1950, 1951, 1955, and 1956, the greatest proportion of young to adults appeared in June or July. In the other years, the greatest proportion of young to adults appeared in September or in October (1953). In the week of September 19 to 23, 1949, nine of 11 red-backed voles taken were young. Eight of these young were caught in traps at stations adjacent to each other, and might have been from the same litter.

The highest population for any trapping period was in 1952.

Forty-five individuals were taken in the week of June 24 to 28 (Fig. 16). The next highest peak was in 1950, when 42 individuals were caught in the week of July 10 to 14 (Fig. 14). The trapping success ratio (number of red-backed voles taken per 100 trap-nights) for the two years was almost the same; 6.75 for 1950 and 6.67 for 1952 (Fig. 22).

Four factors which might favor these high populations were present in both years. These four were: (1) low water in the bog; (2) cool summer seasons; (3) a series of productive years prior to 1952; (4) a high proportion of young in the fall of the previous year. The mean monthly rainfall at Cambridge, Minnesota (Table 2) was the lowest for the seasons 1950 and 1952. The average monthly temperature was also the lowest for these two seasons (Table 1), although in the bog the maximum temperature of 94°F. was recorded on August 10 and 11, 1952. A series of productive years prior to and including 1952 are suggested by these figures: the lowest population figure (3.24 per hundred trap-nights in 1951) for the years 1949 to 1952 was only slightly lower than the highest figure for the last four years (1953 to 1956), 3.27 in 1954. The ratio of young to adults (37.2%) in October, 1949, was the highest for any October, followed by the ratio of 29.4% in 1951.

In each of the two years of highest populations, there was a gradual decline from the midsummer peak to a low in October. This pattern was not comparable with the other years. In 1949,

1951, 1953, and 1956 there was a slight increase in numbers in October from the previous lows. In 1951 the October peak equaled the highest peak of the midsummer season.

The greatest difference in population density from one year to the next was the decline from 1952 (6.67 individuals per 100 trap-nights) to 1953 (1.17 per 100 trap-nights). This probably represents what is sometimes called a "population crash." In 1953, shrews or weasels (predators of mice) or jumping mice were taken and only four white-footed mice and 16 meadow voles were caught. Reasons for this drastic reduction in numbers of red-backed voles might be: (1) high water in the bog, mentioned several times in my field notes, and corroborated by the high monthly rainfall recorded at Cambridge, Minnesota (about ten miles away), which amounted to 3.92 inches for the season; (2) a raccoon that may have hunted the area intensively, for some of the traps were disturbed in the trapping periods of June 22 to 26 and July 14 to 18; (3) a paucity of females in the population, with only seven of 19 individuals (36.8%) being females, the lowest ratio for any year; (4) a high proportion of adults in each period of the previous year, 1952 (Fig. 14).

A similar "crash" was recorded for the same year in southeastern Manitoba by Buckner (1957). He wrote, "...the low numbers of C. gapperi in 1953, and the absence of this species in the trapping records of 1954, except on Plot 3, suggest 'population crashes.'"

Table 4. Summary of sex ratios by years

Year	Females	Males	Ratio of females to males, %
1949	48	51	48.5
1950	100	74	57.5
1951	42	42	50.0
1952	78	94	45.4
1953	7	12	36.8
1954	28	25	52.8
1955	23	26	46.9
1956	6	7	46.2

The two years following 1953 had higher densities of red-backed voles, 3.27 in 1954 and 3.02 in 1955. The average monthly rainfall in 1954 at Cambridge, Minnesota, 4.61 inches, was the highest for any season. It also followed a year of relatively high rainfall (see Table 2). Moreover, both 1955 and 1956 had high rainfalls and this probably had a cumulative effect, raising the water in the bog to a high level. In my field notes of 1955 are repeated references to the high water in the bog, making travel difficult, even during the last trapping period of the season, October 3 to 7. There were seventy-five captures of meadow voles during the season. This was the greatest number of captures in any year and was nearly twice as many as for the previous year (38). This increase in captures of meadow voles suggested some temporary change in the habitat, perhaps a change in size of favorable habitat (discussed in the chapter, The Mammals in the Bog).

In 1956 0.80 red-backed voles per 100 trap nights were taken.

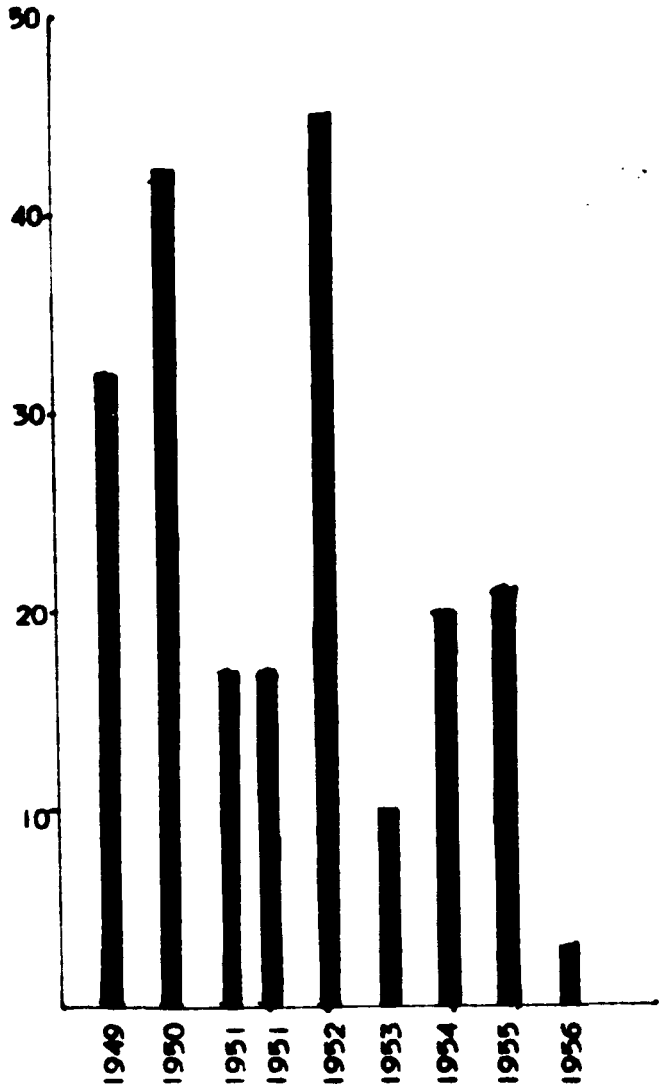


Fig. 19. Number of individuals caught during the peak period of each year. In 1951 there were two equal peaks. Number of individuals along ordinate.

During June 18 to 22 it rained every day, and the water in the bog was "extremely high." During the period of July 22 to 27, the water was "the highest I have ever seen it in the bog." The only other species of mammal taken in the traps during the year was the white-footed mouse. (four). The high water level had probably left little habitat available for occupancy.

The water levels in the bog during the first two trapping periods of 1957 have already been discussed. Nothing was caught.

In the red-backed vole population at Cedar Creek Forest there seemed to be no three-year oscillation in density (Fig. 22) as Morris (1955) has suggested for this species in eastern Canada. Three and four-year oscillations have also been recorded for other species of small rodents, such as the meadow vole (Hamilton, 1937) and lemmings (Elton, 1942, and Pitelka, 1958). For the red-backed voles at Cedar Creek Forest, the first four years of relatively high populations alternated between lows (1949, 1951) and highs (1950, 1952). In 1953 there was a drastic decline in numbers. This same decline (or "population crash") was also recorded for the same year in southeastern Manitoba (Buckner, 1957). There was only a slight increase in numbers in 1954 and 1955, then another decline to a very low population density in 1956. In the only two trapping periods of 1957, no red-backed voles or other species of mammals were trapped. This last decline, from 1954 to 1957, was apparently caused by high water in the bog. Suspected causes for the other fluctuations have

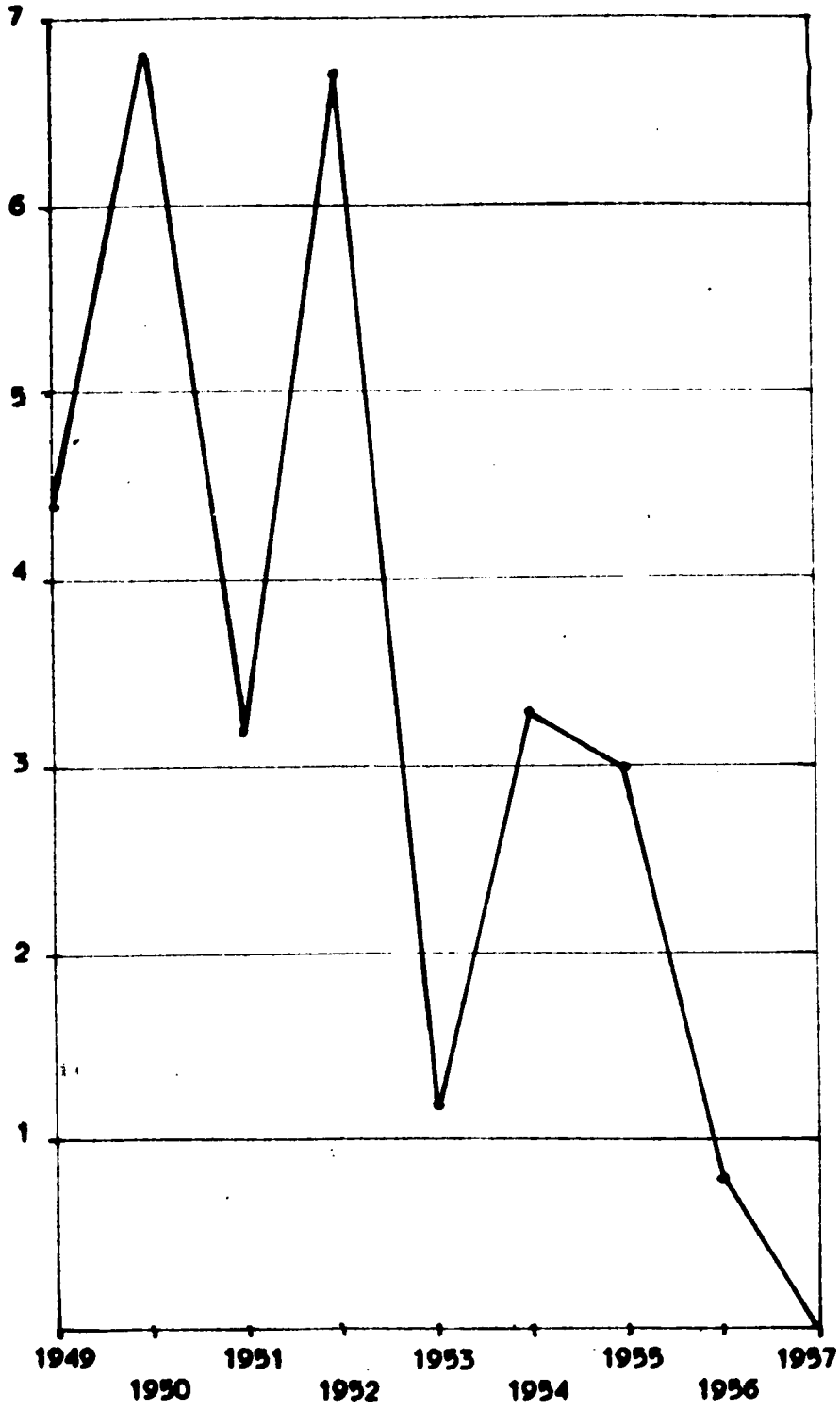


Fig. 20. Annual population of red-backed voles as shown by the number of individuals taken per 100 trap-nights.

already been discussed. At Cedar Creek Forest it was highly probable that some external environmental factors, such as high water level in the bog, temperature, humidity, or some combination of these, was sharply affecting the red-backed vole population.

HOME RANGE OF THE RED-BACKED VOLE

The concept of the home range of a wild animal was probably present in the mind of early man as he hunted the larger mammals for use as food and clothing. But I believe Seton (1909, Vol. 1, pg. 52) first recorded the idea when he wrote, "No wild animal roams at random over the country; each has a home region, even if it is not an actual home."

Burt (1940) defined home range as, "...that area about its established home which is traversed by the animal in its normal activities of food gathering, mating, and caring for young."

This phase of mammalian behaviour has received much attention in the last fifteen or twenty years and many publications have been concerned, if not entirely, at least in part, with home range. The majority of these studies have been done by using live traps, marking the animals, and gaining data by recapturing the marked animals. Calhoun and Casby (1958), Hayne (1949), Mohr (1947), Morris (1955), and Stickel (1954) are among those who have reviewed the methods.

Another way of gaining information is to mark the animals with some radioactive isotope and follow their movements by the use of

Geiger counters. Godfrey (1954) used this method for field voles in England, Johaningsmeier reported on its use for meadow voles in this country at the 1961 meeting of the American Society of Mammalogists, and Kaye (1961) used it for harvest mice.

Several methods are used to calculate home range size from live trapping data. Stickel (1954) grouped these as minimum area method, inclusive boundary strip method, exclusive boundary strip method, observed range length and adjusted range length. The two boundary strip methods are pertinent to this discussion. In each there is a boundary zone around the trap of half the distance to the next trap. The area around each trap in this work was 52 feet square (0.064 acres). In the inclusive boundary strip method, the farthest points of the squares (in which the individual is taken) are connected to form a polygon. The area within this polygon is calculated as the home range size. In the exclusive boundary strip method, the nearest corners are connected.

The inclusive boundary strip method was used in this work. A criticism of this method is that it yields estimates of home range which are too high. In its favor is that it is one of the least subjective methods, it is easy to use, and it has been used by so many workers that it facilitates comparisons between species and between results of different workers for the same species.

The calculated home range of an individual probably rarely coincides with its actual home range (as defined), so the term is

commonly used to designate the area over which a mammal has been trapped. I here use the term to indicate the calculated size which may be only a rough estimate of the actual home range.

All parts of the home range may not be used equally. Patterns of usage may change with the availability of food and cover, with the influence of other individuals, or with the seasonal activities of individuals. One may wonder, if home ranges are so nebulous, why try to calculate them? But they are important in trying to understand the behaviour of a species, in estimating densities, and in trying to learn some basic principles which can be used in population manipulations.

Certain limits are usually imposed on data used in calculating home range in an effort to make the calculated size approach more closely the real size of the home range. An animal taken less than three times is usually excluded from the calculations. So also is an animal which is obviously traveling, such as one caught at widely separated stations in a short period of time.

In this work, the data from individuals captured three or more times were used. Frenzel (1957) showed statistically that, "The use, then, of animals captured three or more times was thought to give mean values of areal movements not significantly different than [sic] those captured four or more times, or five or more times."

Because the same kind of habitat continued beyond the area of trapping, two sets of calculations were made. The first set contained

the data from all individuals taken (more than three times, not traveling) regardless of whether they were caught at edge stations or not. The other set of data includes only those individuals taken at interior stations. These two sets of data are shown in Tables 5 and 6.

Table 5. Home range data in acres for all individuals by year, sex and age

Year	Adult males	Adult females	Imm. males	Imm. females
1949	0.265	0.325	0.135	0.160
1950	0.311	0.265	0.064	0.135
1951	0.403	0.142	0.064	0.064
1952	0.403	0.253	0.064	0.064
1953	0.714	0.448	0.064	0.064
1954	0.296	0.420		
1955	0.160	0.242		
1956		0.256		

The mean calculated home range in acres for all the adults was 0.30 ± 0.02 (2 SE); for the adult males (71) it was 0.33 ± 0.008; for the adult females (60) it was 0.28 ± 0.01. Extreme calculated home ranges for the adult males were from 0.06 to 1.92 acres; for the adult females 0.06 to 1.25 acres. The mean for 15 immatures 0.11 acres; of these, the mean for eight males was 0.096, for seven females 0.13 acres. For the immatures, the samples were so small that only the means were calculated. Extremes for the immature males were 0.064 to 0.135 acres; for the immature females 0.064 to 0.38 acres.

Table 6. Home range data in acres for individuals caught at other than edge stations, by year, sex and age

Year	Adult males	Adult females	Imm. males	Imm. females	Imm. unsexed
1949	0.200	0.405	0.128	0.224	0.282
1950	0.130	0.285	0.064	0.096	
1951	0.083	0.285		0.064	
1952		0.187			
1953					
1954	0.220	0.064			
1955	0.139				
1956		0.256			

The mean calculated home range, in acres, for 30 adults was 0.20 $\pm$ 0.03 (2 SE); for 12 adult males it was 0.15 $\pm$ 0.006; for 18 adult females it was 0.24 $\pm$ 0.002. Extreme calculated home ranges for the adult males were from 0.06 to 0.22 and for the adult females 0.06 to 0.58 acres. The mean for 8 immatures was 0.12 acres (0.06 to 0.26); of these, the mean for three males was 0.10 (0.06 to 0.13), for five females 0.15 acres (0.06 to 0.26).

Table 7. Home ranges in acres of adults taken at all stations and at inner stations only

	Males	Females	Both
All stations	0.33	0.28	0.30
Inner stations	0.15	0.24	0.20

When the habitat beyond the borders of a trapping area appears

to be the same as within the border, animals taken at the border may also be using the area beyond the border. For this reason it would seem that calculated home ranges should be smaller for animals at the edge of the trapping area than those using the more central part of a trapping area. This was not true at Cedar Creek Forest.

Two reasons for this discrepancy are suggested: (1) a greater number of captures was used in the calculations when all stations were included, (2) habitat studies (Gunderson, 1959) showed that the edges of this particular trapping area received more use than the central portion. I believe that the calculated home ranges, from data including edge stations, most nearly approached the real home range of the red-backed voles at Cedar Creek Forest.

Home range estimates for the red-backed vole have been calculated by several workers. Butsch (1954) in a study in northwestern Minnesota gave the average home range of 71 adults as 0.059 acres. His stations were 16 feet apart and the exclusive boundary strip method of calculation was used. Morris (1955) used the same method of calculation and arrived at a figure of 0.6 acres for 15 red-backed voles in a coniferous forest in eastern Canada.

Blair (1941) calculated the average home ranges for four red-backed voles in northern Michigan as 1.30 acres. He used the inclusive boundary strip method. Frenzel (1957) used the same method and calculated the average "areal movement" for 42 red-backed voles in

northeastern Minnesota as 0.83 acres. Unpublished data of Marshall, quoted by Gunderson (1950), gave the home range of five adults as 0.698 acres. In an earlier work at Cedar Creek Forest, Gunderson (1950) calculated the average home range size for three individuals as 0.23 acres, also using the inclusive method. The area trapped was smaller (2.84 acres) and the stations closer (35 feet) than in the present study. The calculated home ranges in the present study were larger than those of Butsch (1954), but less than those of the other workers quoted.

Buckner (1957) gave home ranges of red-backed voles in "cruising radius in feet." He gave cruising radii of 79 feet in one plot and 86 feet in another plot of coniferous forest in southeastern Manitoba. These were calculated from 11 observations in the first plot, 21 in the second plot. The number of individuals involved was not given. Although this is another method used in calculating home ranges, these data are not directly comparable with the other home range calculations available for the red-backed vole.

The wide variation in the calculated home range sizes for red-backed voles may reflect the variables in the techniques used or in characteristics of the different populations. The averages for the calculated home range sizes at Cedar Creek Forest fall somewhere below the mid-range of those calculated by other workers.

LONGEVITY

Information on longevity for small mammals living in the wild is scarce. Usually this information is not actual longevity but a figure derived either from the number of days between first and last capture, or the per cent of individuals surviving from birth for stated intervals of time.

Most workers have been of the opinion that few individuals in a population of small rodents overwinter (Baker and Ranson, 1933; Blair, 1948; Burt, 1940; Frenzel, 1957; Getz, 1960; and Hamilton, 1937).

Still fewer individuals survive two winters. Two workers, Frenzel (1957) and Quimby (1951), each reported two records of jumping mice that lived at least two years. Non-hibernating small rodents have shorter recorded life spans. Blair (1948), using trapping periods about three months apart, has given estimates of the average length of times three species remained on his study plots. For the prairie deer-mouse this was 4.88 ± 2.0 months, for the wood mouse (Peromyscus leucopus) it was 4.64 ± 2.1 months and for the meadow vole it was 4.23 ± 22 months. Frenzel (1957) recorded four meadow voles as living at least 14 months. Getz (1960) recorded two meadow voles that lived at least 11 months on his study area.

In this work, 12 (2.8%) of the 426 live-caught red-backed voles are known to have overwintered. Their history is given in Table 8.

None was known to have survived two winters.

Table 8. History of individuals caught during two seasons

Sex	Number	Days	Dates	Station	Weight, grams
Female	37	321	July 26, 1949	17	7.7
			June 13, 1950	53	17.4
Female	50	276	Aug. 25, 1949	3	13.3
			Oct. 18, 1949	5	12.0
			May 25, 1950	2	18.4
			May 27, 1950	2	15.0
Female	51	257	Aug. 23, 1949	11	14.5
			Aug. 24, 1949	8	13.1
			May 3, 1950	13	13.6
			May 4, 1950	14	15.5
			May 5, 1950	6	15.8
Female	63	235	Oct. 18, 1949	23	14.2
			May 2, 1950	24	17.2
			May 3, 1950	32	17.2
Male	94	351	June 13, 1950	14	8.7
			June 16, 1950	17	9.2
			May 28, 1951	81	18.4
Male	104	370	June 15, 1950	8	18.5
			July 10, 1950	11	17.1
			June 20, 1951	81	18.7
Female	262	224	Oct. 4, 1951	40	9.4
			Oct. 5, 1951	40	11.3
			May 15, 1952	19	16.6
Male	263	265	Oct. 4, 1951	68	----
			Oct. 5, 1951	68	12.9
			May 15, 1952	27	16.4
			May 16, 1952	27	16.1
			June 25, 1952	62	20.6
Male	354	378	July 15, 1953	37	22.4
			July 16, 1953	19	22.4
			July 28, 1954	66	18.7
Female	382	290	Sept. 15, 1954	54	27.9
			Sept. 18, 1954	56	27.3
			June 21, 1955	19	31.4
Male	385	277	Sept. 17, 1954	36	19.3
			June 22, 1955	36	22.7
Male	387	278	Sept. 17, 1954	63	10.0
			Oct. 6, 1954	47	15.4
			June 23, 1955	19	Dead and emaciated

THE MAMMALS IN THE BOG

Ten species of mammals were live-trapped in the bog at Cedar Creek Forest. Of these ten species, five were taken more than 14 times and the other five were taken 14 times or less. The following were taken 14 times or less: water shrew, taken twice (1955); pygmy shrew, three times (1950 and 1951); shorttailed shrew, six times (1949 and 1950); shorttailed weasel, 14 times (1949, 1950, 1952, and 1955); and eastern chipmunk, 14 times (1949, 1950, 1951, and 1952).

The relative abundance of those taken more than 14 times is shown in Table 9. These figures are number of captures (not individuals) taken per 100 trap-nights.

Table 9. Relative abundance for the five most common species based on number of captures (not individuals) per 100 trap-nights.

Year	Species				
	S. c.	P. l.	C. g.	M. p.	Z. h.
1949	0.62	0.49	7.23		0.26
1950	0.27	0.46	10.84	0.46	0.39
1951	2.35	0.08	5.82	0.62	0.58
1952	0.54	0.39	11.03	0.83	0.27
1953		0.25	2.22	0.99	
1954	0.70	0.12	4.69	2.34	
1955	0.25	0.56	4.38	4.63	0.31
1956		0.25	0.80		

S. c. *Sorex cinereus*
P. l. *Peromyscus leucopus*
C. g. *Clethrionomys gapperi*
M. p. *Microtus pennsylvanicus*
Z. h. *Zapus hudsonius*

Of the five species taken more than 14 times, the red-backed vole and the white-footed mouse were the only two caught each year. Of the others, the meadow vole was taken in six consecutive years. There was an increase for each year from 1950 to and including 1955. In that year the figure for the meadow vole was slightly higher (4.63) than for the red-backed vole (4.38). This increase over the six years might be due to an increase in the size of favorable meadow vole habitat. A windstorm in June of 1952 blew down white cedars and tamaracks on the south and east side of the open areas nearest stations 40 and 51 (Fig. 2). This favored the expansion of the cattail, grass, and sedge habitat. In 1956 no meadow voles were taken, but the water was so high that this area was partly inundated.

Jumping mice were taken in the area in the first four years and also in 1955, but they were taken so sporadically that most of them likely were transients. The habitat in the bog was probably not suitable for jumping mice. Quimby (1951) found, "...that jumping mice prefer more or less moist and open habitats."

There is no clear evidence of three- or four-year oscillations in the numbers of any mice in the bog. Peak densities for the white-footed mouse and meadow vole were in 1955, for the red-backed vole in 1952 based on number of captures; (1950, based on number of individuals), and for the jumping mouse in 1951.

Reports of unusual abundances of shrews ("irruptions") occur in the literature. Davis (1940) reported an unusual concentration of

Cryptotis and Fowle and Edwards (1955) reported an unusual abundance in 1947 of the shorttailed shrew in eastern Canada. Of the four species of shrews taken in Cedar Creek Forest (Table 3), the masked shrew was the most abundant, although it was taken in only six years. In 1950 there were 0.27 captures per 100 trap-nights. In 1951 the number rose sharply to 2.35, the maximum, and the following year it declined sharply to 0.54. No reasons for this concentration could be detected. Fowle and Edwards (1955) suggested reasons for the irruption of Blarina in 1947. They wrote, "It seems most likely that the increase in numbers of Blarina resulted from the reproduction beginning in March 1947 and from the exceptionally high survival of young." However, at Cedar Creek Forest no masked shrews were taken in 1951, prior to July 31. There were 36 captures of this species in a four-night trap-period in August. Thirty-four of these were dead, so at least 35 individuals were caught. It would seem that these were not all resident individuals; some must have moved into the area from elsewhere.

The small numbers of shorttailed shrews taken can best be explained by the habitat requirements of this species. It is most often taken in drier deciduous woods or open areas. Pruitt (1953) wrote, "Blarina is, generally speaking, an animal of the deciduous forests."

Mammals known to be present in the bog, aside from those trapped, were: raccoon, foxes (both the red and gray), red squirrels,

cottontail rabbits, snowshoe hares, and white-tailed deer.

At no time was there any information which might signify an unusually heavy predation on mice. This might have been expected with the high population of masked shrews in 1951. Neither the red-backed nor meadow vole were at their lowest density that year. The white-footed mouse density was, but this could not be correlated in any way with predation. Raccoons and foxes were known (either by seeing them or seeing their sign) to hunt the area regularly.

WATER AND THE DISTRIBUTION OF THE RED-BACKED VOLE

Toward the southern edge of its geographic range the red-backed vole seems to inhabit more humid habitat than it does farther north. Bailey (1929) wrote of this animal in describing his experiences in Sherburne County, Minnesota, "Sometimes rare but usually may be found in small numbers in any timber or brushland that is not too dry. Generally abundant in tamarack swamps when these are not entirely under water." Both Hatfield (1938) and Quimby (1944) found red-backed voles along the border of spruce-fir and tamarack swamps at Cloquet, Minnesota. Butsch (1954) found the greatest number of these voles in edaphic climax forest with moist, heavy ground cover in northwestern Minnesota. In a study in central New York, Townsend (1935) found, "At Conquest, in a large area of dense, moist woods, the red-backed mouse was the most abundant species, representing an estimated 51% of the small mammals, and a population per acre

of 58."

Some studies have shown the red-backed voles favoring upland situations, but these areas seem to be away from its southernmost distribution. At Sugar Island, Michigan, red-backed voles characterized the upland mixed forest according to Pruitt (1951). In the Quetico Provincial Park, Ontario, it was reported by Cahn (1937) as occupying every habitat except swampy places. On State Island, on the Canadian border of Minnesota, Frenzel (1957) found that, "Red-backed voles demonstrated highest incidence of capture in mixed hardwoods and mixed conifers, with the shore shrub and hardwood conifer types being used to a lesser extent."

The red-backed vole, as revealed by live trapping, was the most abundant small mammal in the bog during the study (Table 3). One of the most obvious characteristics of the bog was the presence of water. Certainly this characteristic must play some role in influencing the abundance of the various species of small mammals.

At Cedar Creek Forest, food probably did not exert a great deal of differential pressure at any one time on the abundance of the most common mice on the bog. Several authors (Seton, 1909, Townsend, 1935, and later workers) have stated that the red-backed vole is omnivorous.

The water in the bog might influence the different species of animals in different ways, both directly (because of fluctuation of water levels) and indirectly. Drinking water is necessary for most small

mammals to rid the body of nitrogenous wastes, to take part in the chemical reactions, and in many climates, to cool the animal by evaporation.

The red-backed vole (in the Midwest) is near the southern periphery of its geographic range at Cedar Creek Forest, where other factors associated with water, particularly temperature, might perhaps become critical.

Several exploratory experiments were conducted to determine the influence of water requirements on the abundance of red-backed voles at Cedar Creek Forest. The first of these was to determine whether the red-backed vole and white-footed mouse differed in daily water consumption. Live-trapping data revealed the meadow vole to be second and the white-footed mouse to be third in abundance of the rodents, but the white-footed mouse was taken each year. The meadow vole is a microtine, more closely related and more similar in behaviour and habits to the red-backed vole than to the white-footed mouse. Further, there may be other explanations for the smaller numbers of meadow voles (compared with red-backed voles) than those concerned with water requirements. Several authors have shown that the meadow vole occurs most frequently in graminoid vegetation (Lantz, 1907; Bailey, 1900; Blair, 1940; Eadie, 1953; Mossman, 1955; Getz, 1961; Gunderson, 1950; and Schmidt, 1931, among others). Only a very small portion of the study area had grass-like vegetation (Fig. 2). It is also possible that the temperature

tolerance of the two species differs. Wiegert (1961) has shown the optimal temperature for the meadow vole to be between 25 and 29° C. Opsahl (1959) gave the optimal temperature for the red-backed vole as 26.0° C.

Daily water consumption for the red-backed vole and the white-footed mouse was measured under laboratory conditions for a period of 25 weeks. Water consumption experiments in rodents have most often been conducted with mice of the genus Peromyscus. As early as 1922 Dice (1922) reported that Peromyscus maniculatus bairdii drank from 1.14 to 3.75 cc. of water per day. Ross (1930) was another early worker using Peromyscus. Chew (1951) found that Peromyscus leucopus drank 5.36 cc. daily at 17.8° C., and 62.5% relative humidity. Williams (1959) tested water consumption of intergrades between Peromyscus maniculatus osgoodi and P. m. rufinus when fed varying diets. He found water consumption initially increased with an increase in protein consumption. Little work has been done comparing water consumption in two or more genera of mice.

The animals used in this experiment were fed commercial rabbit pellets. At various times, samples of this food when oven dried were found to contain about five per cent water. Random measurements of food consumed by the mice daily, varied from one to three grams. A daily ration of food would contain 0.05 to 0.15 cc. of water.

The animals were kept in galvanized wire cages 9 x 9 x 15 inches. The floor trays were covered with sawdust. The nest boxes were wooden live traps with the back doors removed. When it was necessary to examine or weigh the animals, or clean the cages, the back door was replaced and the animal chased into the trap. Cotton was used for nesting material. Drinking tubes were attached to the sides of the cages with broom clips, which made removal of the tubes easy.

Many methods have been used for measuring water consumption. The straight drinking tube with a fine tip, angled downwards, has been used, but this method has been criticized as wasting too much water. A hanging drop of water is lost each time a mouse drinks. There are about twenty drops in one cubic centimeter of water.

The apparatus that I used was an inverted 50 ml. graduated centrifuge tube. The part from which the animals drank faced up, eliminating the loss of the hanging drop. The only loss would be by evaporation. This loss averaged 0.4 cc a day.

The basement of the museum furnished a fairly constant environment for this experiment. The daily minimum and maximum temperatures and the relative humidity were averaged for each week. The weekly average of minimum temperatures varied from 69.2°F (week of Dec. 28, 1960, to Jan. 3, 1961) to 79.0°F. (Oct. 26 to Nov. 1, 1960). Weekly average maximum temperatures varied from 71.0° F. (Jan. 25 to Jan. 31, 1961) to 80.0°F. (Oct. 26 to Nov. 1, 1960). The

weekly average relative humidity varied from 15.0% (Jan. 18, to Jan. 24, 1961) to 3.0% (Oct. 26 to Nov. 1, 1960).

Mammals acquire water for physiological processes in several ways. The ability to maintain a favorable water balance, by utilizing water content of food and metabolic water, and reducing water loss through evaporation and urine, has been documented by the Schmidt-Nielsens (1948). Lindeborg (1952) has shown that some small mammals, notably Perognathus and Peromyscus were able to conserve water, by preventing water loss through skin and lungs. He found that the meadow vole was unable to prevent water loss and its daily intake was as high as 10.85 cc.

As anyone knows who has kept red-backed voles or meadow voles, the amount of water consumed is great. Odum (1944) showed that Clethrionomys gapperi maurus drank almost ten times as much water as did Peromyscus leucopus under similar conditions. He made no corrections for body weights, so the amounts for each species are not strictly comparable. He found that a 33.8 gram Clethrionomys drank 28.4 cc. of water in a 24-hour period. This turned out to be (by my calculation) 0.84 cc. per gram of body weight. If one cubic centimeter of water weighs one gram, this individual drank water equivalent to 84% of its body weight per day.

The results of my experiments (Figs.21 and 22) show the average amount of water consumed per day in cubic centimeters per gram of

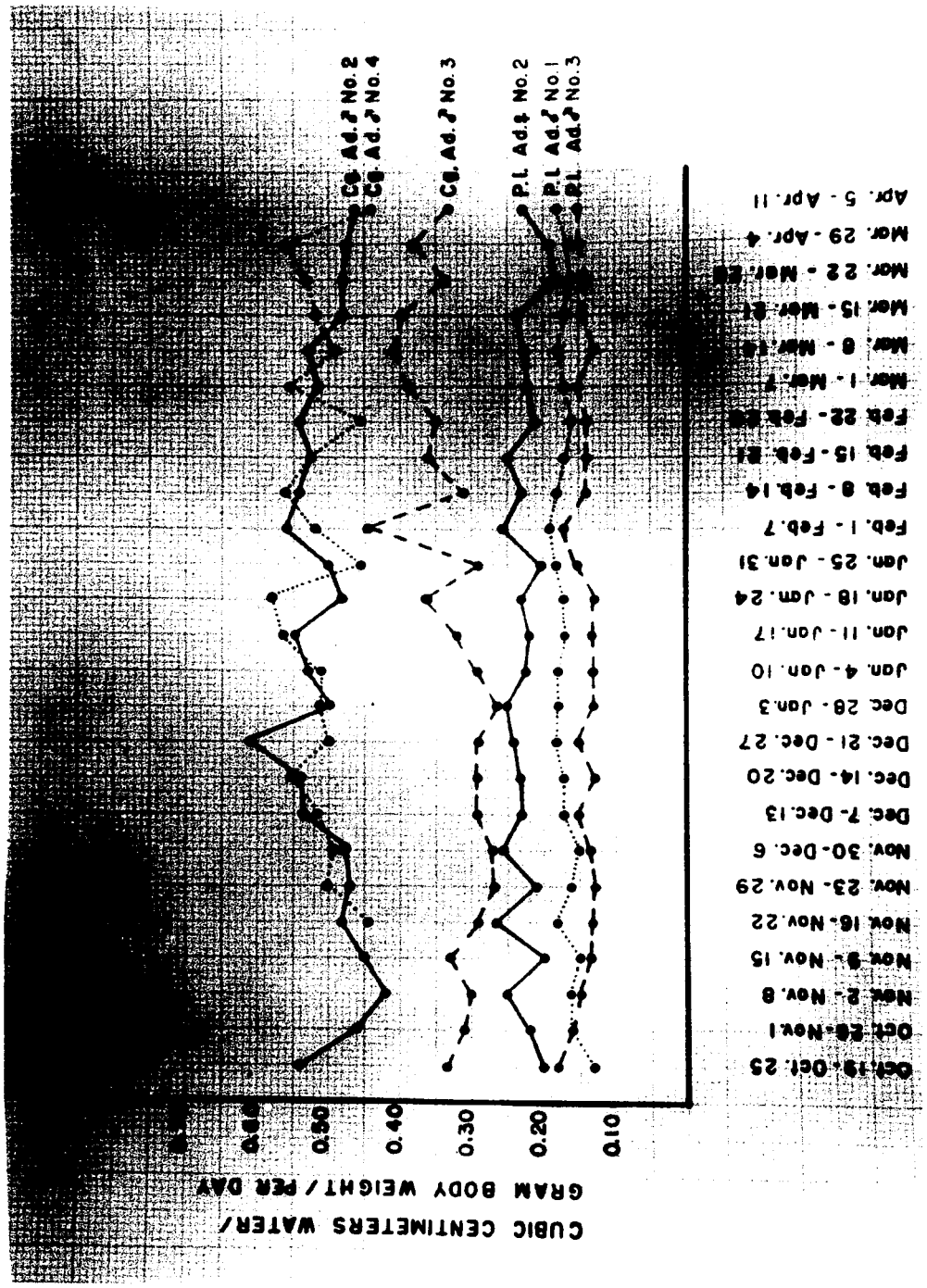


Fig. 21. Weekly averages in cubic centimeters of water per gram of body weight daily for each individual.

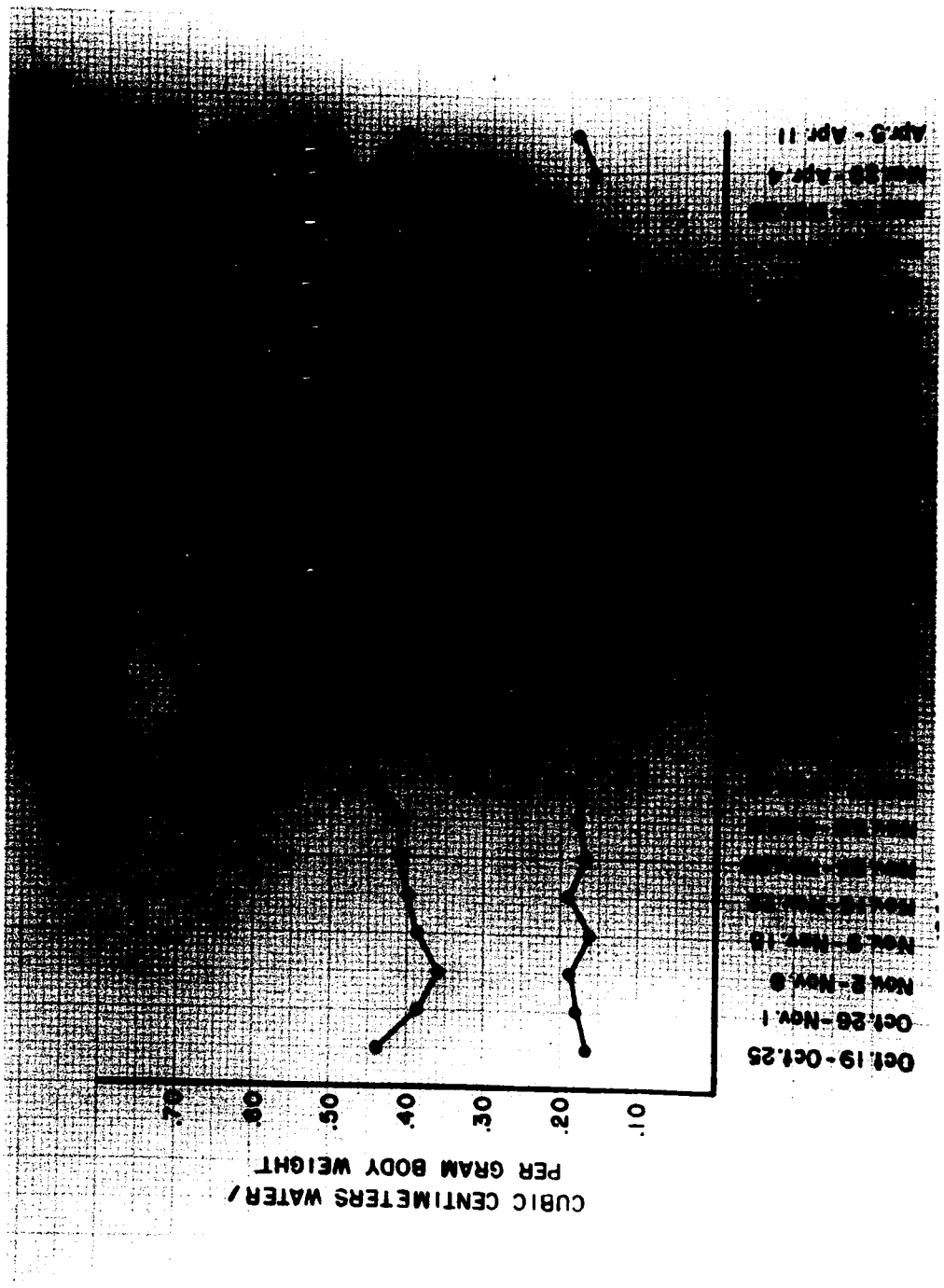


Fig. 22. Weekly averages of cubic centimeters of water per gram of body weight for each species.

body weight on a weekly basis for individuals of two species. The top three lines (Fig. 21) are for the red-backed vole, the bottom three lines for the white-footed mouse. The first line is for an adult male red-backed vole, whose average weight for the period was 25.1 grams, varying from 23.0 to 26.0. Daily extremes of water consumption were from 8 to 19 cc., but this last figure is extremely questionable. There may have been some undetected leakage, or an error in recording information. The second line shows water consumption for an adult male red-backed vole whose average weight was 20.2 grams, varying from 17.3 to 21.8. Extremes of daily water consumption were from 7.0 to 11.5 cc. The third line is for a red-backed vole whose average weight was 26.9 grams, varying from a low of 19.9, when caught, to a high of 29.8 towards the end of the experiment. Extremes of daily water consumption were from 10.0 to 14.0 cc.

Of the lower three lines, the first is for an adult male white-footed mouse whose average weight was 13.7 grams, varying from 11.6 to 15.9. Extremes of daily water consumption varied from 2.0 to 3.5 cc. The next is for an adult male white-footed mouse whose average weight was 17.0 grams, ranging from 14.9 to 18.8. Extremes of daily water consumption varied from 2.0 to 4.0 cc. The last line is for an adult male white-footed mouse whose average weight was 24.1 grams, varying from 19.0 to 26.6 grams. Extremes of daily water consumption were from 2.5. to 4.5 cc.

Figure 22 shows the average weekly water consumption for each species and further delineates the differences between them. Finally, bringing the calculations down to one figure for each species the red-backed vole drank 0.44 cubic centimeters per gram of body weight daily, the white-footed mouse 0.18. From this evidence it would seem logical to conclude that the availability of free water for physiological processes is more important to the red-backed vole than to the white-footed mouse.

To test for the availability of water in the vegetation in the summer months, four samples from the bog and four from the upland were air dried (107.0°C.) and compared for water content. A pair of samples (bog and upland) was taken on July 18 and 21, and again on August 2 and 15, 1961. They were brought to the laboratory in plastic bags and air dried to a constant weight. They were randomly chosen and consisted of surface clippings of an area three feet square.

The species composition of the ground vegetation in the bog differed from that of the upland. The commonest plants in the bog samples were: Clintonia borealis, Cornus canadensis, Dryopteris disjuncta (Ledeb.), Galium sp., Maianthemum canadense, Menyanthes trifoliata var. minor, Mitella nuda, Onoclea sensibilis, Trientalis borealis, Ulmus americana (seedlings), Vaccinium angustifolium, Sphagnum sp., grasses and sedges. The commonest plants in the upland samples were: Pteridium aquilinum, var. latiusculum,

Aralia nudicaulis, Aquilegia canadensis, Galium sp., Quercus ellipsoidalis (seedlings), Smilacina stellata, Vaccinium angustifolium, grasses and sedges.

Table 10. Original weight of vegetation samples

Date	Bog	Upland
July 18, 1961	159.2 grams	130.6 grams
July 21	251.2	150.5
August 2	325.5	65.6
August 15	85.1	51.3

Table 11. Percentage of water in bog and upland vegetation

Date	Bog	Upland
July 18, 1961	75.94%	66.23%
July 21	70.22	68.37
August 2	79.88	58.24
August 12	53.70	46.00
Average	69.93	60.21

These two samples were too small to treat statistically, but there was an indication that the vegetation of the bog contained more water than that of the upland. There also was more vegetation (in grams) per square yard in the bog than in the upland, evident also when walking through these areas.

Another experiment was devised to find out if vegetational water decreased the amount of free water consumed by the animals. This experiment was done in much the same way as the earlier water

consumption experiment. Ten adult red-backed voles were used, eight males and two females. These were divided into two groups of four males and one female. One group was given only commercial rabbit food (alfalfa pellets) for six weeks, July 25 to September 24. The other group was given green vegetation daily in addition to the pellets. These pellets contained about five per cent water, or about 0.05 to 0.15 cc. of water per daily ration, as calculated for the earlier water consumption experiment. The information was summarized for weekly periods. The minimum temperatures where this experiment was conducted varied from 78.6°F. to 80.4°F., the maximum temperatures varied between 80.8 and 82.8°F. Relative humidity varied from 50.6% to 64.0%.

Table 12. Water consumption in cubic centimeters per gram of body weight in two groups of adult red-backed voles, given rations of different water content

Sex	Ave. Weight	Dry alfalfa pellets	Dry alfalfa pellets and green vegetation
Female	18.1	0.48	0.48
Male	24.9	0.54	0.45
Male	27.9	0.35	0.32
Male	31.3	0.29	0.24
Male	23.7	0.54	0.41
Male	27.2	0.43	0.41
Male	21.3	0.54	0.55
Male	29.4	0.33	0.19
Female	22.9	0.35	0.28
Male	15.3	0.26	0.25
Average		0.411	0.358

The average difference in water consumption between the two groups was so slight that the *f* test for variance of sample means (with equal samples) was used to see if there was a significant difference. The calculated *f* value, 1.95, was far less than the tabular *f* value, 4.41, at the 95% level. Therefore, there was no significant difference between the two samples in this experiment. One should not draw the conclusion from this that the voles do not derive some water from vegetation. These individuals had been in captivity for some time and may have acquired a "preference" for the alfalfa pellets.

Both Getz (1961) and Pruitt (1953) have pointed out that the soil moisture in the bogs that they studied was higher than in the other habitats. In my work, relative humidities were measured four inches below and four inches above the surface, at ten different stations in the bog and ten different stations in the upland on August 5, 1961. Time did not permit more adequate sampling. Recording instruments would be necessary for making precise comparisons. For instance, the relative humidity may have changed at the first station by the time a reading is obtained at the last station. A battery-operated electric hygrometer indicator was used to obtain these data.

Table 13. Relative humidities four inches below surface and four inches above surface in the bog and in the upland

	Four inches below surface		Four inches above surface	
	Bog	Upland	Bog	Upland
	67.0	67.0	62.0	50.0
	82.0	80.0	77.0	62.0
	71.0	71.0	68.0	67.0
	72.0	72.0	68.0	67.0
	79.0	76.0	70.0	70.0
	74.0	67.0	74.0	65.0
	75.0	69.0	74.0	65.0
	79.0	74.0	65.0	62.0
	71.0	70.0	70.0	60.0
	76.0	74.0	70.0	67.0
Ave.	74.6	72.0	69.8	63.5

Although the difference was not great, the relative humidity in the bog was higher than in the upland both below and above the surfaces.

These four exploratory experiments suggest some reasons for the varying abundance of the three species of mice. Both the red-backed (first in abundance) and meadow vole (second in abundance) need more free water than the white-footed mouse (third in abundance). At Cedar Creek Forest, this water would be more available in the bog, than in the nearby uplands. The meadow vole is found in grassy habitats without tree cover. This type of habitat occupied only a very small portion of the bog. The white-footed mouse, which consumes less water than the other two species, may find conditions more favorable elsewhere than in the bog.

SUMMARY

A population of red-backed voles (Clethrionomys gapperi Vigors) was studied for eight and one-half years (1949 to 1957) in a bog at Cedar Creek Forest, Anoka and Isanti Counties, Minnesota.

The study area was located in a white cedar (Thuja occidentalis) bog near Cedar Lake. Cedar Lake was formed in the remains of an ice-block depression left when the Grantsburg sublobe of ice receded after the last glaciation. Because the area is unique it has been set aside as a study area by the Minnesota Academy of Sciences and the University of Minnesota. The Forest is a part of the Anoka Sand Plain, formed from the fluvial deposits of the Mississippi River as it followed the recession of the Grantsburg sublobe in a southwesterly direction over the region now called the Anoka Sand Plain.

Red-backed voles were live-trapped, marked, and recaptured for home range, population, and longevity data. Traps were placed 52 feet apart in a grid pattern; a strip 26 feet wide (one-half the distance between traps) bordered the outside lines of traps. This square plot, with an area of five acres, was sampled periodically through eight and one-half seasons. Each trapping period was for five days (four nights). The first period of each season was in early May, the last in October. There were seven or eight trapping periods in each of the first four years and five in each of the next four years. In 1957 there were only two. The trapping periods were scheduled

in a manner to sample the early spring, summer (breeding), and fall populations.

Each vole was assigned to one of two age groups, immature (young) or adult. Evidence indicated that these red-backed voles were capable of breeding at about two months of age, at which time they weighed approximately 11.0 grams. When they first left the nest (weaning time) the individuals weighed between 5.6 and 7.9 grams. Four young, probably only a day or two out of their own nest, were taken together in a trap; their balance was poor and their actions were clumsy. Their weight ranged from 7.0 to 7.9 grams. Another individual, taken at another time, of about the same physical abilities, weighed 5.6 grams.

The seasonal fluctuations in population density varied from a low in the spring to a high in midsummer or in early fall. The ratio of young to adults was highest in June and July in four of the years (1950, 1951, 1955, and 1956), in September in three of the years (1949, 1952 and 1954), and in October one year (1953).

There seemed to be no three- or four-year oscillation in the population density of red-backed voles at Cedar Creek Forest. Densities in the first four years of relatively high populations alternated between lows (1949, 1951) and highs (1950, 1952). In 1953 there was a sharp decline in numbers. Suggested reasons for this were: high water in the bog, and/or a paucity of females (36.8%) in the populations. Also, there was possible predation by raccoons,

although they hunted the area in other years also. A similar decline was recorded by another worker in southeastern Manitoba. There was a slight increase in numbers of red-backed voles for the years 1954 and 1955, then another decline to a very low density in 1956. In 1957 none was taken in two trapping periods (May and July). This last decline, from 1954 to 1957, was believed to result from high water in the bog.

The data gathered on population densities were used also to calculate home ranges for the red-backed voles. The term "home range" was used in this work to express the calculated area, in acres, over which an animal moved, as shown by live-trapping. The "inclusive boundary strip method" was used in calculating home ranges of individuals. The squares for each station (52 feet square) at which the individual was taken, were connected at their farthest points, and the area within this polygon was calculated in acres. This information was divided into two groups of data. In one group the information from all individuals taken three or more times was used to calculate home range area. In the second group only individuals taken at stations located on the inner part of the plot were used. Excluded from the latter group were individuals caught at stations on the border of the trapping plot.

The mean home range (using individuals at any station) for 131 adults was 0.30 acres; for 71 males it was 0.33 acres (extremes 0.06 to 1.92); for 60 females it was 0.28 acres (extremes 0.06 to 1.25).

The mean for 15 immatures was 0.11 acres. The mean home range, excluding individuals captured at edge stations, for 30 adults was 0.20 acres; for 12 males it was 0.15 acres (extremes 0.06 to 0.22); for 18 females it was 0.24 acres (extremes 0.06 to 0.58). The mean for eight immatures was 0.12 acres. For the adults, the home range was larger when individuals using edge stations were included in the calculations.

Data on longevity for small mammals living in the wild are scarce and are given either as the number of individuals surviving from birth to stated intervals, or time elapsed (in days or months) between first and last captures. It is generally believed that few individuals live through one winter. In the present study, 12 of 426 red-backed voles overwintered, but none was known to have lived through two winters. The greatest number of days between first and last capture for a male was 378; for a female it was 321.

Ten species of small mammals were trapped in the bog at Cedar Creek Forest. From live trapping results, indications were that the red-backed vole was the most abundant species of rodent and the masked shrew the most abundant species of shrew. An "irruption" of masked shrew populations occurred in 1951.

The red-backed vole, as revealed by live-trapping, was far more numerous in the bog than any other species of small mammal. Some experiments were set up in an attempt to determine the causes of this. Food was ruled out because all the species of small rodents in the bog

were omnivorous. The plot as a whole was probably not optimal habitat for the meadow vole because the area of graminoid vegetation without tree cover was small. The red-backed vole and the white-footed mouse were the only two species taken every year. Daily water consumption for these two species was measured in the laboratory during a 25-week period. The red-backed voles (3 individuals) drank a daily average of 0.44 cubic centimeters per gram of body weight, while the white-footed mice (3 individuals) averaged 0.18 cubic centimeters per gram of body weight per day. This would indicate that free water to drink was important for the red-backed vole.

Another experiment, conducted to determine whether there was more water available in the vegetation of the bog than in that of the upland, indicated that the bog vegetation contained more water, 69.93% by weight, than did that of the upland, 60.21%.

No significant difference in daily water consumption was found when red-backed voles were fed alfalfa pellets only, which contained about 5% water, or when fed alfalfa pellets and green vegetation. It may be that the voles "preferred" the pellets to green vegetation. This might invalidate the experiment. The relative humidity in the bog and that in the upland were compared in one experiment. Again these data are very limited. In 20 observations (ten in the bog; ten in the upland), the relative humidities four inches below and four inches above the surface were higher in the bog (69.8% and 74.6%)

than in the upland (63.5% and 72.0%). With the exception of the daily water requirement experiment, I do not consider these laboratory experiments to be conclusive, but rather I view them as indicators for research which might be productive.

APPENDIX I

Dates of live-trapping periods,
324 trap-nights for each trapping period

1949:
May 10-14
May 30-June 3
June 21-July 1
July 25-29
Aug. 22-26
Sept. 19-23
Oct. 17-21
Total trap-nights, 2268

1950:
May 1-5
May 23-27
June 12-16
July 10-14
Aug. 7-11
Sept. 4-8
Sept. 25-29
Oct. 1-5
Total trap-nights, 2592

1951:
May 7-11
May 28-June 1
June 18-22
July 9-13
July 30-Aug. 3
Aug. 20-24
Sept. 10-14
Oct. 1-5
Total trap-nights, 2593

1952:
May 12-16
June 2-6
June 24-28
July 21-25
Aug. 4-8
Aug. 25-29
Sept. 15-19
Oct. 6-10
Total trap-nights, 2592

1953:
May 5-9
June 22-26
July 14-18
Sept. 1-4
Oct. 5-9
Total trap-nights, 1620

1954:
May 10-14
June 21-25
July 26-30
Sept. 14-18
Oct. 4-8
Total trap-nights, 1620

1955:
May 2-6
June 20-24
July 18-22
Aug. 29-Sept. 2
Oct. 3-7
Total trap-nights, 1620

1956:
May 7-11
June 18-22
July 23-27
Aug. 27-31
Oct. 15-19
Total trap-nights, 1620

1957:
May 6-10
July 1-5
Total trap-nights, 648

Total trap nights for all years, 17,732

APPENDIX II

Summary of trapping results for each period and year

Dates	F.	M.	Yng.	Ad.	Cap.	Ind.
1949:						
May 10-14	1	0	0	1	1	1
May 19-June 3	4	5	1	8	17	9
June 27-July 1	18	14	14	18	56	32
July 25-29	9	6	6	9	22	15
Aug. 22-26	6	6	3	9	17	12
Sept. 19-23	4	7	9	2	19	11
Oct. 17-21	6	13	7	12	32	19
	48	51	40	59	164	99
1950:						
May 1-5	5	4	0	9	13	9
May 23-27	6	4	1*	10	18	11
June 12-16	9	12	12	9	36	21
July 10-14	17	25	12	30	77	42
Aug. 6-11	18	11	9	20	43	29
Sept. 4-8	17	6	5	18	36	23
Sept. 25-29	15	6	3	18	32	21
Oct. 16-20	13	6	2	17	26	19
	100	74	44	131	281	175
1951:						
May 7-11	1	1	0	2	6	2
May 28-June 1	2	5	0	7	10	7
June 17-21	12	5	12	5	25	17
July 9-13	0	9	0	9	19	9
July 30-Aug. 3	3	8	1	10	16	11
Aug. 20-24	9	5	5	9	27	14
Sept. 10-14	5	2	4	3	9	7
Oct. 1-5	10	7	5	12	39	17
	42	42	27	57	151	84
1952:						
May 12-16	4	8	0	12	20	12
June 2-6	3	5	1	7	12	8
June 24-28	13	11	1	23	38	24
July 21-25	21	24	6	39	72	45
Aug. 4-8	15	18	3*	31	60	34
Aug. 25-29	11	13	3	21	42	24
Sept. 14-18	6	11	5	12	29	17
Oct. 7-10	5	4	1	8	13	9
	78	94	20	153	286	173

APPENDIX II (Cont'd)

Dates	F.	M.	Yng.	Ad.	Cap.	Ind.
1953:						
May 5-9	0	0	0	0	0	0
June 22-26	2	2	0	4	9	4
July 14-18	2	8	1	9	18	10
Aug. 31-Sept. 3	0	1	0	1	2	1
Oct. 5-9	3	1	1	3	7	4
	7	12	2	17	36	19
1954:						
May 10-14	0	0	0	0	0	0
June 21-25	4	5	0	9	9	9
July 26-30	8	7	1	14	28	15
Sept. 14-18	11	9	7	13	30	20
Oct. 4-8	5	4	1	8	9	9
	28	25	9	44	76	53
1955:						
May 2-5	0	0	0	0	0	0
June 20-24	5	12	2	15	24	17
July 18-21	9	12	0	21	34	21
Aug. 29-Sept. 2	5	1	0	6	7	6
Oct. 3-7	4	1	0	5	6	5
	23	26	2	47	71	49
1956:						
May 7-11	1	0	0	1	0	1
June 19-22	1	2	1	2	3	3
July 23-27	1	1	0	2	3	2
Aug. 27-31	1	0	0	1	1	1
Oct. 15-19	3	3	0	6	6	6
	6	7	1	12	13	13
1957:						
May 6-10	0	0	0	0	0	0
July 1-5	0	0	0	0	0	0
	0	0	0	0	0	0

Key:
F. = Females Yng. = Young Cap. = Total number of captures
M. = Males Ad. = Adult Ind. = Total number of individuals

*Number contains unsexed individuals; therefore, female and male total does not equal total individuals for that line.

APPENDIX III

Data on individuals used in home range calculations

Individual	Number of times caught	Trap-revealed home range, acres
1949:		
Adult male 5	3	0.192
Adult female 6	3	0.128
Adult male 7	5	0.320
Adult female 9	6	0.320
Adult female 15	5	0.576
Adult male 17	3	0.192
Imm. male (?) 19	3	0.160
Imm. male 20	3	0.128
Imm. male 22	3	0.128
Adult male 24	4	0.480
Adult female 26	3	0.128
Adult female 31	7	0.164
Adult male 41	3	0.128
Adult female 48	6	0.640
Adult female 56	6	0.448
Imm. female 57	3	0.160
Adult female 61	3	0.192
Adult male 65	3	0.224
Adult male 67	3	0.320
1950:		
Adult female 50 (2 summers)	3	0.448
Adult female 51 (2 summers)	5	0.480
Adult male 63 (2 summers)	3	0.224
Adult female 79	3	0.224
Adult male 83	11	0.544
Adult female 86	4	0.320
Adult male 88	5	0.864
Adult male 90	4	0.544
Adult male 93	6	0.320
Adult male 95	8	0.192
Adult male 97	4	0.352
Imm. female 100	3	0.064
Imm. female 108	3	0.384
Adult male 109	4	0.128
Imm. male (?) 111	3	0.064
Adult female 112	4	0.320
Imm. female 113	3	0.128
Adult male 115	5	0.480

APPENDIX III (Cont'd)

Individual	Number of times caught	Trap-revealed home range, acres
Adult male 117	3	0.128
Adult male 120	4	0.128
Adult male 121	3	0.224
Adult male 125	3	0.576
Adult male 126	3	0.128
Adult female 128	4	0.320
Adult male 133	4	0.192
Adult male 135	3	0.128
Adult female 136	3	0.192
Adult female 141	3	0.192
Adult female 142	3	0.128
Adult male 144	4	0.288
Adult female 145	6	0.128
Adult male 147	3	0.224
Adult female 150	3	0.192
Imm. female 160	3	0.064
Adult male 165	6	0.608
Adult male 169	3	0.192
Adult male 176	3	0.064
Adult female 182	4	0.224
1951:		
Adult female 209	4	0.192
Adult female 210	3	0.064
Adult male 210a	4	0.192
Adult male 215	7	1.920
Adult male 217	4	0.416
Adult male 218	7	0.320
Adult male 220	5	0.396
Adult male 226	4	0.480
Adult male 230	4	0.064
Adult male 234	6	0.384
Adult female 241	4	0.064
Adult male 242	3	0.064
Adult female 243	3	0.352
Adult female 244	3	0.128
Adult male 252	4	0.128
Imm. male (?) 253	4	0.128
Adult male 254	3	0.192
Adult male 255	3	0.288

APPENDIX III (Cont'd)

Individual	Number of times caught	Trap-revealed home range, acres
Imm. female 258	3	0.064
Imm. male 260	3	0.064
Adult female 261	3	0.064
1952:		
Adult female 265	4	0.192
Adult male 266	5	0.384
Adult male 267	3	0.064
Adult female 269	3	0.128
Adult female 270	3	1.248
Adult female 272	9	0.224
Adult female 274	5	0.128
Adult male 276	4	0.064
Adult female 277	3	0.128
Adult female 278	4	0.224
Adult male 279	4	0.192
Adult female 281	5	0.320
Adult male 282	16	0.704
Adult male 285	4	0.352
Adult male 290	3	0.192
Adult male 291	5	0.384
Adult female 292	3	0.256
Adult male 293	9	1.12
Adult female 293a	5	0.256
Adult male 294	4	0.064
Adult female 295	8	0.064
Adult female 296	3	0.064
Adult female 297	3	0.576
Adult male 299	5	0.064
Adult female 300	3	0.064
Adult male 304	4	0.672
Adult female 307	7	0.320
Adult female 311	5	0.128
Adult female 313	3	0.576
Adult female 314	3	0.064
Adult female 315	3	0.192
Adult female 317	3	0.896
Adult male 322	3	0.192
Adult male 323	3	0.256
Imm. male 326	3	0.064

APPENDIX III (Cont'd)

Individual	Number of times caught	Trap-revealed home range, acres
Adult male 333	3	0.128
Adult female 334	3	0.416
Adult male 337	4	0.256
Adult male 338	3	0.128
Adult female 346	3	0.064
1953:		
Adult male 349	3	0.384
Adult female 350	5	0.448
Adult male 352	3	0.320
Imm. male 353	3	0.064
Adult male 354	3	1.440
1954:		
Adult female 367	4	0.992
Adult male 369	4	0.704
Adult male 370	3	0.192
Adult female 371	6	0.128
Adult female 374	3	0.128
Adult male 375	5	0.064
Adult female 376	4	0.064
Adult female 377	5	0.320
Adult male 379	3	0.224
Adult female 380	5	1.248
Adult female 384	3	0.064
1955:		
Adult male 391	3	0.224
Adult female 392	3	0.256
Adult male 393	5	0.192
Adult male 395	3	0.128
Adult male 398	3	0.064
Adult male 399	3	0.288
Adult female 405	3	0.224
Adult male 408	3	0.064
Adult female 418	3	0.256
1956:		
Adult female 422	3	0.256

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