MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 79

An Analysis of Some Physical Factors Affecting the Local Distribution of the Shorttail Shrew (*Blarina brevicauda*) in the Northern Part of the Lower Peninsula of Michigan

BY
WILLIAM O. PRUITT, JR.

ANN ARBOR
UNIVERSITY OF MICHIGAN PRESS
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AN ANALYSIS OF SOME PHYSICAL FACTORS AFFECTING THE LOCAL DISTRIBUTION OF THE SHORTTAIL SHREW (*BLARINA BREVICAUDA*) IN THE NORTHERN PART OF THE LOWER PENINSULA OF MICHIGAN*

INTRODUCTION

In biology one of the basic premises often forgotten or ignored is that an organism cannot be considered apart from its environment. Environment can be classified into the physical and the biotic conditions in which the organism exists. Many aspects of the biotic environment of small mammals have been studied—community relations, life histories, predator-prey relationships, population dynamics, and genetics—but the physical environment has been less studied. This, perhaps, is due to technical difficulties inherent in such investigations, resulting from poor or scanty instrumentation, and to an intellectual preoccupation with the community concept, which, in my opinion, overemphasizes the biotic controls and is, in its usual form, highly subjective. It may even reach absurdity (certain food-chain diagrams) or become metaphysical (the "superorganism" idea). If local distribution and habitat selection may be logically explained in terms of basic physical factors, such an explanation is to be preferred to one that concerns relative availability of food supply, for example, and it certainly is preferable to one that involves more complex and rather nebulous sociological phenomena.

An organism must have a range of optimum conditions for existence, as well as upper and lower limits of tolerance for heat, moisture, light, and possibly other physical factors in various combinations; but just what the limits are for any given species is usually unknown. For many plants the minimum moisture content of the environment is known or can be ascertained. For animals, especially mammals, the search for it properly belongs in the laboratory if definitive results are to be obtained. Before the animal is subjected to dessicators and thermal chambers, however, the field should be roughly delimited by investigations of the animal in a natural state and of the environment and habitats in which it is found. For one particular kind of small mammal (*Blarina brevicauda kirtlandi*) this problem is simplified in the northern part of the Lower Peninsula of Michigan, where the animal comes in direct contact with large amounts of environmental matrix

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which are unsuitable for it. The purpose of this study was to investigate factors which might prohibit *Blarina* from occupying this apparently unsuitable environment and to contrast these factors with those in environments in which *Blarina* was known to exist.

Shelford (1912), who early recognized the importance of physical factors of the environment, stated that "forest development is accompanied by marked changes in soil and physical factors; animal distribution is more closely correlated with differences in *physical factors* than with species of plants." Chenoweth (1917), who studied *Peromyscus leucopus,* postulated that evaporation is the most important factor in determining habitat, even more important than temperature. His mice reacted to evaporation, whether produced by movement, dryness, or heat. Normal behavior occurred in air of low evaporative power. When evaporation was increased, the mouse was stimulated and reacted negatively. He also postulated that the essential factor for *Blarina*'s existence seemed to be plenty of moisture. Hardy (1945) found that soil texture influenced the local distribution of small rodents, both directly and indirectly. He also summarized the more important work on soil influences. Blake (1926) gathered data on soil temperatures throughout the year for his study of soil insects. His plots also had *Blarina* present. Jameson (1949) noted the temperature differential in mid-May between air and a small mammal tunnel below the leaf litter. He found that winter temperatures in the tunnels deviated little from 32°F. His study plots were all well populated by *Blarina,* and he was unable to suggest any environmental factor which might affect its local distribution. He minimized the importance of leaf litter and leaf mold in affecting distribution of *Blarina,* but suggested that the presence of a mor humus layer with its larger population of arthropods might influence the local distribution of *Sorex fumeus.* He also noted the effects of types of humus (mor or mull) upon the local distribution of burrowing mammals.

Green (1925) suggested the importance of soil in limiting small mammal distribution in the northern part of the Lower Peninsula. He believed that the sandy soils of the region were warmer than clay soils and that they thus accounted for the presence of such mammals as the prairie mole (*Scalopus aquaticus*) at latitude 45°N. He mentioned *Blarina* as being "plebeian" in his study area, although he took only three specimens, two "under matted dead sedges on the banks of Mole Brook" and the other "under a large decaying log in the coniferous swamp bordering Mouse Brook." He also thought that the winds blowing in from "icy Lake Superior" had a cooling effect on the soil, but currently it is generally conceded that the lake winds have a modifying effect on the macroclimate.

This subject has a direct bearing on the larger fields of zoogeography and animal dispersal, for the process of range extension is the same in both magnitudes—invasion and ecesis of a habitat. An animal in nature extends its range only by a series of successful invasions of new areas. The factors limiting dispersal on a continental order of magnitude are essentially the same as those acting locally, as from the bottom to the top of a fallen log, differing only in extent.

ACKNOWLEDGMENTS.—I wish to express appreciation to the University of Michigan Biological Station for use of facilities, to the Director, Dr. Alfred H. Stockard, for providing employment which made it possible for me to conduct this study at the Station, and to Mr. Clem Bur, Maintenance Supervisor of the Biological Station, for his constant aid while I was there. I am grateful to Dr. William H. Burt for his assistance and suggestions during the course of this study and for his critical reading of the manuscript. Especial thanks must go to my wife, Erna N. Pruitt, for her help as field secretary and curator. I am indebted to the University of Michigan for a University Fellowship during 1951–52, which made possible the completion of this study.

GENERAL DESCRIPTION OF THE REGION

Field work was carried on from 15 June 1950 until 16 August 1951, while I was in residence at the University of Michigan Biological Station, near Cheboygan, Michigan. Preliminary investigations in this area had been carried on during the summers of 1948 and 1949.

Cheboygan and Emmet counties are at the northern tip of the Lower Peninsula of Michigan, bounded on the north by the Straits of Mackinac, on the west by Lake Michigan, and on the northeast by Lake Huron. The area is underlain by Devonian rocks which outcrop only to the north and to the southeast of the area studied. The surface topography has been formed by glacial action and by the action of the postglacial Great Lakes. A more nearly complete description of the topography is given under the detailed account of the separate study areas.

Foster *et al.* (1939) described this region as follows:

> Originally a dense forest covered all the land, except a few bogs and marshes which supported a marsh grass, sedge, or shrub type of vegetation. Four distinct types of forest, based on the original forest growth, are represented in the county: (1) the hardwood forest which consists of hard maple, beech, elm, basswood, yellow birch, and hemlock; (2) the pine forest consisting of red and white pine; (3) the swamp coniferous forest consisting of cedar, spruce, balsam fir, and tamarack; (4) the hardwood-coniferous forest consisting of a mixture of beech, elm, basswood, spruce, balsam fir, and cedar.

Gates (1912) noted the relationship between fertility of the soils and the distribution of the forest types. His classification was "better upland" (hardwoods), "poorer soils" (pine land), and "moist lowland" (cedar bogs).

With the exception of a few scattered areas the entire region is an almost classic example of the misuse of natural resources. Lumbering, in the latter part of the past century, first took all the pines and then the hardwoods.

A few stands of hardwoods remained until World War I, when they were cut. The only remnant of hardwoods resembling the original cover is on Colonial Point, Burt Lake. Even this is slowly succumbing to "selective cutting."

After the lumbermen came fire, which swept over the region repeatedly. In the earlier days the attitude of the local people was one of indifference; fires burned unchecked for weeks, being fought only when they endangered a habitation. Such treatment has reduced some areas to virtual biological deserts, sand covered with reindeer lichen (*Cladonia*), with scrubby aspens (*Populus grandidentata* and *P. tremuloides*), and with pin cherry (*Prunus pennsylvanica*). Large stretches of country are now covered with a more or less thrifty aspen association, and in places the pine forest is re-establishing itself (Gates, 1930). The swamp conifer lands have suffered less from fire; most are now covered by the climax cedar-spruce. Thus, the present vegetational cover may be grouped into three main types—hardwood forests and farms on the better soils (loams and sandy loams), various stages of pine succession on the sands, and swamp conifers on the peats and mucks (Fig. 1).

This study originated as an investigation of possible succession of small mammal faunas in these vastly different areas. Five study areas were established: (1) an area of aspen, jack pine, and red oak, which was burned experimentally in 1948 and is now covered by waist-high aspen, red maple, and red oak; (2) a mature aspen association area; (3) a mature pine area; (4) an area of "demivirgin" hardwoods; (5) an area of climax swamp conifers. These study areas cover the main vegetational types—three on the pine land and its seral stages, and one each on the hardwoods and swamp conifers, or three on sand, one on sandy loam, and one on muck. When it was discovered that *Blarina* could not be found that year (1949) on the pine sere, a wholly new problem opened up, namely, an investigation of the prime environmental differences in the several areas.

Soil types were determined by use of the following sources: Foster *et al.* (1939), Michigan State Highway Department (1946), Donahue (1935), a soil map of the Biological Station tract made by Professor L. J. Young of the School of Natural Resources, unpublished preliminary soil survey data made available by the late Professor W. F. Ramsdell, and independent field observations.

A more intimate acquaintance with these study areas soon showed striking climatic differences between some and a similarity among others. An early morning trip from the Burn to the Bog and then to the Hardwoods showed marked temperature differences, both of the air and of the soil. When these observations were checked with the published United States Weather Bureau records for the region and with the records from the summer weather station on the Biological Station campus, great discrepancies were noted.

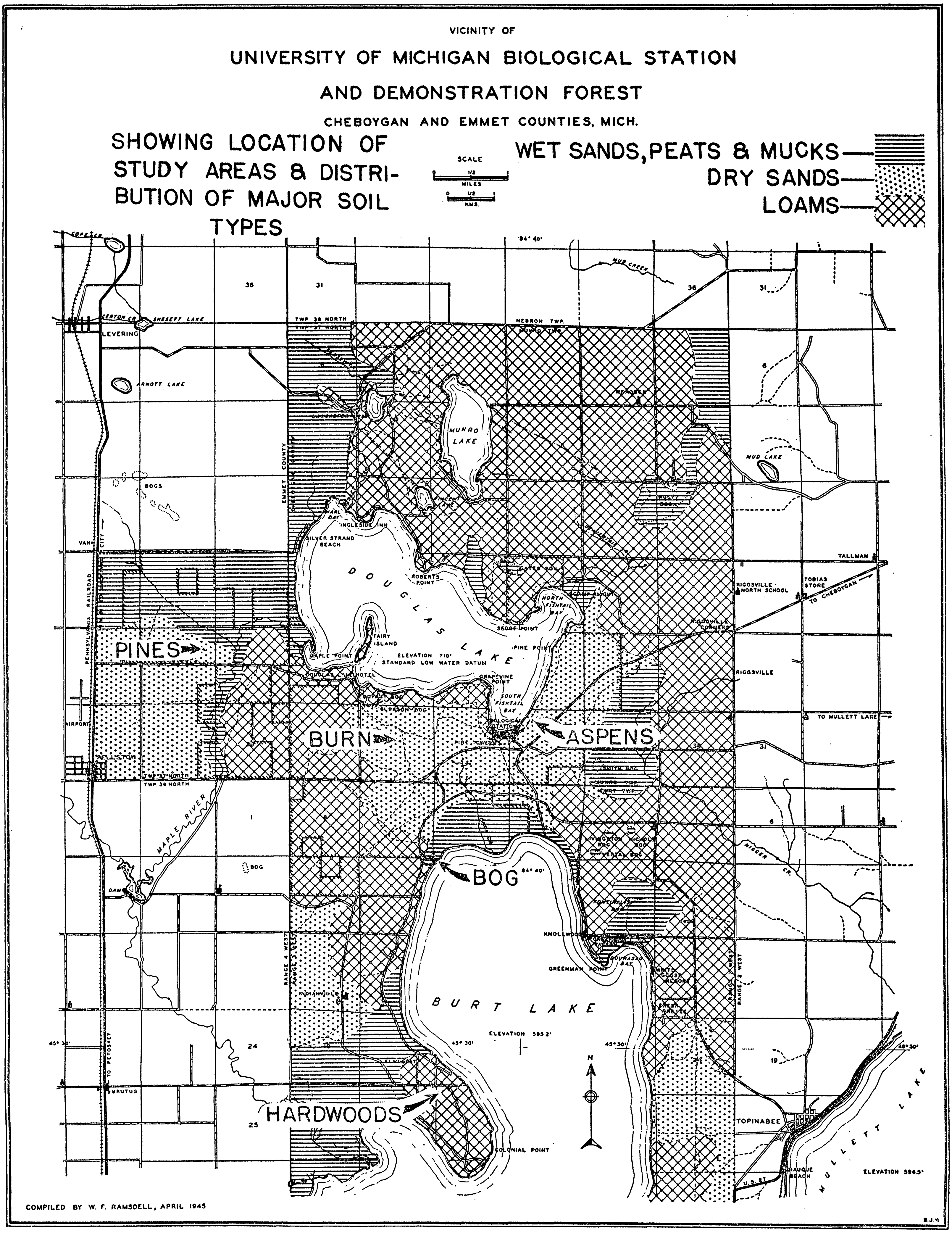

FIG. 1. Study areas and distribution of major soil types.

Awareness of the importance of the microclimate is well summed up by Geiger (1950), who indicated that the usual meteorological summaries are no longer sufficient and may even be misleading. Most plants (and animals, too) live in the zone of disturbance which is avoided in macroclimatological observations. It has been shown that the macroclimatological data taken by the Weather Bureau can be used only in a very broad and general way by ecologists. Wolfe, Wareham, and Scofield (1949) have made an important contribution along this line to the development of an American school of microclimatology.

The macroclimate of the Biological Station region is known only from the records of the United States Weather Bureau stations at Pellston Airport and at Cheboygan, which are published in the monthly summaries "Climatological Data," and from the summer records of Dr. F. C. Gates on the Station campus, published in the *Annual Reports* and in the *Papers of the Michigan Academy of Science, Arts, and Letters,* from 1920 through 1937. I am indebted to Dr. Gates for the summer black-bulb thermometer readings. Foster (1939) recorded:

> [This macroclimate is] characterized by long cold winters, short cool summers, mild autumns, late cold springs, long days of sunshine during the summer, prevailing westerly winds, low evaporation, and an average of about 26 inches of rainfall. Hail storms, sleet storms, and destructive winds are very rare.
>
> The average frost-free season is 134 days at Cheboygan, from May 20 to October 1, inclusive. It ranges within the county from 140 days in the extreme northern part, where the climate is moderated by the lake, to about 116 days in the south-central part, where the altitude is greater, and the influence of the lake less . . . . Frosts have occurred during every month of the year except July, but they are rare in summer.
>
> The mean annual rainfall varies within the county to some extent. At Cheboygan it is 26.31 inches. At Gaylord in Otsego County, it is 29.52 inches, and this more nearly corresponds to the rainfall in the southern part of Cheboygan County. The amount of rainfall in all sections generally is sufficient for all crops grown, as the greater part falls during the growing season, or in May, June, July, August, and September. Extended droughts are very rare. The average snowfall is 56.9 inches.

Gates (1930) in describing the climate stated that the vegetation of the region is an expression of the integration of climatic and edaphic factors, but that this is not always apparent, as the factors are measured at the present time. He stated that precipitation is most abundant in winter and spring, with a long dry period in the summer and fall, and noted the importance of this long dry period in paving the way for fire "the bane of the development of the region."

METHODS

The plaster-block method for continuous measurement of available moisture of the soil, as described by Bouyoucos and Mick (1940), was used in this study with some modifications. The plaster blocks were obtained from Wood and Metal Products Company, Bloomfield Hills, Michigan. Three blocks were buried at each station, one each at depths of one, three, and six inches below the ground surface.

Soil temperatures were obtained by two different methods. At each station a block of soil 3½ by 12 by 4 inches was removed, then a four-sided cage of hardware cloth and screen wire was placed in the hole, open side down and open end facing north. In this cage a Taylor Six-type maximum-minimum thermometer was buried at a depth of three inches. The removed soil block was trimmed on the bottom to fit the hole and was placed over the cage. At the open end another block of soil was cut out and used as a door or plug which was removed when the thermometer was taken out for reading and resetting, and was replaced snugly after the thermometer was inserted. By careful handling the plug remained unbroken surprisingly well. When a plug finally crumbled, another was cut out of the soil nearby. The set maximum temperatures of the soil and the instantaneous thermistor readings were usually the same; when differences did occur they were small.

The second set of soil temperatures was obtained with thermistors. These were mounted in assemblies (Pruitt, 1952) which were buried, one beside each plaster block. All temperatures are given hereafter in Fahrenheit degrees.

Since the same kind and length of wire were used for both moisture- and temperature-sensitive elements, additional resistance calibration was unnecessary. All wires were tagged and brought up along a post which had previously been driven into the ground at the station. The ends of the wires, with jacks, were placed in a small wooden box on top of the post four feet above the ground. On the north side of the box, under protection of an overhanging roof, was a Taylor Six-type maximum-minimum thermometer. Thermistor and soil moisture readings were taken with a Simpson Model 260 volt-ohm-milliammeter. Bouyoucos and Mick (1940) experienced difficulty in using direct current at constant voltage for measuring conductivity of the blocks; such factors as hydrolysis of the block material and dissociation of the absorbed soil solution caused faulty readings. Preliminary use of the ohmmeter showed that in the soils under consideration erratic readings such as were obtained by Bouyoucos and Mick did not occur. Regarding difficulty of obtaining satisfactory correlation between block resistance and soil moisture, my later observations confirmed theirs. Since a comparison of relative moisture of the several areas, rather than the actual moisture figures, was of paramount importance, it was felt that use of an ohmmeter was justified. This use is especially justified when comparative costs and ease of handling in the field are considered. Bouyoucos and Mick (1947) have later used an ohmmeter modification of their Wheatstone bridge circuit for irrigation control work.

Upon completion of the field observations on 16 August 1951, the block resistances were recorded for a final time, and immediately thereafter the soil surrounding each block was taken up and sealed in a small glass jar. Later, samples of the soil from each of these jars were analyzed for moisture content. Water held by a pF of less than approximately 2.7 was removed by centrifuging the samples at 1,000X gravity for 35 minutes, and then all water was removed by oven-drying. The results of this series of analyses are compared with moisture determinations made by the electrical resistance method (Table I). It must be borne in mind that, at the present time, detailed calibrations of the plaster blocks in the particular soils under consideration have not been made. The figures in the right-hand column of Table I are calculated from previously calibrated soils (Bouyoucos and Mick, 1940) which resemble these soils closest in mechanical analysis.

TABLE I

Comparison of Soil Moisture, Mechanical and Electrical Methods

*Area and Depth in Inches	Per Cent Loss (Centrif.)	Per Cent Loss (Centrif. + Oven-Drying)	Total Per Cent Loss	Per Cent Moisture (Elec. Resis.)
B-6	2.85	3.05	3.9	1.5
B-3	2.6	1.25	2.7	1.6
B-1	2.0	3.6	6.6	1.5
A-6	3.0	1.3	4.1	1.5
A-3	2.9	2.0	3.3	1.5
A-1	5.1	18.5	26.6	1.5
P-6	1.5	1.3	2.8	1.5
P-3	1.3	2.0	3.3	1.5
P-1	4.6	17.9	21.3	1.5
H-6	3.1	9.1	12.0	5.5
H-3	7.8	19.8	26.2	5.5
H-1	19.7	28.3	42.5	6.0
S-6	57.4	71.3	87.8	55.0
S-3	46.8	69.7	84.4	50.0
S-1	26.1	78.4	84.2	50.0

* B=Burn, A=Aspens, P=Pines, H=Hardwoods, S=Bog.

I am deeply grateful to Mr. G. P. Larson and the Michigan State Highway Department Soils Testing Laboratory for their technical advice and for use of facilities in making the centrifuge and oven-dry determinations.

When a station was visited, a standardized procedure was followed. First, the v-o-m was hung on a hook below the box; next, the air maximum, minimum, and set maximum temperatures were read and recorded, and the thermometer was reset. The soil thermometer was then extracted, read, recorded, reset, and replaced. Next, the v-o-m was zeroed, connected to the proper leads and resistances at one, three, and six inches for the thermistors, and the blocks were read and recorded. An area with a radius of two feet

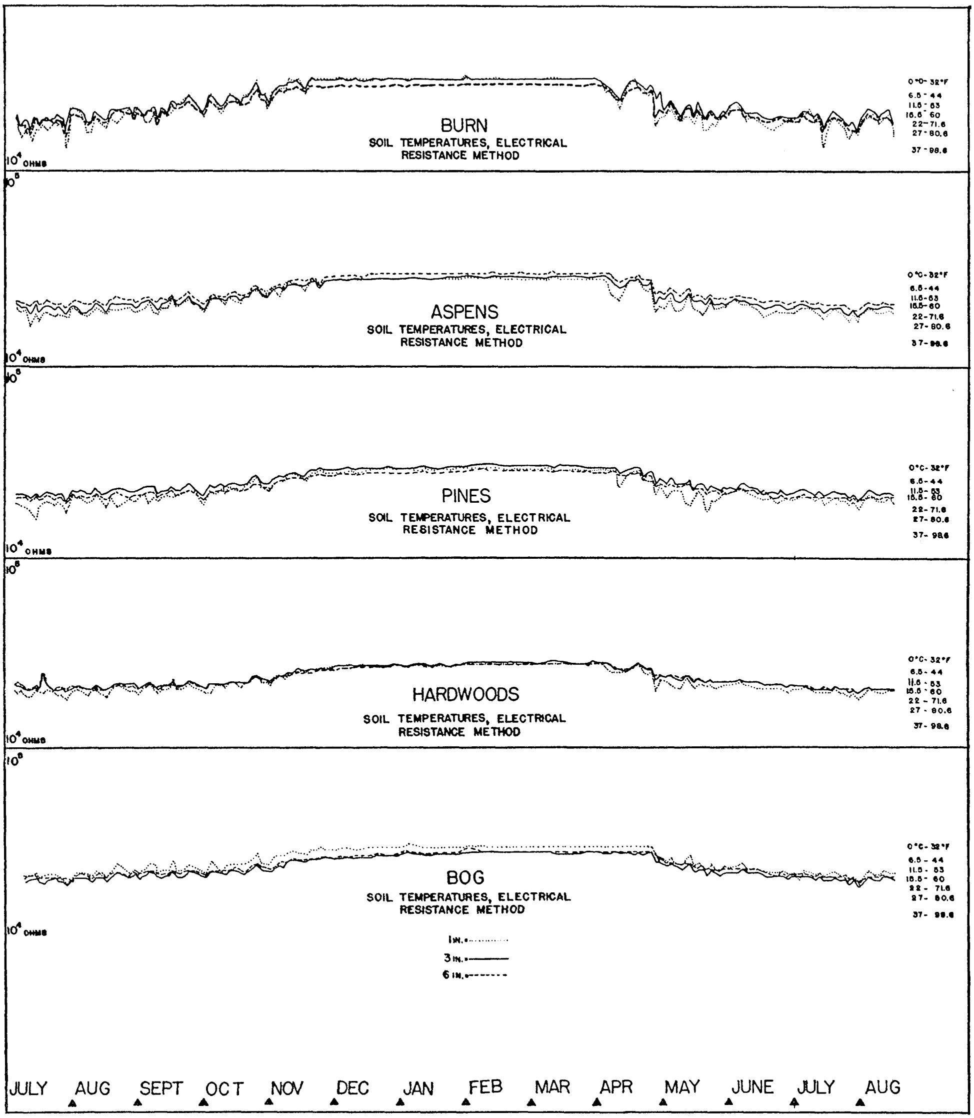

FIG. 2. Soil temperatures, electrical resistance method.

around the blocks and thermistors was never stepped on, even with snowshoes. The value of this protected area was seen in the second summer (1951) of the study. Beech seedlings, dogtooth violets, and bracken came up on the tested areas among the thermistors and blocks and above the soil thermometer cage.

The close agreement of the three-inch thermistor (Fig. 2) and the set maximum temperatures of the soil testify to the accuracy of this simple method of burying a maximum-minimum thermometer for soil temperature, as contrasted with the elaborate precautions taken by some workers to avoid contaminating temperature influences (Li, 1926). In the region chosen for this study, where the winter is continuously cold, such a method of taking soil temperatures is feasible. The only difficulty came in late February and in March when spring thawing occurred during the heat of the day. Low night temperatures and cold snaps caused an ice layer to form over the ground surface of some areas, making extraction of the soil thermometer difficult. Two thermometers were broken during the early spring of 1951. In a region farther south, where the winters are characterized by such alternating freezing and thawing, this method would not be practical.

Thus, the forest floor at a depth of from one to six inches was sampled for temperature and comparative moisture. This zone is the part of the habitat most used by *Blarina*. To be sure, *Blarina* emerges frequently, as is shown by its occurrence in owl pellets and by tracks upon the snow surface. Its food gathering activities are mainly subsurface, however, as Seton (1909) recognized, who characterized *Blarina* as a "threader of mouse-tunnels, and a digger in moss, fallen leaves, and loamy soil . . . . " He defined the habitat of *Blarina* as the "inter-world" between the true forest floor and the carpet of dead leaves which covers it. Merriam (1884) not only recognized the fact that *Blarina's* activities were mainly subsurface, but also noted that it was more abundant in the hardwoods than in the coniferous forests of the Adirondacks. Hamilton and Cook (1940), too, mentioned this sphere of activity. They recognized the importance of snow cover in relation to local distribution of small forest mammals.

Intensity of solar radiation was measured by means of a self-registering black-bulb thermometer *in vacuo*, on the campus of the Biological Station. Unfortunately, this instrument broke on 5 May 1951, preventing continuation of the observations. The black-bulb thermometer has certain limitations and restrictions regarding conversion of its temperatures to those of natural conditions. These limitations tend to minimize the representation of the severity of the soil climate, not to exaggerate it for " . . . . the black bulb thermometer does not indicate the extremes of surface temperature which are possible under peculiar local conditions in the microclimate" (Geiger, 1950).

In order to compare the vegetation of the several study areas, a modified point-observation method was used. This method was originated by Stewart and Hutchins (1936) for calculating range use, and was modified by Gates (1949) for use in forested areas. Briefly, the method is as follows: A circular (actually octagonal) quadrat, usually of 0.8 meter radius, having an area of two square meters, is selected. The observer estimates the amount of area covered by each classification of vegetation in the quadrat. As an aid a white card 10 by 10 cm. is sometimes used for a standard of comparison. With practice surprising accuracy is obtained. Several faults of this method are obvious, namely, habitual over- or underestimation by an observer and the errors inherent in observations made by different people. The ease of setting up a quadrat, however, and the great flexibility of the method are important points in its favor.

In this study ten permanent quadrats were set out on each area. The quadrats were situated along a line through the center of the area. A center stake for each quadrat was set up at regular intervals along this line, regardless of location in reference to advantageous spots. Each quadrat was given a marker with a painted key number.

Gates's method was modified as follows: Eight stakes were placed at regular intervals around, and 0.8 meter from, the center marker, making an octagon essentially two square meters in area. On squared paper the position of each plant in the several categories was mapped, and the area covered by each was noted, either by size of symbol or by marginal notations. Herbaceous layer, shrub or bracken layer, tree layer, and actual ground litter were the categories chosen. By using different colored pencil leads I was able to plot all categories on one map of each quadrat. In this manner the vegetation of each area was sampled by mapping a total of 20 square meters. These samples could be revisited and compared during the season.

DESCRIPTION OF AREAS

Burn.—The Burn area is in Cheboygan County, NE 1/4 sec. 32, T. 37 N., R. 3 W., on the high plain of outwash sands and gravels which lies to the east of Glacial Lake Algonquin Pellston Island (Leverett and Taylor, 1915). The substrate is Rubicon sand. The original vegetation, red and white pine, was removed in the 1870's. After repeated burnings there developed an open forest of aspen, birch, red maple, and red oak, with a scattering of young pines. In 1948, an area 300 by 425 feet was cut and burned experimentally to provide a study plot for classes in plant ecology. At the present time the sand on this plot is mostly bare, but is partly covered with burned and charred logs and roots. Aspen is reinvading swiftly, as is also bracken fern. Many sprouts of red maple are coming up from stumps. Vegetation has a maximum height of four and one-half feet. It is interesting to note that the young aspens on this area lost their leaves some three weeks earlier than the more mature trees nearby. This area probably is not truly representative of most aspen-pine burns, since the surrounding forest acts as a snow fence, causing snow to pile deep on it. Less snow cover, however, would accentuate the severity of the soil winter.

Aspens.—This area is in Cheboygan County, NW 1/4 sec. 34, T. 37 N., R. 3 W., just east of South Fishtail Bay in Douglas Lake, on a hill that originated as a sand spit from Glacial Lake Algonquin Topinabee Island. The lower western boundary of the plot is formed by the wave-cut bluff above the beach level of the Nipissing stage of Douglas Lake. The substrate is Rubicon sand, which here lies in a strip between the moist Eastport sand along the present lake level and Roselawn sand to the east beyond the crest of the hill. The original vegetation of the area was red and white pine, with white pine probably predominating. It was lumbered in the 1870's and thereafter was subjected to repeated fires, the last of which took place in 1912. The present vegetation consists of a forest of mature aspens with some red maple, white birch, and a scattering of pines. Several huge blackened stumps and logs remain to remind one of the size of the trees in the original forest.

PINES.—The Pine area is in Emmet County, NE 1/4 sec. 26, T. 37 N., R. 4 W., on what is known as the Pellston Flats, which were part of the bed of Glacial Lake Algonquin, between Pellston and Brutus islands. The substrate is Rubicon sand. The original vegetation consisted of both red and white pine. The area was cut in the 1870's and thereafter was subjected to repeated fires, the last of which occurred in 1892. The succession on this area has been followed by Dr. F. C. Gates and other botanists at the Biological Station through the aspens to the pines which now cover it. Red pine is dominant, with a scattering of white pine, some red maple, white spruce, and aspen. The ground surface is very irregular, with mounds one to three feet high every 10 to 15 feet and with low spots between. This area is of especial interest since it serves as the only example in existence illustrating the composition of the forest that originally covered the sandy areas of the region.

HARDWOODS.—At the beginning of this study an area of second-growth sugar maple and beech just east of Munro Lake, Cheboygan County, SE 1/4 sec. 9, T. 37 N., R. 3 W., was gridded as a study area and was trapped in 1949. Although further investigation was abandoned, certain data from the plot are used in this study.

The principal hardwoods plot is situated in Cheboygan County, NW 1/4 sec. 28, T. 36 N., R. 3 W., on the property of Mr. Alfred Dau on Colonial Point, sometimes called Indian Point. The substrate is Emmet sandy loam, smooth phase. The topography of the area is level, but the ground surface is marked by irregularities similar to those on the Pine area, which seem to be characteristic of forest climaxes (Lutz and Chandler, 1946). These depressions are possibly of some importance in promoting a stable moisture regime, since free water was present in them from 4 April to 14 May 1951. The forest floor is covered with a deep layer of leaf litter and decaying branches, twigs, and logs. The vegetation is mature sugar maple, beech, and hemlock, with accompanying yellow birch, ironwood, red oak, and red maple. The understory is mainly young sugar maple, with some beech and hemlock. This area has been excellently analyzed botanically by Braun (1950).

Bog.—This area in Cheboygan County, SW $\frac{1}{4}$ sec. 4, T. 36 N., R. 3 W., is known locally as the Hermit's Bog, a part of the large swamp, Reese's Bog, lying along the north shore of Burt Lake. The substrate is Carbondale muck, with a sand base at a depth of about 40 cm. The entire swamp has been logged and burned in the past. The original vegetation, to judge from the immense fire-blackened stumps and logs, was white cedar and some white pine. The present vegetation is almost entirely white cedar, with some white spruce and a few white pine, aspen, and birch. The forest floor is covered with needles from the dominant conifers, but the low spots, stumps, and logs are covered with mosses and liverworts.

PROCEDURES

Areas were visited and instruments read every other day from 10 July 1950 until snow made such regular rounds impractical. While snow was on the ground the areas were visited once every four to seven days. After snow melted in the spring of 1951, the rounds were made every other day until the middle of June, when they were made every Tuesday, Thursday, and Saturday, until 16 August 1951, when the field work was terminated.

Areas were visited in a rotating plan in order to minimize the effect of time of day. For example, one round would be in the order Burn-Pines-Hardwoods-Bog-Aspens. The following round would go Aspens-Burn-Pines-Hardwoods-Bog, and so forth. During the late spring, summer, and fall it was possible to visit all areas in about two and one-half or three hours. During the winter months when some areas could be reached only on snowshoes the entire round might take as long as six hours. At no time was it impossible to visit all areas on any particular round on one day. The rounds were made in the morning, from about 8:30 to 11:00, when air temperatures were usually nearly midway of their daily fluctuation, thus giving a more exact record of the preceding range and making it possible to reset the thermometer so that it could accurately record the ensuing range. The position of the set maximum soil temperatures varied, however, since the rate of heat penetration varied in the different soils.

COMPARISON OF AREAS

Figures 3 and 4 show the progression of the maximum and minimum air and soil temperatures; Figure 5 shows the progression of block resistances on the several areas throughout the year. Close inspection of these records reveals several important facts.

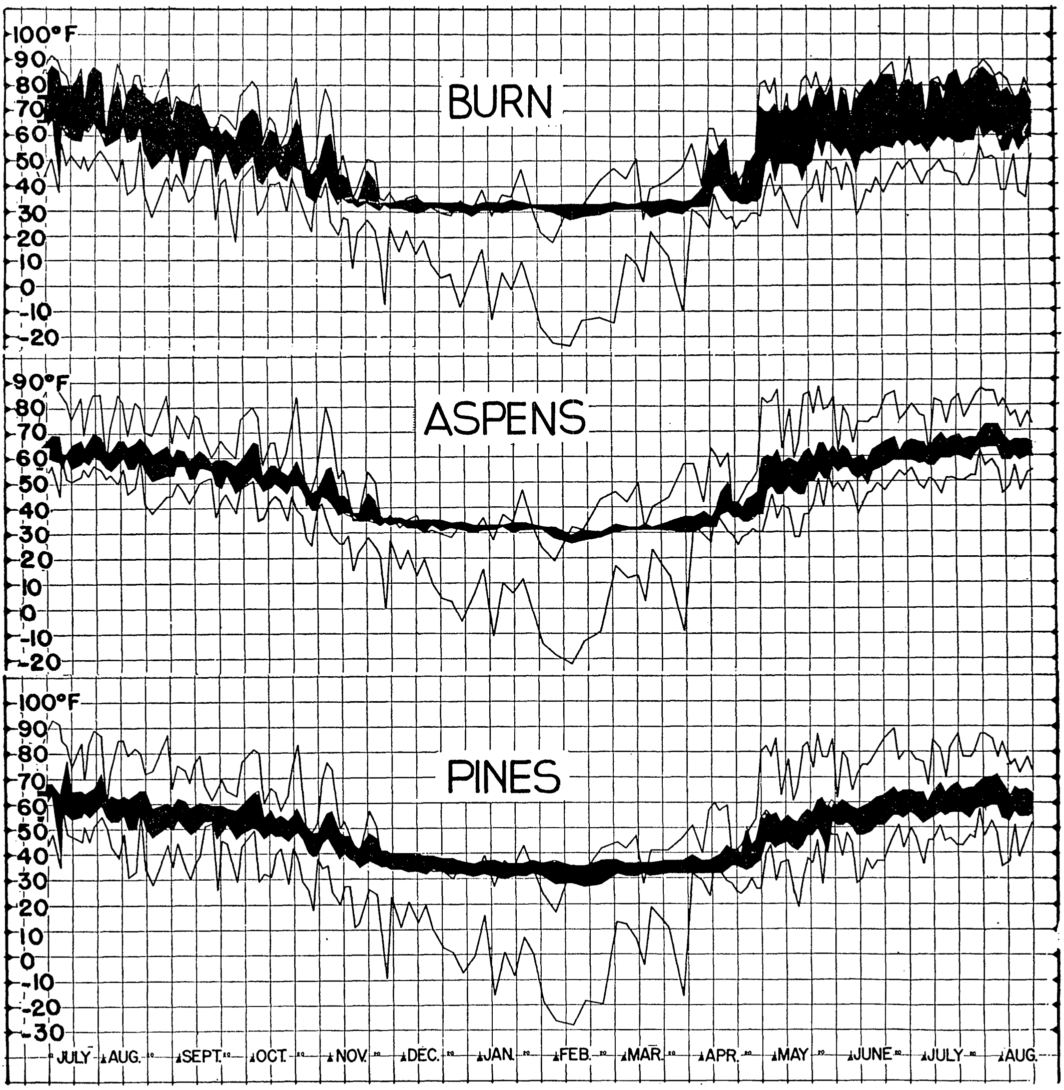

FIG. 3. Maximum and minimum soil (shaded) and air temperatures.

BURN.—In general, compare the fluctuations of air temperature on the Burn with the records of the black-bulb radiation thermometer on the Station campus (Fig. 6). The close agreement of the two sets of fluctuations should be noted and also the close agreement of soil temperature with air temperature. This pattern of air and soil temperatures agrees closely with the theoretical Stage 1 of the formation of the phytoclimate as postulated

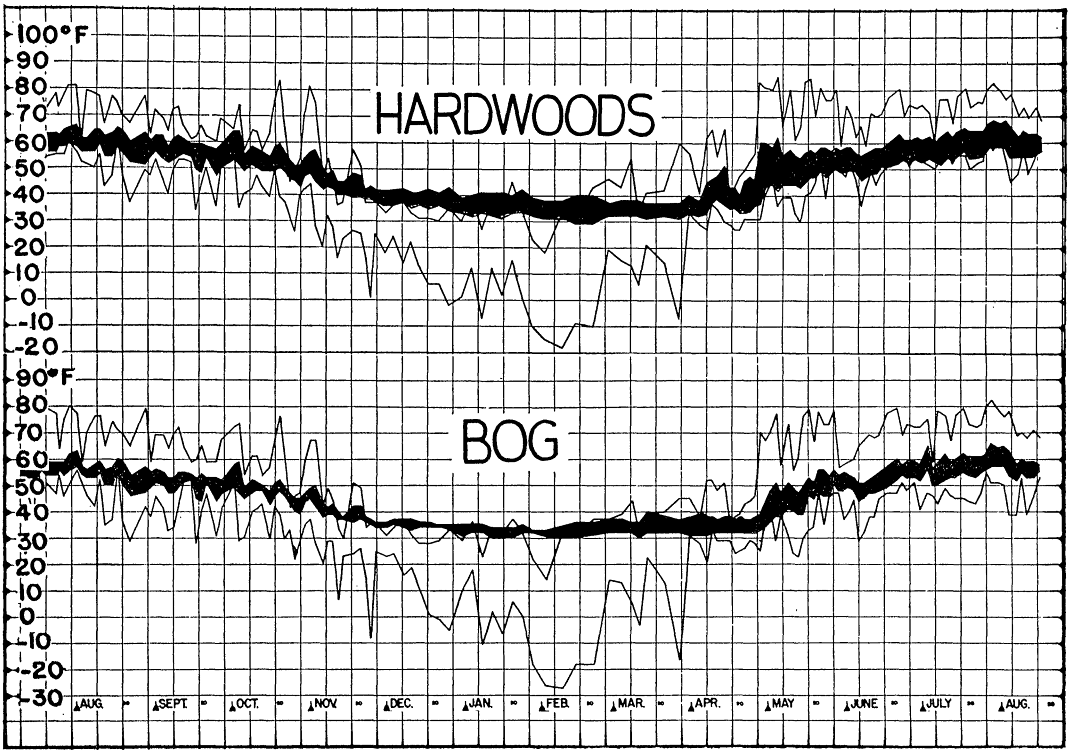

FIG. 4. Maximum and minimum soil (shaded) and air temperatures.

by Geiger (1930). During the months of May, June, July, August, and September the average monthly spread ranges from 18° to 23°. In October and November the spread of air temperatures is from 27° to 28° with a soil spread of 8° to 14°. As soon as snow covered the ground permanently in mid-November its insulating effect caused the soil temperatures to cease their agreement with the air temperatures. There was still some fluctuation, however, up to 35° and down to 27°, averaging 3°, 2°, 4°, 3°, respectively, for the months the snow covered the ground. More important than the fluctuations is the fact that for long periods, as from 25 January to 20 February, the soil was frozen to at least three inches in depth and did not show any alternate freezing and thawing.

The advent of spring to the air of the Burn is gradual, with successively higher maxima over a period of time. The soil, however, still undergoes winter conditions until the snow cover melts, and then suddenly the temperature regime of summer is re-established, with its fluctuations and high maxima.

The degrees of soil maxima for June, 1951, for example, are: 75, 65, 74, 77, 80, 82, 70, 84, 84, 75, 81, 82, 79, and the corresponding air maxima are: 78, 66, 78, 76, 73, 78, 80, 85, 89, 77, 80, 91, 76; on eight readings they average 3.7° above the soil maxima and on five readings 3.2° below the soil maxima. Such conditions of soil climate are shown graphically in Figure 3. It must be remembered that these temperatures are at a depth of three inches. At the surface and immediately thereunder the conditions would show an even greater fluctuation. Temperatures as high as 101° at a depth of one inch were measured, while the corresponding air temperature was 74° and the temperature at three inches was 86°. In this same region Gleason (1917) recorded a surface temperature as high as 140°F. on bare soil in the sun during an intense heat wave in the latter part of July.

To summarize, the temperature regime of the Burn surface-soil layers is characterized by marked fluctuations, wide extremes, permanent winter freezing, and sudden release from winter conditions in the spring.

ASPENS.—The temperature relations of the soil in the Aspens are quite like those of the Burn, with the fluctuations and extremes modified and somewhat smoothed (Fig. 3). The peaks of soil temperature are still present and generally agree with the peaks of air temperature, but do not follow them exactly. The same sudden cessation of fluctuation comes with the arrival of snow. The soil freezes to a depth of at least three inches and only occasionally thaws, and for the period 4 through 25 February did not thaw at all. The arrival of spring is more gradual; soil temperatures increase their maxima but retain the winter minima until the last of March. Thereafter, the summer temperature regime is in force. Quite violent fluctuations, similar to those on the Burn, are noted until about the first of May, when the canopy begins to close. This type of soil climate corresponds closely to Geiger's Stage 3.

PINES.—The temperature regime in force in the Pines is quite modified from that on the Burn, but the relation is still to be seen in the wide daily range (Fig. 3). The fluctuations of soil temperature are still present in greatly modified form, with occasional independent action, as from 20 to 30 October. With the arrival of snow the soil resists the extremes of air minima for a longer period of time. Freezing takes place at three inches, but the temperature here at no time remains long below the freezing point.

Snow conditions in this open conifer forest are different from those in the deciduous areas. Snow, instead of sifting down evenly over the entire area, is caught to a certain extent by the pine foliage and then falls to the ground in blobs from the size of a snowball up to that of a bushel basket. This compacts the snow cover, probably reduces its insulating property, and favors the formation of a hard, granular, icy cover in late winter and early spring when radiation is intense enough to cause noon and early afternoon melting. At this time the surface of needle litter, one or two

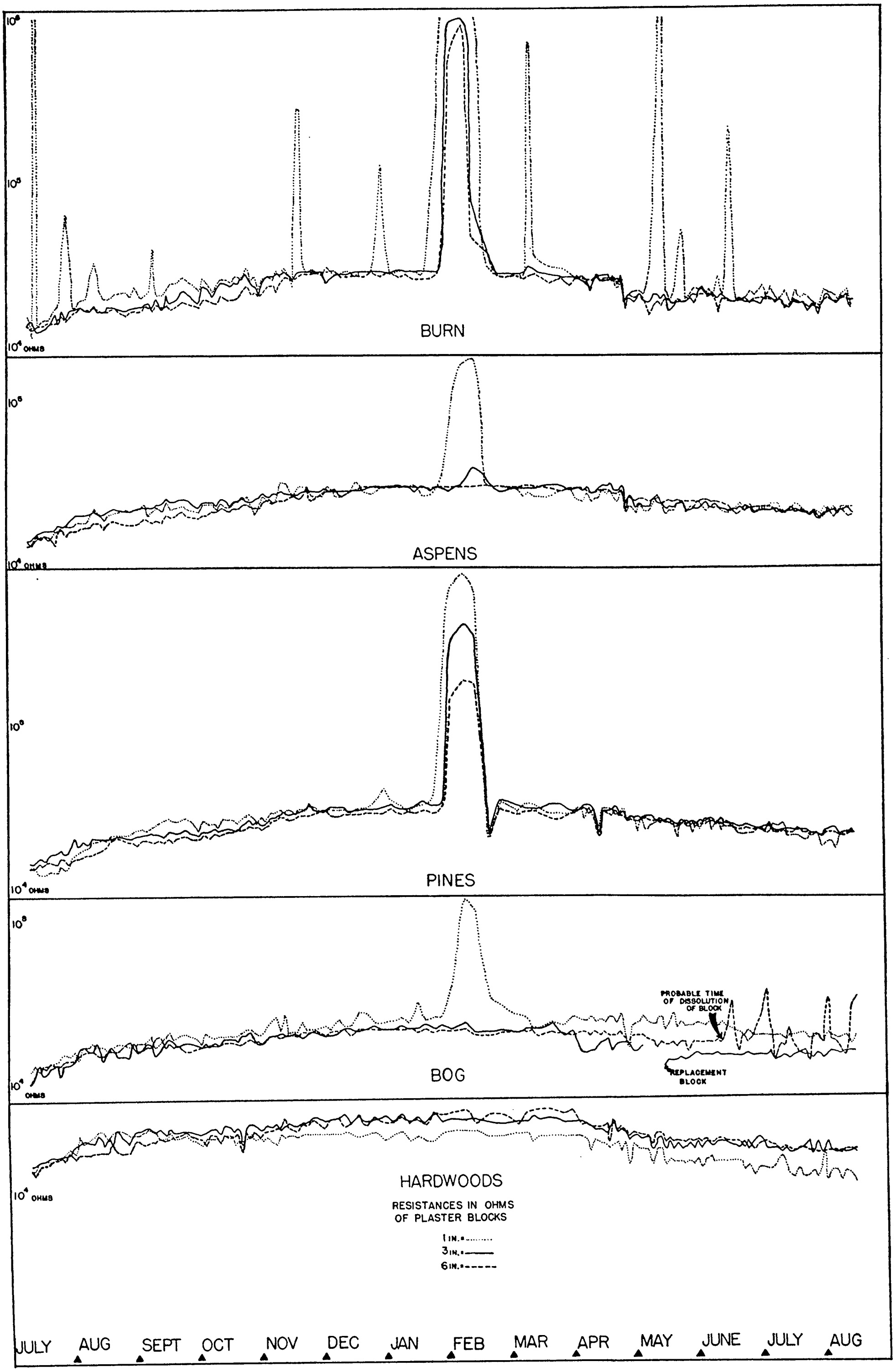

FIG. 5. Resistances of plaster blocks, in ohms.

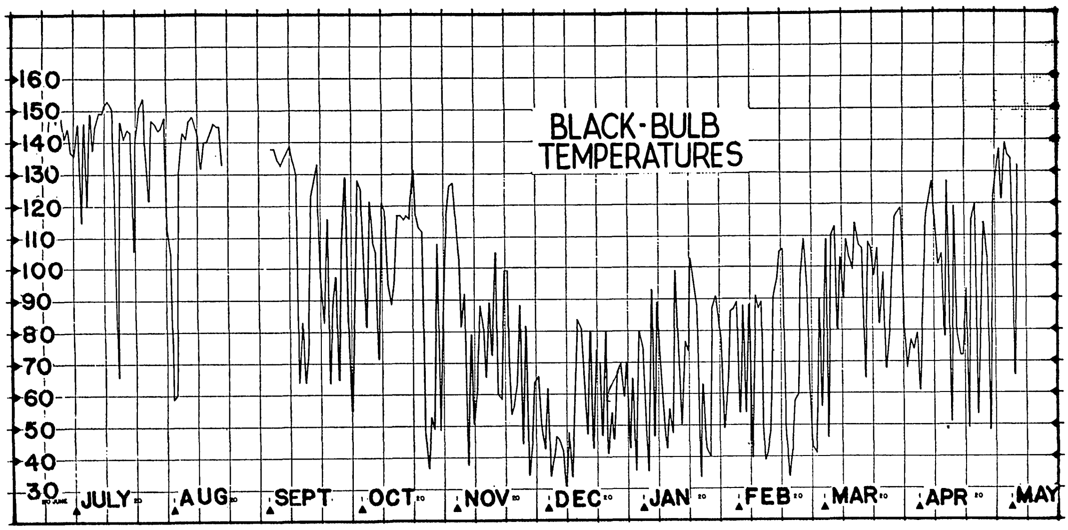

FIG. 6. Readings of black-bulb radiation thermometer.

inches deep, is frozen into a hard, interlocking and interwoven mass, quite impervious to burrowing.

Mackinney (1929) did not believe that the amount of compaction of the snow cover affected in any way its insulating properties either on bare or on litter-covered soil. He noted the physical effects of litter on friability of soil even below the freezing point. My data, though not conclusive, would seem to indicate that the amount of compaction of the snow cover is of importance to its insulating properties.

HARDWOODS.—Temperature conditions of both air and soil in this area are markedly different from those prevailing in the pine sere. At no time during the warmer periods (July to October, 1950; May to August, 1951) was this area the warmest in air temperature, and at no time during the colder period (November to April, 1950–51) was it the coldest. During spring and fall it was several times the warmest of the areas. The characteristic of the temperature regime is its stability. Fluctuations are present, but they are not violent nor of great extent. Monthly average spreads of soil maxima and minima range only from 6° to 12°. Close study of the chart of temperature (Fig. 4) shows numerous instances where soil temperature is more or less independent of air temperatures. The greatest fluctuations occur in October and early November, and again in April and early May, when the canopy is incomplete and snow cover is lacking or intermittent. The arrival of the permanent winter snow cover causes even further reduction in fluctuations of soil temperature. The soil temperature at three inches dropped below freezing several times, but at no time was the soil maximum below 32°, the lowest maximum being 38°, the absolute minimum, 29°. From the charted records it may be seen that the daily spread of soil temperatures remained remarkably constant throughout the winter. Snow on this area sifted over the whole ground surface, with very little adhering to the trees; thus, it formed an even, fluffy, insulating layer. The thick layers of litter and humus, even though there might be ice crystals in the upper part, did not form the solid impenetrable mass that characterized the pine sere but remained friable and easily penetrated by a small mammal. The cover of snow on this area was melting almost continually from the ground surface upward, probably because of the heat produced by decomposition of the leaf litter. This condition kept the leaf litter more or less saturated with moisture. The presence of so much free moisture with its high latent heat of fusion was probably an additional factor tending to stabilize the temperature regime. This state agrees quite closely with Geiger's Stage 4.

Bog.—The Bog, with its dense canopy and its substrate of continually decomposing peat and muck having a high water content, was the most stable of all environments measured. Monthly average air temperature spreads ranged from 20° (December) to 51° (February). If the month of February with its sudden thaw is excluded, the greatest range is 32° (May). Soil temperatures, on the other hand, had monthly average spreads from 3° to 8°, the greatest single spread being 13° on 4 May 1951, three days after the last snowbank melted, when the air temperatures showed a spread of 48°. Study of the charted air and soil temperatures shows several characteristics (Fig. 4). The soil temperature is almost completely divorced from the fluctuations of the air temperature. The range of average maximum and minimum soil temperatures is remarkably constant from month to month (in degrees)—6.0 (July), 5.9, 5.6, 3.8, 2.4, 3.1, 4.5, 5.8, 6.2, 8.4, 6.0, 7.3, 7.0. The daily maxima are much more stable than the daily minima. Freezing occurs on the surface, but at no time does the soil at a depth of three inches remain completely frozen; the maximum is never below 32°F. When freezing does occur, the soil environment remains for the most part penetrable, similar to that of the Hardwoods.

Comparisons of soil temperatures.—In late winter and early spring, when the solar radiation is increasing in intensity, the Aspen and Burn areas were the sites of peculiar melting conditions. On these areas the winter winds had tended to hollow out spaces in the snow around the bases of trees, stumps, and logs. With the increased incoming radiation these hollows soon melted free, exposing the soil and litter surface to the effects of great outgoing radiation at night. Around the base of nearly every aspen tree, stump, slash pile, and log there was an area of intense and deep soil freezing. In the Bog the dense canopy prevented wind action; indeed, the snow seemed even deeper around tree and stump bases. At the time of increased

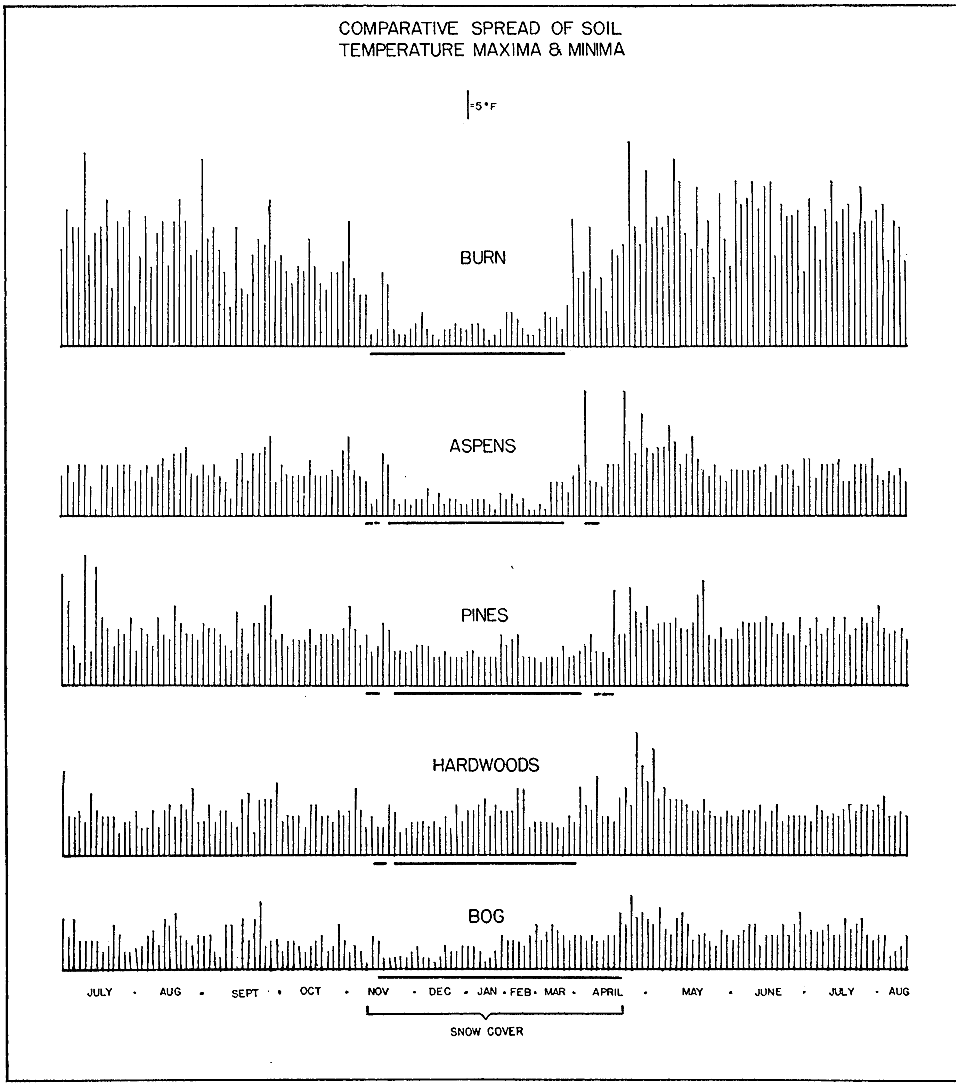

FIG. 7. Range of maximum and minimum soil temperatures of all areas at a depth of three inches, all plotted to the same base line.

radiation exchange, these vulnerable potential hibernacula and nest sites had even more protection from freezing than did other parts of the same area, in contrast to conditions on the Burn and Aspen areas. In the mature Hardwoods the trunk-space area was relatively calm, even in winter, and the snow was not scooped out around the tree bases as on the Burn and Aspen areas.

Figure 7 shows the spread of maximum and minimum soil temperatures of all areas at a depth of three inches, all plotted to the same base line. During periods of no snow cover, it may be seen that the Burn, Aspens, and, to a lesser extent, the Pines, have similar spreads of temperature, similar fluctuations, and comparable extremes. In contrast, the Hardwoods and the Bog show great stability of temperature, similar lack of marked fluctuations, and a narrower range of extremes.

During periods of snow cover the Burn and Aspens show little fluctuation in temperature, but this stability is under the freezing point most of the time. The Pines show more fluctuations, but again, much of the time the temperature is below the freezing point. There is no marked change in the general pattern of fluctuations in the Hardwoods and Bog at this time, only a slight decrease in magnitude, and, in addition, the general range of the temperature is above the freezing point.

The only time of the year in which the Hardwoods resemble the pine sere in lack of stability of temperature is in the early spring before the canopy closes. Even then, the Hardwoods are far more stable than is the Burn.

Thus, during the period of no snow cover, the representatives of the pine sere form a comparable group characterized by marked fluctuations of temperature, as contrasted with the Hardwoods and the Bog, which have greater stability of the temperature regime. During periods of snow cover and low air temperatures, the representatives of the pine sere form a comparable group characterized by soil freezing and great reduction in amount of fluctuation, as contrasted with the Hardwoods and the Bog, which are characterized by higher temperatures and no great change in amount of fluctuation.

Soil moisture.—Inspection and comparison of the records in Figure 5 show that the comparative moisture contents of the soils of the several areas exhibit similar relations and differences. The Burn is again the most variable, having no available moisture in the top one inch of the soil several times during snow-free periods. During the winter, when the soil is frozen, no moisture is available. The Aspens are much more stable, but the surface one inch and, for a time, three inches, had a sharp drop in moisture. In some respects the Pines resemble the Burn more than they do the Aspens. There was a prolonged and marked lowering of the moisture in January and early February; the sharp return to "normal" readings coincided with the February thaw. The Hardwoods are again the most stable, lacking the sharp peaks and valleys in the moisture regime. The Bog is difficult to analyze. In early May the three-inch block gave erratic readings and was replaced. In late June the six-inch block also began to give suspicious readings but was not replaced. When the blocks were recovered in mid-August, the original three-inch block was eroded completely away, and the six-inch block was eroded so much that only a thin skeleton of plaster was left, which disappeared at the touch. In spite of the high peak of resistance at one inch in early February, moisture seemed plentiful. Possibly this decrease in available moisture, which was probably due to freezing, may have passed the threshold of tolerance of *Blarina,* or this amount of freezing may have reduced the amount of available matrix for burrowing and tunneling to a point where only those *Blarina* later caught on the area could forage for enough food to enable them to survive.

These data on comparative available moisture do not indicate free water, but water in the sense of physiological availability to plants. They do serve, however, as an indication of the moisture in the atmosphere of a cavity or tunnel through the soil. Infinite resistance in a block means that probably little or no capillary moisture remains, the only moisture present being hygroscopic, which is believed to be only a molecular film, without the properties of water and probably incapable of escape to the atmosphere at these temperatures. It was noted on the Burn that at block resistances of above 50,000 ohms no water of condensation formed on the soil maximum-minimum thermometer case.

In general, then, the representatives of the pine sere again form a comparable group bound together by less available moisture, more fluctuations in amount of moisture, and periods during the winter of little or no available moisture. The Hardwoods stand by themselves as an area of great moisture stability, higher level of moisture, and no winter freezing. The Bog is also in a class by itself, having a far higher level of available moisture than any other area. The surface freezing makes it comparable to the pine sere in one respect, namely, part of the microhabitat of *Blarina* is unavailable at times during the year.

VEGETATIONAL DIFFERENCES.—Vegetation was sampled on two occasions, the first in the period 10–19 May 1951, and the second in the period 9–12 August 1951. Sampling in this manner at the beginning and at the peak of the growing season allows certain conclusions to be drawn concerning the stability of the environments sampled. The importance of light and its intimate relationship with temperature have been noted by many authors (Daubenmire, 1947; Weaver and Clements, 1938; Geiger, 1950). Study of Figure 8 reveals that the sampled environments fall into two separate groups. One, the Burn-Aspens-Pines group is characterized by a tremendous increase in the amount of cover produced by the herbaceous and shrub or bracken layers; the other, the Hardwoods-Bog group shows, in general, no such great increase; indeed, there is even a decrease in the Bog. When the Hardwoods were sampled in May the vernal aspect herbaceous societies were present, but after the canopy closed such a category practically disappeared. The shrub layer shows an increase, but this is due almost entirely to leafing out of two extremely shade-tolerant perennials, beech and sugar maple saplings. The canopy of the Burn-Aspens-

Pines group, however, is either lacking or thin enough to allow sufficient light and heat for vigorous plant growth to penetrate to ground level. If it were not for the shade given by bracken fern (*Pteridium aquilinum*) even more light and heat would reach the ground during the period of most intense solar radiation, as is the case on the Burn.

Vegetation was also sampled by the tree-count method on 3 November 1951. A strip two meters wide adjoining and parallel to the row of point-

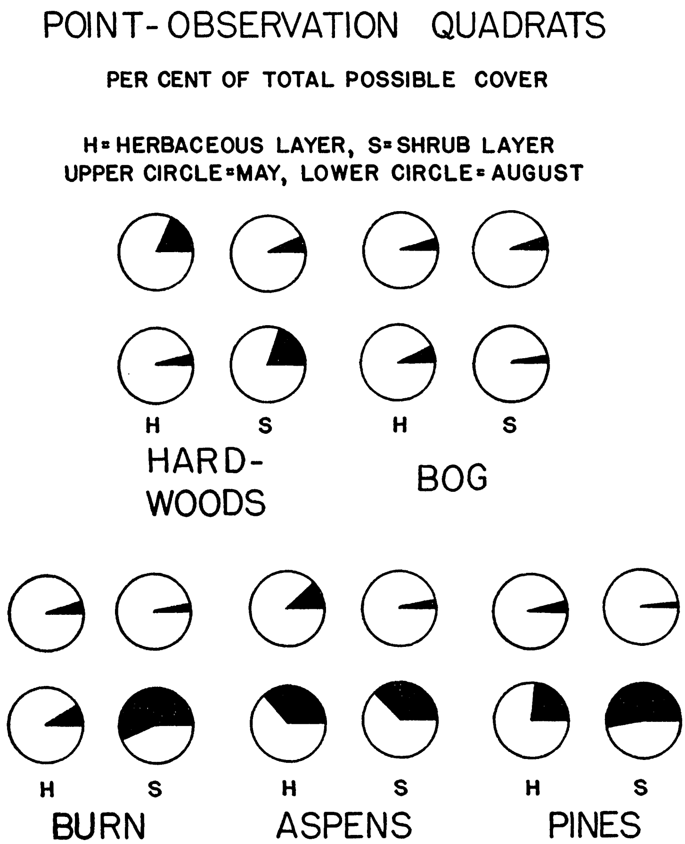

FIG. 8. Analysis of cover in the lower strata of vegetation.

observation quadrats was surveyed, and all trees breast high or higher were counted and separated into the following size classes (in inches): 0–3, 3–6, 6–12, 12+, DBH (Table II). The Burn area was not sampled in this manner since only a few tree species had reached this height.

Comparison of vegetational differences is not of major importance to this problem because vegetation is essentially a function of the primary physical factors of temperature and moisture, along with soil structure and

TABLE II

NUMBERS OF TREES ON THE STUDY AREAS BY SIZE CLASSES

	Hardwoods				Bog				Aspens				Pines			
Size Classes (DBH)	0–3	3–6	6–12	12+	0–3	3–6	6–12	12+	0–3	3–6	6–12	12+	0–3	3–6	6–12	12+
Pinus strobus	..	..	..	..	..	..	1	..	..	..	..	..	9	1	1	..
Pinus resinosa	..	..	..	..	..	..	..	..	3	..	..	..	3	2	1	6
Picea glauca	..	..	..	..	6	11	5	1	..	..	..	..	1	1	..	..
Abies balsamea	..	..	..	..	2	1	..	..	..	..	..	..	..	..	..	..
Tsuga canadensis	4	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..
Thuja occidentalis	..	..	..	..	45	23	3	..	..	..	..	..	..	..	..	..
Populus grandidentata	..	..	..	..	..	..	3	..	63	24	1	..	16	..	..	..
Populus tremuloides	..	..	..	..	..	..	..	..	..	..	..	..	10	..	..	..
Betula lutea	..	4	2	1	..	..	..	..	..	..	..	..	..	..	..	..
Betula alba	..	..	..	..	..	..	1	1	22	1	..	..	4	..	..	..
Quercus borealis	..	..	3	4	..	..	..	..	9	6	..	..	..	..	..	..
Acer pennsylvanicum	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Acer spicatum	2	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Acer saccharum	50	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..
Acer rubrum	..	1	..	2	..	..	..	..	18	..	..	..	15	..	..	..
Tilia americana	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Fagus americana	11	1	2	4	..	..	..	..	..	..	..	..	..	..	..	..

chemistry. Since the primary factors have already been measured, these vegetational differences are included so that rough comparisons may be made with the mass of data accumulated by other investigators who have relied heavily upon vegetational analyses.

DESCRIPTION OF TRAPPING

Discussions concerning the relative merits of snap versus live trapping are many. Certain types of studies, those having to do with home range, movement, and survival, obviously require live trapping; however, the investigator using live traps never actually possesses the animal studied except for short periods. All he knows must be gleaned from necessarily hasty observations made during the few fleeting moments while the animal is in the hand. Many investigations have been carried out on areas which were populated by trap-hardy animals and the less trap-hardy *Blarina*. As the work proceeds, the ratio of surviving *Blarina* to the trap-hardy animals usually becomes less and less. This cannot help having a marked effect on the results, since the "balance of nature" is upset at a most inopportune time. It may be better to study the mammals on any area from a number of thin temporal cross sections which are complete in their data rather than from thicker temporal cross sections, the accuracy of which may be open to serious doubt. In addition, the use of snap traps provides specimens for future more complete studies of age, molts, food, abnormalities, variation, and so forth, data for which are incomplete when taken only from observations on live animals.

In this study, in which estimated or calculated populations for a large area were not desired—indeed, such estimates and calculations characterize the state of mind which is the antithesis of that needed to appreciate the concept of detailed autecology and microhabitat—snap traps were used, as a comparative segment of the different areas was desired. Also, the quadrats were trapped for six consecutive nights in order to have a check on influx of animals to repopulate the decimated area. The detailed data for *Blarina* comprise a separate report which will appear elsewhere.

The 300- by 400-foot areas were gridded for placement of 100 Museum Special traps, 30 by 40 feet apart, thus making the enclosed area actually 270 by 360 feet, with a larger "effective area." The plots were gridded in the early spring of 1951, before the leaves unfolded, by using a 300-foot steel tape and a right-angled sighting device made of four strips of wood. At each proposed trap site a strip of red cloth was hung to a branch above the tape mark, or if no branch or twig was near, one was stuck in the ground so that the marker was over the tape. To each marker was stapled a bit of card with the row number and trap number in India ink. It was necessary to identify each trap in order to plot the position of each animal taken. This practice was invaluable in running the lines to prevent skipping a trap. Complete coverage of the areas would have been very difficult if the traps had not been numbered.

Traps were set in the afternoon before the first day of the trapping period. Bait used was a mixture of peanut butter, rolled oats, bacon grease, and chopped raisins. Identical bait was used on all areas. Each trap was set directly under the red marker. A handful of leaf or needle litter was removed, and the trap was placed in the depression thus formed. All traps were tied to nearby trees, branches, or fallen limbs. In the 3,000 trap-nights of the 1951 season of this study only two traps were lost.

Traps were visited daily, between 8 and 10 A.M., and were rebaited when necessary. All animals caught were placed in small paper bags, on the outside of which were written the area and trap number. Each area was trapped

TABLE III

TRAPPING RESULTS, 1951

Species	Burn	Aspens	Pines	Hardwoods	Bog
Peromyscus leucopus	14	10	1	4	1
Blarina brevicauda	0	3	5	40	4
Sorex cinereus	0	0	0	0	31
Citellus tridecemlineatus ..	3	1	0	0	0
Napaeozapus insignis	0	0	0	1	1

for six nights; then the traps were taken in, checked, and the following afternoon, if possible, set out on the next area. The Hardwoods area was trapped from 24 to 29 June, the Pines area from 1 to 6 July, the Bog area from 9 to 14 July, the Aspens area from 15 to 20 July, and the Burn area from 23 to 28 July. By trapping in this order the three "climax" areas were compared in quick succession, and the Burn, the area with environment most unfavorable to shrews, was trapped last, giving the small mammal populations the longest time to build to a maximum. Thus, the comparative trapping results (Table III) indicate that populations on the Aspens and Burn are probably lower than recorded, and that the Hardwoods population probably would have been even larger if it had been trapped later in the season.

In addition to the animals listed in Table III, one *Tamias striatus peninsulae* was taken on the Burn and one *Glaucomys sabrinus macrotis* was taken in the Bog. These are not included in any calculations since the traps were not designed to catch animals of such a size. Moreover, by far the greatest *Tamias* population of any area was in the Hardwoods, which fairly swarmed with chipmunks in 1951.

A similar series of trapping periods conducted in 1949 on the Burn, Aspens, Pines, and the Munro Lake Hardwoods produced the catch shown in Table IV.

Because of the difficulty of accurately setting up an area in the tangled cedar swamps, quadrat trapping was not done in that part of the region until 1951. Numerous trap lines in several cedar swamps, however, had established the presence of *Blarina* and *Sorex* as a sizable part of their fauna.

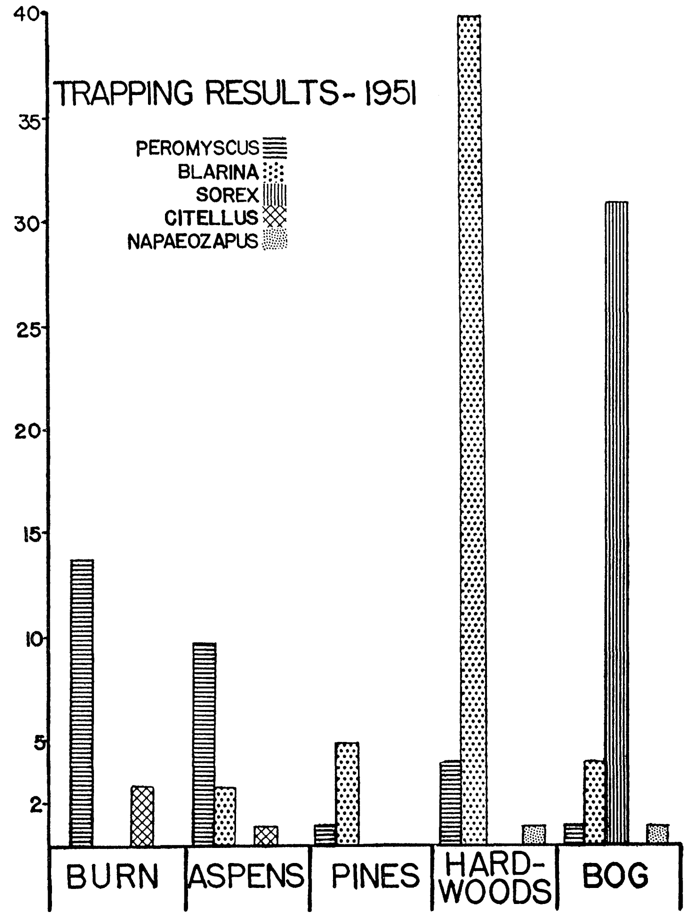

FIG. 9. Total trapping results, 1951.

With environmental segregation such as has been shown to exist between the study areas, one would expect to find a segregation in the kinds of small mammals present. Study of Tables III and IV and Figure 9 shows this to be the case. *Citellus tridecemlineatus*, the thirteen-lined ground squirrel, a prairie form which is expanding its range northward as the land utilization pattern changes from all forest to forest and fields (Burt, 1948), was found breeding only on the Burn. A young adult was taken on the Aspen area, and one was observed passing through that area on 12 May 1951. *Peromyscus* was found on all areas, but in strikingly different

TABLE IV
TRAPPING RESULTS, 1949

Species	Burn	Aspens	Pines	Munro Lake Hardwoods
Peromyscus leucopus	18	15	7	12
Blarina brevicauda	0	0	0	2

numbers. The highest number was taken on the Burn. Undoubtedly, many of these actually were resident in the surrounding aspens. From study of the daily trapping record it was found that of five *Peromyscus* caught the first night of trapping, all were in either the outside or next to outside row of traps. During the 1949 trapping a similar peripheral take was noted. In both years the Burn yielded, respectively, three and four more *Peromyscus* than did the Aspens. Possibly these were the only *Peromyscus* resident on the Burn, the others taken (see Table V) having drifted in from

TABLE V
DAILY TRAPPING RECORD

Species	June 24–29						July 1–6						July 8–13					
	Hardwoods						Pines						Bog					
Blarina	17	9	6	2	3	3	4	..	..	..	..	1	..	..	1	1	..	2
Sorex	..	..	..	..	..	..	..	..	..	..	..	..	1	1	16	5	5	3
Citellus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Peromyscus .	1	1	..	..	1	1	..	..	..	..	..	1	..	..	..	..	..	1
Napaeozapus	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..

Species	July 15–20						July 22–27					
	Aspens						Burn					
Blarina	..	..	1	..	1	1	..	..	..	..	..	..
Sorex	..	..	..	..	..	..	..	..	..	..	..	..
Citellus	..	..	..	..	1	..	2	1	..	..	..	..
Peromyscus .	5	1	..	2	2	..	5	1	2	3	2	1
Napaeozapus	..	..	..	..	..	..	..	..	..	..	..	..

the surrounding aspen upland. On the Aspen area five *Peromyscus* were taken the first night, one the next night, none the next, two on each of the following nights, and none the last night. If the "three nights rule" as expounded by Bole (1939) and Mohr (1943) is followed, the resident population on this area was six (Tables V and VI). The solitary *Peromyscus* taken in the Pines in 1951 was captured on the last night of trapping, in the second from the outside row. Of the four *Peromyscus* taken in the Hardwoods, one was taken on each of the first two nights, then none until the last two nights. The last two were taken in peripheral traps. The single *Peromyscus* taken in the Bog was trapped on the last night. From these data it appears that in the region studied *Peromyscus* has a high population center in the aspen areas, whereas areas of heavy canopy, coniferous areas, and those with stable soil temperature and moisture regimes have fewer *Peromyscus*.

The segregation of *Blarina* is sharply marked. During the 1949 trapping these shrews were not found on any representative of the pine sere, but two were taken in the Munro Lake Hardwoods area. Trapping in 1951 showed that *Blarina* had apparently invaded the later stages of the pine sere in small numbers. The Aspen area, bounded on the west by the steep slope of the Nipissing bluff of Douglas Lake, was adjacent to a strip of environment close to the lake where *Blarina* had been taken. Individuals have

TABLE VI
THREE NIGHTS' CATCH

Hardwoods		Pines	
Blarina	32	*Blarina*	4
Peromyscus	2	*Peromyscus*	0
Napaeozapus	1		
Bog		Bog—Revised	
Blarina	1	*Blarina*	2
Sorex	18	*Sorex*	26
Peromyscus	0	*Peromyscus*	0
		Napaeozapus	1
Aspens		Burn	
Blarina	1	*Blarina*	0
Peromyscus	6	*Peromyscus*	8
		Citellus	3

many times been seen crossing a road which runs through the woods below the Nipissing bluff, parallel to the western boundary of the Aspen area. Undoubtedly, this was the source of the invaders. The unsuitability of the Aspen area as a permanent *Blarina* habitat is emphasized by the complete failure to take any animals in 1949, even though this suitable environment was adjacent. The general unsuitability of the Pine area for *Blarina* is shown by the absence of specimens in 1949. In the 1951 trapping, however, four of these shrews were taken on the first night and no more until the sixth night.

The Hardwoods are the greatest population center for *Blarina*. The night by night catch there followed the anticipated curve almost exactly: 17 the first night, then 9, 6, 2, 3, and 3 on each of the last two nights, as the resident population was trapped out, and the area began to be repopulated by indrifting.

The status of *Blarina* in the Bog is uncertain. None was taken until the third and fourth nights of trapping (one each night), and two on the sixth night. The great harvest of *Sorex* did not begin until the third night. Possibly the low frequency of *Blarina* on this area may be explained by the fact that some winter soil freezing occurred, thus restricting the foraging movements of *Blarina; Sorex,* however, being so much smaller, was able to infiltrate the network of moss and needles, even though it was frozen.

The mammal showing the most marked segregation and restriction to a particular environment is *Sorex cinereus,* this species being found on the Bog only. After the first night of trapping, one trap was missing, one contained raccoon hair, and one *Sorex* was caught. On the second night only five traps were unsprung, and many were pulled aside to the limit of the string. Slugs and snails undoubtedly accounted for some, and raccoons and red squirrels for the rest. One *Sorex* was taken that night. The third night resulted in 16 *Sorex* caught, and the three successive nights produced 4, 5, and 3. There may be two causes for these catches. The possibility that unusual weather conditions influenced the catch may be ruled out. Neither the instruments on the plot nor the records at the Biological Station show any unusual trends at this time. The more likely possibility is that the raccoon and red squirrel interference took place before the peak of *Sorex* activity. If this is assumed to be the case, then the catch from the third night on followed the expected catch very closely, as if the population were being exposed to trapping for the first time.

Napaeozapus was represented by one individual on each of two areas, Hardwoods and Bog. With so few individuals no final conclusions may be made, but it is suggestive that they were taken on the most stable areas. Blair (1941) found that the home ranges of *Napaeozapus* in hardwood forest in Alger County, Michigan, varied from one to nine acres, which possibly explains why only one individual was taken in six nights of trapping on each of these areas. The presence of this animal is another small link in the connection between Hardwoods and Bog environment.

DISCUSSION

This study will be considered successful and will have fulfilled a worthwhile purpose if it focuses attention on the fact that natural history and distributional studies that do not take into account all of the environmental conditions to which the animals are exposed are of little value. This same criticism may be applied to many zoogeographic studies, for, in the final analysis, the geographic distribution of an animal is but the historical sum of the various successful invasions of, and restrictions from, a number of habitats. Because so many studies are carried out in the summer months only, one is prone to lose sight of the fact that these summer months are but a small part of the yearly cycle of the seasons to which the local fauna is exposed.

Before starting this study I had erroneous ideas about the rigorous conditions with which small animals have to contend in a region which is usually covered in winter by the extended polar air mass. I now believe that these mammals have a more stable bioclimate than do the same kinds which live farther south, on the fluctuating edge of the polar air mass, where the weather is variable, with alternating periods of freezing and thawing and with only intermittent snow cover.

Blarina is, generally speaking, an animal of the deciduous forests. Its range, with a few exceptions (peninsular Florida and the easternmost prairies), is concurrent with the distribution of the Eastern Deciduous Forest, as outlined by Braun (1950), and coincides almost exactly with the Canadian, Carolinian, Austroriparian, Texan, and Illinoian Biotic Provinces of Dice (1943). Over a large part of its range it may truly be said to be ubiquitous, apparently occurring in a great variety of habitats. At the periphery of its range it encounters factors, both biotic and physical and combinations of both, which limit its further expansion. The combination of these factors usually forms a tangled, interconnected web almost impossible to unravel. In the northern part of the Lower Peninsula of Michigan *Blarina* apparently meets a series of conditions which simplify this phenomenon.

Dice (1938) noted that the important mammalian habitats of the Canadian Biotic Province are predominantly of two types—hardwood forest and swamp or bog. He recognized the importance of the pine forest in this Biotic Province, but noted that the pine forests have a sparse mammal fauna and that no mammal seems restricted to this habitat. In Cheboygan County the pine forest (and its remnant sere) occupies a minimum of 19 per cent of the total land area, whereas approximately 40 per cent is bog or lakes with bog tendencies (calculated from Foster *et al.,* 1939). Since these areas interdigitate with those of the hardwoods (sands with loams and mucks or peats), the *Blarina* population, instead of being more or less continuous over this region, is split up into many pockets or residual centers and is restricted from invasion and ecesis of the sandy upland environment because of freezing of the soil in winter and extreme heat and dryness in summer. Only in wet or cool summers or in winters with an excess of snow and mild temperatures can it extend its local range to include these areas. The literature abounds with references to *Blarina* tunnels through and upon snow and surface trails made when the temperature was as low as –20°F. (Merriam, 1884). These, however, are more or less temporary uses of the surface. The animal must return to its subnivean environment to gather the bulk of its food and to rest. This environment, therefore, must remain unfrozen and available, with no extensive frozen crust to deny entrance or exit. Pearson (1947) suggested that the shrews used in his metabolism study (*Blarina brevicauda* and *Sorex cinereus*) probably could not stand temperatures higher than 71° to 80°F. for long periods. Soil temperatures on the Burn exceeded this many times. Chew (1951) investigated the water metabolism of *Blarina,* as well as that of *Peromyscus leucopus* and *Microtus ochrogaster.* He found that *Blarina* had a higher intake of water, both in food and as free water, than did the other two mammals studied, and, moreover, that in nature it was also subject to less evaporation than were the other two. When compared under experimental conditions, however, *Blarina* lost more water by evaporation than did the other two. He attributed this to greater water intake, or physiological differences, or a physiological inability to conserve evaporative losses. He also noted that *Blarina* ate food of high water content, from 60 to 90 per cent. Additional water needed by the animal must come from that found free in the environment. If the environment has no free water, either because it is actually nonexistent, or is unavailable (in the form of ice), then this factor is indicated as a cause of distributional restriction. Observations on captive specimens of *Blarina* indicate that comparatively high humidity is important in keeping them alive for any length of time.

Another factor of great potential effect on *Blarina* is the physical character of the soil. *Blarina* is not highly specialized for a fossorial existence, but uses tunnels already present or pushes through the matrix by a series of jerky thrusts. The sands of the pine sere, having comparatively few rootlets and other binding material in the upper layers, usually fall back in place behind a burrowing creature, forcing it repeatedly to create a new passageway in its movements. The humus zone of the Hardwoods is formed of layer after layer of decomposing leaves, which can be separated easily. Lower down in the humus layer the decomposing midribs and veins of hardwood leaves, as well as a reticulum of fine rootlets, serve as a binder or reinforcement to keep the tunnel intact. An animal does not work at top speed during all its waking hours or while foraging for food. If its tunnels constantly closed behind it, and if the matrix were such that it had to work continuously at maximum effort, *Blarina* might not be able to forage widely enough to encounter sufficient food items to meet its already high intake requirements.

During the summer of 1950, live trapping by Miss Cecilia Banwell at the Biological Station disclosed the presence of a sizable *Blarina* population on an "aspen area," which was on Rubicon sand, NW 1/4 sec. 33, about one-half mile east of the Burn area studied. Close study of this area revealed the fact that part of it was a shallow northeast-southwest valley and the accompanying southeast-facing slope. This valley and the slope caught and held the fallen leaves which were deposited thickly by the prevailing northwesterly and westerly winds. Later investigation showed that the snow cover at this spot was from one and one-half to two and one-half times as deep as on the surrounding aspen upland. Thus, topography caused the formation and continuation of an isolated microhabitat suitable for *Blarina,* in the midst of the shrewless aspen upland. This spot is less than onequarter mile from the High Springs ("head of the Gorge"), an area of hemlock, yellow birch, and white pine, with a very thick humus layer and abundant moisture from the numerous seepages and running springs, where *Sorex cinereus, Sorex palustris, Blarina,* and *Napaeozapus* have been taken. It is conceivable that in a moist, cool summer enough individuals of *Blarina* could spread from this permanent center to stock the nearby upland pocket.

Of all the upland areas under consideration, the Pines gives the best indication of becoming a "*Blarina* area." Although it is superficially a climax area, many years of needle accumulation and decay will be necessary to rebuild a humus layer comparable to that in a virgin stand. When that occurs, *Blarina* will probably be found resident there regardless of the usual climatic fluctuations.

Thus, it may be postulated that *Blarina* was originally distributed rather widely in the Douglas Lake region. Lumbering and fires have so impoverished the sandy uplands, and cultivation has so changed the loams that today *Blarina* is limited to mature hardwood stands, with minor centers of population in coniferous swamps and bogs. From these centers of population it is restrained from permanently invading the adjacent sandy uplands because of freezing of the soil in winter and excessive heat and dryness in summer. As plant succession on the impoverished areas slowly returns humus to the soil and thereby approximates the original conditions of moisture and temperature, friability and penetrability, *Blarina* reinvades these areas from the permanent population centers.

This reinvasion keeps pace with the re-establishment of suitable microclimatic and bioclimatic conditions on successive areas. Until suitable year-round conditions are established, the presence of *Blarina* on any area is limited to seasons when the environmental bridge connects the area with a population center. Later, as the microclimate and bioclimate approach continuous optima, more individuals of *Blarina* are in the environment for a longer time, until finally the original population center has expanded to include the new area within its limits. The speed and intensity of this process is regulated by population pressure and a great many known and unknown biotic factors. This process is the basic element of extension of range, as well as of species survival in a time of major environmental instability.

SUMMARY

1. On a series of five study areas in the northern part of the Lower Peninsula of Michigan, illustrating the main forest associations and soil types of the region, physical conditions (soil moisture, temperature, freezing, and penetrability) of the environment of *Blarina brevicauda* were recorded and analyzed for a period of 14 consecutive months. Previously, two summers had been spent in preliminary investigation of the small mammals of the region.

2. The physical analysis shows that the areas called the Burn, Aspens, Pines, Hardwoods, and Bog form a series having increasing stability of soil temperature. In regard to depth and amount of winter freezing the relation is Burn, Aspens, Pines, Bog, and Hardwoods, in decreasing amounts.

3. The physical analysis shows that the Burn, Aspens, Pines, Bog, and Hardwoods stand in that relation to one another as regards year-round presence of available soil moisture.

4. Quadrat trapping (approximately 4,000 trap-nights) indicates that, at the time of trapping, *Blarina* was not present on the Burn, rarely in the Aspens, occasionally in the Pines, regularly in the Bog, and in great numbers in the Hardwoods. In contrast, *Peromyscus leucopus* was present on all areas, but in almost reverse concentration. *Citellus tridecemlineatus* was found only on the Burn and Aspens, breeding only on the Burn, *Napaeozapus insignis* only in the Hardwoods and Bog, and *Sorex cinereus* only in the Bog.

5. Because of these relationships, it is postulated that in this region *Blarina* has a major center of population in the hardwoods (loams), a minor center in coniferous swamps and bogs (peats, mucks, or wet sands), and is present in the dry sandy uplands only to the extent that winter freezing and excessive summer heat and dryness of soil allow it. As succession proceeds, and changes in the soil and humus environment occur, *Blarina* keeps pace by invading the newly accessible areas.

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