MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 109

Microclimates and Local Distribution of Small Mammals on the George Reserve, Michigan

BY

WILLIAM O. PRUITT, JR.
Box 282, College, Alaska

ANN ARBOR
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN
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INTRODUCTION

WHILE doing the field work for a problem on the local distribution of the shorttail shrew (*Blarina brevicauda*) in northern Michigan, I was continually impressed by the importance of the snow cover in the formation and preservation of a microhabitat suitable for this mammal. At that time I resolved to do a similar study in a region which usually did not have permanent winter snow, but which had only an intermittent cover with accompanying alternate freezing and thawing of the top layers of the soil. Consequently it was rare good fortune to be able to spend the period from September 1952 through August 1953 on the Edwin S. George Reserve, in southeastern Michigan, pursuing such an investigation.

I am grateful to the University of Michigan Museum of Zoology, through its director, the late Dr. J. Speed Rogers, for a Reserve Fellowship during this period and for furnishing housing on the Reserve itself. Dr. Irving J. Cantrall, Curator of the Reserve, gave many valuable criticisms and comments and much physical aid during the course of the study. I am indebted to Dr. J. S. Veatch for much information about the soils of the different study areas. I am grateful to Mr. Lawrence Camburn, Custodian of the Reserve, for the use of his shop and tools in the construction of various items of field equipment. Especial thanks must go to my wife, Erna N. Pruitt, for her constant aid and encouragement and for her good nature during the strain of the all-night trapping sessions.

THE EDWIN S. GEORGE RESERVE

Since its establishment in early 1930, a great deal of biological research has been done on the E. S. George Reserve and several excellent descriptions of the Reserve have been published. These may be found in papers by Murie (1936), Burt (1940), Rogers (1942), Cantrall (1942), and Sutton (1949). For details, the reader is referred to them. Suffice it to say that the Edwin S. George Reserve comprises some 1300 acres in Livingston County, Michigan. It lies in the "pot-hole" country of southeastern Michigan, is hilly, and covered with a mosaic of mixed oak-hickory woodland and old fields in several stages of recovery from agriculture. A number of swamps, bogs, and small ponds are scattered over it.

The U. S. Weather Bureau station at Howell, 14 air miles to the north, has continuous records for 25 years. Since 21 September 1949, weather observations have been recorded on the Reserve under standard Weather Bureau conditions. As will be noted later, these standardized observations (USDA 1941: 915, and George Reserve files) sometimes have only incidental agreement with the actual environmental conditions in the microhabitats of the small mammals. The rainfall on the Reserve was 29.78 inches in 1952 and 26.12 inches in 1953, while the "normal" for the region appears to be 31.23 inches per year, as measured at Jackson, Michigan, 25 air miles to the southwest.

DESCRIPTION OF AREAS

In order to study the physical environment of the small mammals of the Reserve, seven study areas were established. Each plot was approximately one acre (210 feet square), and was gridded for the placement of 100 traps. The letters and numbers in the following descriptions (e.g., R–21) refer to the master grid plan of the Reserve as it was in 1952–53. This master plan is kept in the Reserve files.

AREA NO. 1. NORTHEAST HARDWOODS, R–21.—This area was part of an extensive oak-hickory forest and was situated in a "cove" or steep hollow on the northwest slope of a steep southwest-northeast ridge, locally known as the "Esker." The leaf litter was deep and friable, and was formed on a sandy substrate. The soil was young, with not much if any podzolization, and was composed of inwash from the eroded ridge. There were a few pebbles but no clay layer. The "F" horizon was 1 to 1.5 inches deep, the "H" horizon was 2 inches deep and had a pH of 4 to 4.5. Next there was a 6 to 12 inch brown layer with a pH of 4 to 4.5. The coloring resulted from a non-ferrous organic stain. Below this was a medium-coarse, yellow-brown sand on down for at least 30 inches. Later, as the soil matures, the brown organic stain will undoubtedly be leached out and a gray layer will be formed. The absence of clay was probably owing to the vagaries of glacial deposition, since the slope of the ridge had a variegated pattern of clay and sand "pockets." At the northeast corner of the plot there was such a pocket of silt and clay, to which my moisture records could not apply.

AREA NO. 2. DRY HARDWOODS, R–20.—This area was on a hilltop near area no. 1 and was part of the same open oak-hickory forest. The substrate was a sandy loam with considerable clay. There was an "F" horizon .5 inch deep, followed by 1 to 2 inches of a dry, gray leached layer with a pH of 5.5. Next came a dry, pale yellow clay at about 24 inches; this continued down for at least 36 inches. It was all underlain by a limey sand and gravel at 40 inches or more. Tree roots occurred on the surface, then came a gap, then a deep layer in the clay, and then very deep rootlets extended on down into the limey layer. According to Dr. J. S. Veatch (personal communication), there was originally a dense forest of white oak, occasional sugar maple, and possibly some beech, white ash, and hornbeam here. Because of the clay, Dr. Veatch has stated that this site is more moist than the usual ridge top on the Reserve and could not have been an "Oak Opening." The soil was a typical gray-brown podzol with the lime leached out to a deep layer and may be classified as Hillsdale fine sandy loam.

AREA NO. 3. SOUTHWEST WOODS, F–7, 8.—This area was in mature oak-hickory forest with a sassafras understory. The substrate may also be classified as Hillsdale sandy loam. The "F" layer was from 1 to 1.5 inches deep, followed by an "H" layer 1 to 2 inches deep, with pH 7, then less than 1 inch of gray layer, then a light yellowish sandy clay which met a stiff clay with a pH of 4 to 5 at 30 inches. There was no limey layer until about 48 inches below the surface. The clay layer held water and still had nutrients even though the pH was low. This was responsible for the more mesic conditions and the fine forest on this area. The yellow color indicates youth; when mature it would become red.

AREA NO. 4. DRY FIELD, M, L–9.—This area was in an upland old field with a sparse cover of composites and grasses and a ground cover of *Polytrichum* and *Tortula.* The substrate may be classified as Bellefontaine loamy sand, and was a medium to coarse sand with a suggestion of clay at 40 inches. At the northeast corner of the area there was a pocket of coarse sandy loam to a depth of about 30 inches, then a mixture of this loam with a reddish clay.

AREA NO. 5. WET FIELD, K–9.—This area encompassed a "swale" or depression in the same upland field as area no. 4. There was a dense cover of *Poa* and *Rubus,* with scattered *Aster* and other composites. The substrate was a loamy, fluffy sand with a buried silt loam at about 24 inches, extending down to about 40 inches, which was, in turn, deeply underlain by organic matter. The silt loam was at the surface and extended for a depth of 20 inches at the actual microclimate station, as well as at other parts of the plot where *Rubus* occurred. Undoubtedly this area at one time was a pothole and the silt was the old bottom, while the sand was the inwash from the surrounding upland. This was the reason for the variegated pattern of silt and sand.

AREA NO. 6. BARE AREA, G, F–20.—This is the same area that was designated by Cantrall (1942) as the "Blowout." White pines (*Pinus strobus*) had been planted here at the same time as those growing in S–24, in the fall of 1928. While the pines in S–24 are now 15 to 20 feet high, the pines on this area were stunted by deer browsing to a maximum height of one foot. There were scattered *Quercus velutina* and *Juniperus communis* in the east half of the plot, and over the whole area there was a sparse herbaceous cover of grasses and composites with a nearly complete cover of *Polytrichum piliferum, Tortula,* and other mosses. The substrate may be classified as Coloma sand, medium to coarse, predominantly quartz. Typically the top inch or so is inwash followed by 6 to 10 feet of yellow-brown sand. This area had been under cultivation at one time and, therefore, an artificial "H" horizon 4 to 5 inches deep had been formed. This was brown with a little humus and a pH of 4.5 to 5.5. Next was a layer of yellow sand with a pH of 4; at 40 inches, was yellow sand with a pH of 4.5. Still deeper the pH changed to 6, and at 4 feet to 5.5. A boring to 7 feet revealed all sand and still no clay. The pH of the sand immediately under the *Polytrichum* layer beneath an oak was 4. This area was not a "blowout" or an old lakeshore bar, but a deposit of the glacial drift.

AREA NO. 7. TAMARACK AREA, I–9.—This area was in a swamp that was covered by a thick growth of *Larix laricina, Acer rubrum, Rhus vernix, Ulmus americana,* and *Cornus racemosa,* with a dense ground cover of grasses, sedges, Christmas fern, *Sphagnum,* and other mosses. The substrate was Rifle peat, a black woody peat for a depth of 12 to 15 inches, then a brown fibrous peat (derived from the sedges and grasses which had preceded the forest) to an undertermined depth. This forest undoubtedly had been intact for a long time in order to deposit 12 to 15 inches of peat. Surface water had a pH of 8, surface peat a pH of 7, sphagnum under a "mound" a pH of 6.5, and water wrung from sphagnum a pH of 4.5 to 5.

METHODS

The methods of investigation used in this study were basically the same as those used previously (Pruitt, 1953). Certain differences in equipment and techniques should be noted. On each study area the following physical factors were recorded: maximum and minimum temperatures at 4 feet above the ground and at 3 and 9 inches below the soil surface. Instantaneous readings of soil temperatures by means of thermistors mounted as described by Pruitt (1952) were made at 1, 3, and 6 inches below the soil surface, and instantaneous readings of available moisture of the soil were made at the same depths. The sensitive elements for determining soil moisture were Bouyoucos plaster blocks. On the areas having extremes of soil moisture conditions (Tamarack, Bare, and Dry Field), Bouyoucos nylon soil moisture units were also installed at the same depths as the plaster blocks.

In the center of each area a post was set to support a small wooden box. This box contained the ends of the leads and the jacks of the wires that led from the soil thermistors and moisture units. On the north side of the box, under an overhanging wood roof, was a Six-type maximum-minimum thermometer. The soil thermistors and plaster blocks were buried 1 to 2 feet from the base of the post and were protected from disturbance by a wire fence strung on short wooden stakes. On the opposite side of the post was a soil well. This contained a 4-sided wooden box fitted with a removable wooden cover; the floor was earth. The maximum-minimum thermometers were attached to metal drawers which fitted into metal tubes projecting horizontally into the soil at 3 and 9 inches deep, respectively. The tubes were made of galvanized down-spouting, rectangular in cross-section, closed at the distal end with a tight-fitting wooden plug, and sealed with an asphalt compound. The proximal end of the drawer was also equipped with a tight-fitting wooden plug to minimize convection currents with the well proper. The sod or leafmold from the excavation was used to cover the overhanging lid. The thermistor and block resistances were measured with a Bouyoucos Wheatstone Bridge as well as with a Simpson Model 261 volt-ohm-milliammeter.

PROCEDURES

As in my previous study in northern Michigan, procedures during this study on the George Reserve were to measure the small mammal populations inhabiting each study area and to measure and analyze certain physical factors of their environment throughout an annual cycle of the seasons.

Areas were visited every other day from 18 September 1952 until 30 July 1953, with rare exceptions. Areas were visited in rotation in order to minimize any effect of time of day. First, air temperatures were read, recorded, and the thermometer reset, then the soil well temperatures were read, recorded, and the thermometers reset. Care was taken to read the soil thermometers quickly so that exposure to the air temperature in the soil well was kept to a minimum. Next, the thermistors and plaster blocks (and nylon units, if present) were read with the Wheatstone Bridge and recorded, then checked with the ohmmeter and these results recorded. The entire round of the seven study areas took 2 to 3 hours. Areas were visited in mid-morning when air temperatures were usually midway of their daily fluctuations.

On 30 July 1953 the blocks and nylon units were taken up and calibrated. Each was fixed in a small metal pan and surrounded with 100 to 300 grams of the soil which had surrounded it in the field. The soil was then soaked and allowed to air-dry once to assure a firm bond between it and the block. It was then resoaked and again air-dried. During this period

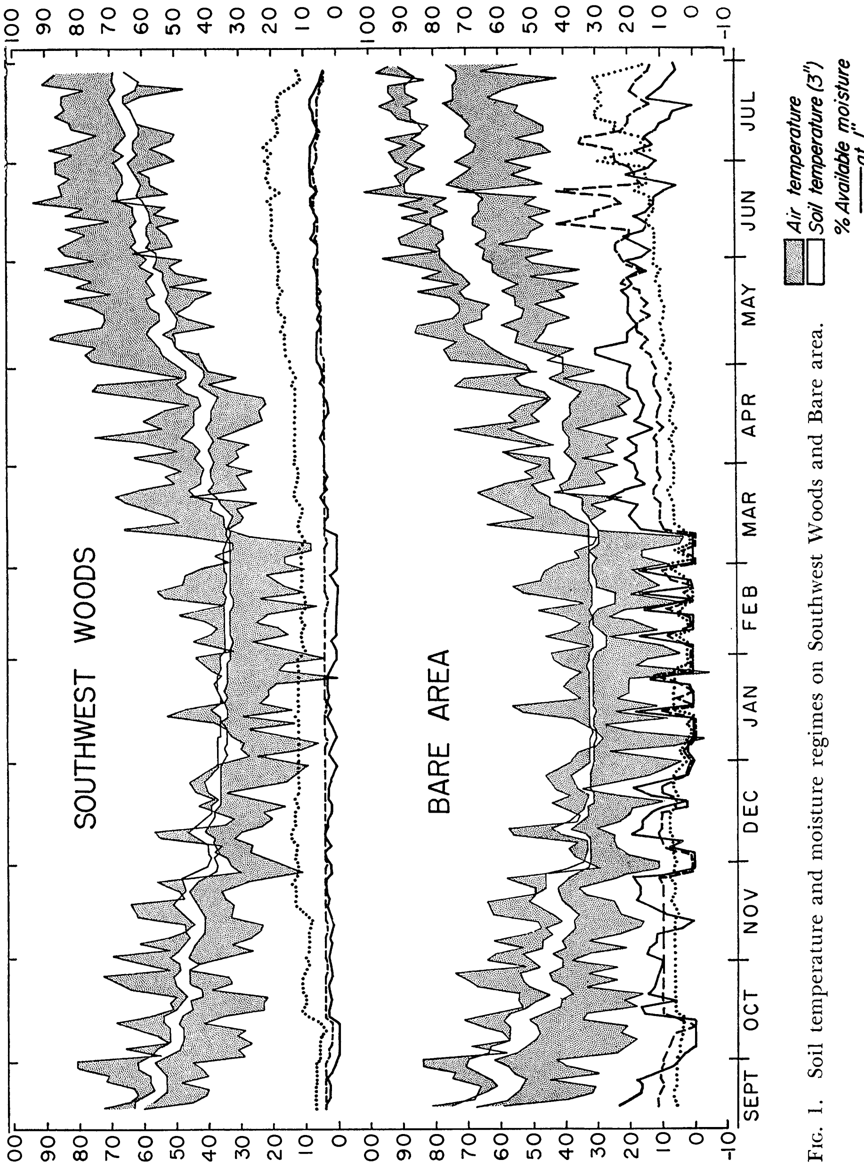

FIG. 1. Soil temperature and moisture regimes on Southwest Woods and Bare area.

of air-drying, weights of the soil and resistances of the blocks were recorded periodically. After the tare of the pan, block and wires was subtracted, the percentage of moisture was calculated. From these and the resistances a calibration curve was drawn for each depth on each area. These calibration curves were used to construct the graphs of soil moisture in Figure 1.

COMPARISON OF AREAS

Because of space limitations, the complete temperature and soil moisture records presented here are only for Southwest Woods and the Bare area; they represent the extremes of terrestrial environmental conditions on the Reserve. The complete records for the other areas are on file at the E. S. George Reserve.

Figure 1 shows for Southwest Woods and the Bare area the progression of maximum and minimum air and soil temperatures and soil moisture throughout the ten and one-half months of this study. Figure 2 shows the comparative spread of miximum and minimum soil temperatures at a depth of 3 inches for all areas.

BARE AREA.—Although concurrent data from a black-bulb thermometer were not available for this study, soil temperatures on the Bare area show a striking agreement in yearly progression with the "normal annual solar radiation" received at East Lansing, Michigan, 32 air miles to the northwest of the Reserve (Crabb, 1950: 35). The reader is referred to the agreement between temperature trends of exposed sandy soil and black-bulb readings in northern Michigan (Pruitt, 1953: 17, 21, 23). In the terminology of Geiger's (1930) succession of phytoclimates, the Bare area appeared to represent Stage I. No area sampled on the Reserve appeared to truly represent Geiger's Stage IV or the actual climax in phytoclimates.

The absolute minimum soil temperature at 3 inches below the surface was 21 degrees F., which occurred on 17 February 1953. The absolute maximum at this depth was 100 degrees F., which occurred on 21 and 30 June 1953. During the summer months, the soil at 3 inches, and for July, the soil at 9 inches also, exceeded the lethal limit for *Blarina* that was suggested by Pearson (1947).

As has been pointed out before (Pruitt, 1953), *Blarina* and other subterranean mammals without extensive fossorial morphological adaptations must have an environment with an unfrozen or easily penetrated matrix in order to utilize their home range successfully. The Bare area, as did the Burn in northern Michigan, showed soil freezing that was extensive both in depth and time. This is best shown by the graph of soil moisture (Fig. 1). When the Bouyoucos plaster block freezes, the resistance shows a marked increase (Rowland, Stolzy, and Crabb, 1955). As Bouyoucos and McCool

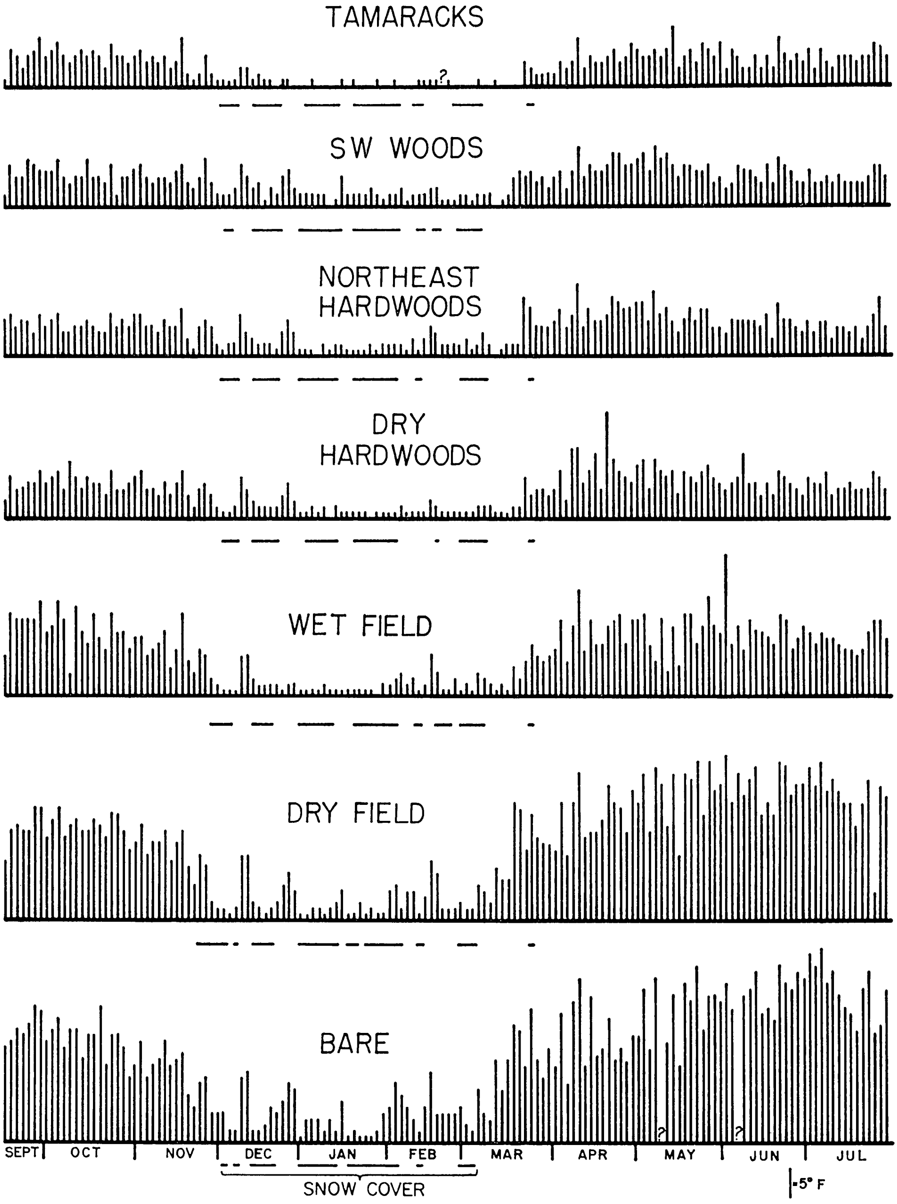

FIG. 2. Extremes of soil temperature, all plotted to the same base line; all areas.

(1916) have shown, the soil solute may not freeze at precisely 32 degrees F. Thus, the block resistances are better indicators of soil freezing than are temperatures alone. Using block resistances as an indicator, it will be seen that the soil on the Bare area underwent recurring periods of freezing and thawing as deep as 6 inches below the surface from late November to early March.

As has been suggested by Chew (1951), and as will be demonstrated later, *Blarina* apparently requires air with low evaporative power, probably saturated, to survive. Reference to Figure 1 shows that moisture in addition to being unavailable for a good portion of the winter months because of freezing, is also unavailable in at least the top inch of soil at several times during the warmer periods of the year.

Thus, on the Bare area, the only time during this study that some physical factor was not probably in excess of the lethal limit for *Blarina* was from mid-March to early May. According to Blair (1940) this is before the peak of breeding on the Reserve. At this time of the year, then, the population is near the low point in its annual oscillation. Minimal populations are not conducive to expansion into submarginal habitats.

DRY FIELD.—Soil temperature conditions on this area were generally similar to those found on the Bare area. The fluctuations were not quite so marked and the extremes not quite so harsh. The absolute minimum at 3 inches below the surface was 23 degrees F., which occurred on 18 February 1953. The absolute maximum at this same depth was 95 degrees F., which occurred on 21 June 1953. During January, February, and early March the soil froze and thawed repeatedly. During June and early July the soil temperature here, as on the Bare area, exceeded the probable lethal limit of *Blarina*. The only time that physical factors allowed *Blarina* to inhabit this area was from mid-March to the latter part of May, again during the annual minimum of population size.

WET FIELD.—This area lay in a well-marked "cold pocket." The topography caused cold air drainage into it from the north and northwest while woods on the south hindered the flow of cold air on down the slope. The lowest air temperature during my stay on the Reserve was recorded here, a −12 degrees F. during the period 25–27 January 1953. The minima for the other areas at this time were: Bare, −5; Dry Field, −5; Tamaracks, −5; Dry Hardwoods, −3; Northeast Hardwoods, −1; Southwest Woods, 0. The minimum at the North Gate Station, taken under standard Weather Bureau conditions, at this time was −1.5 degrees F. The effect of the cold air drainage is more striking when it is remembered that the Dry Field station was about 450 feet north and the Tamarack station was about 600 feet southwest of the Wet Field station. The absolute maximum air temperature on this area was 104 degrees F., which occurred on 21 June 1953. In spite of such extremes of air temperature the soil temperatures were remarkably stable; the absolute minimum at 3 inches was 25 degrees F., on 18 February 1953, and the absolute maximum at the same depth was 79 degrees F. on 30 July 1953. The soil temperature approached the lethal limit for *Blarina,* but did not remain there for long periods as it did on the two previous areas. Likewise, the winter soil freezing was shallow and not of long duration. Undoubtedly there were patches of unfrozen soil all winter. Of the three non-forested areas this one gave the best indication of allowing *Blarina* to inhabit it during years with more rainfall, snow, and a higher *Blarina* population. That this is true is indicated by the fact that Blair (1940, 1948) took *Blarina* on his "blue-grass meadow" on the Reserve only in summer and fall, not in the spring when populations were at a low level.

DRY HARDWOODS.— Although this was the most variable of the forested areas, the soil temperature and moisture regimes were nevertheless quite different from those of the open areas. The absolute maximum at 3 inches below the surface was 71 degrees F. on 21–23 July 1953, and the absolute minimum at the same depth was 29 degrees F. on 18 February. The soil moisture was more stable than in the open areas, although the extremely dry year of 1952 was evident in the total absence of available moisture in mid-October of that year. The surface one-inch froze intermittently during February 1953, but only on 18 February, at the time of absolute minimum air temperature, did the soil freeze at 3 inches. The effect of the forest canopy on moderating the air temperature is shown by the fact that these extremes ranged only from –3 (27 January 1953) to +97 degrees (21 June 1953).

NORTHEAST HARDWOODS.—This area showed a moisture and temperature regime quite similar to the preceding area. The temperature at 3 inches below the surface was slightly more stable during the warmer periods of the year when the forest canopy was complete, but slightly less stable during the winter, probably because the greater moisture content of the soil sometimes facilitated evaporative cooling. Because of the mosaic of clay and sand existing on this area, the moisture levels and soil temperatures recorded during this study are valid only for the floor of the cove in the immediate vicinity of the station.

SOUTHWEST WOODS.—Since this area was the closest approach to the climax of any on the Reserve, as far as vegetation was concerned, one would predict that the soil conditions here would be the most stable of any. In some respects this was true, but by and large this area showed more fluctuations in soil moisture and temperature than would be expected in this soil type and under trees of this size. The absolute minimum air temperature was 0 degrees on 27 January 1953, while the absolute maximum was 93 degrees on 21 June 1953. The absolute minimum soil temperature at 3 inches below the surface was 30 degrees on 7 January and 20 February, while the absolute maximum at the same depth was 70 degrees on 21 June, 21–23 July, and 30 July. The surface one-inch froze several times in early January and remained frozen during most of February and early March. The soil moisture at one inch reached zero during early October 1952. The soil temperatures for this area may have been influenced after 9 May by a break in the forest canopy that occurred when, between 7 and 9 May, a large oak that stood 15 feet northeast of the station fell in a northwesterly direction, leaving a large hole in the forest canopy above and to the north of the station. The break was so situated that it did not allow direct solar radiation onto the station, but the air currents in the trunk-space area were undoubtedly affected.

TAMARACK AREA.—Although this area was lower down the same slope from where the Wet Field was situated, it did not exhibit any signs of being a "cold pocket." As is common in most swamps and bogs, the soil temperatures showed the presence of a large amount of water by having their fluctuations fewer and of smaller magnitude than those on the more mesic and xeric areas. While the air temperatures ranged from –5 degrees on 27 January 1953 to +96 degrees on 21 June, the soil temperature at 3 inches below the surface ranged only from 31 degrees on 4 March to 70 degrees on 21–23 and 30 July. Examination of the records showed that the periodic fluctuation of soil temperature was quite small. Before the end of the study all the plaster units had dissolved, that at one inch on 8 April, the one at 3 inches on 13 July, and the one at 6 inches on 27 July. The surface one-inch of soil froze intermittently during early January, most of February, and early March. Except for the very dry fall of 1952, the moisture regime on this area was one of either nonavailability or excess, either physiologically nonavailable by freezing or saturated to above the field capacity.

DESCRIPTION OF TRAPPING

It is fairly well agreed among mammalogists that the quadrat method of sampling small mammal populations is the most accurate (Bole, 1939), and that, as far as indicating size of populations, live-traps furnish data as reliable as those given by snap-traps (Goodnight and Koestner, 1942). As noted later, this latter premise is not always true. Hayne (1949) concluded that, for more accurate population estimates, the probability of capture must be high. His data also confirm the belief that, barring unusual incidents, a trapping period of three nights is sufficient to catch essentially all the small mammals on a given area, provided that the area contains enough traps to cause a high probability of contact.

Investigators working with vertebrates on the George Reserve are restricted from utilizing the valuable technique of removal trapping. Thus, my data on the George Reserve populations, sampled by live-trapping, are not strictly comparable with the results of my northern Michigan study which utilized removal-trapping. They may be used comparatively between the different areas on the Reserve, however.

Each area was gridded for the placement of 100 traps. This "saturation trapping" insures a high probability of capture. Traps used were a mixture of Sherman, Blair, and Burt models. A great aid to night trapping was one-inch squares of red and yellow Scotch-lite stapled to the tops of the markers.

Some workers (Blair, 1941) have recommended the use of rubber-tipped forceps to remove mice from live traps. I found that it was far easier to slip a small soft cloth sugar sack over the end of the trap, open the end into the sack, and then blow into the front of the trap. The animals invariably jumped into the sack from which they could easily be removed by grasping the scruff of the neck with the fingers. There was also less chance of injuring the animal with this method. Animals were marked by toe-clipping, using the numbering system used by Evans (1951).

Traps were usually set in the afternoon. To get information on periods of activity, at first they were checked at two-hour intervals for 24 hours, but later they were checked at three-hour intervals for usually two or three complete nights. They were also checked at comparable intervals during the intervening days.

The trapping periods were as follows: *Dry Field:* 11 November 1952, 7–8–9 February 1953, 30–31 March, 1–2 April 1953, 6–7–8–9 June 1953, 6–7–8–9 July 1953. *Wet Field:* 13 November 1952, 9–10–11 February 1953, 2–3–4–5 April 1953, 10–11–12–13 June 1953, 9–10–11–12 July 1953. *Bare Area:* 15 November 1952, 10–11–12 March 1953, 28–29–30 April, 1 May 1953, 27–28–29–30 June 1953, 22–23–24–25 July 1953. *Southwest Woods:* 19 November 1952, 6–7–8 March 1953, 19–20–21–22 April 1953, 23–24–25–26 June 1953, 19–20–21–22 July 1953. *Tamarack Area*: 21 November 1952, 24–25–26 February 1953, 25–26–27–28 April 1953, 30 June, 1–2–3 July 1953, 27–28–29–30 July 1953. *Dry Hardwoods:* 23 November 1952, 13–14–15 February 1953, 6–7–8–9 April 1953, 16–17–18–19 June 1953, 12–13–14–15 July 1953. *Northeast Hardwoods:* 27 November 1952, 22–23–24 February 1953, 11–12–13–14 April 1953, 19–20–21–22 June 1953, 15–16–17–18 July 1953.

RESULTS OF TRAPPING

There was marked ecological segregation among the small mammals on the Reserve. Those kinds on which I have distributional data fall into three classes: (1) species with wide ecological distribution, as *Peromyscus leucopus,* (2) those restricted to stable, mesic environments, as *Blarina, Sorex,* and *Synaptomys,* and (3) those restricted to xeric, unstable environments, as *Peromyscus maniculatus.* The total number of individuals live-trapped on the seven study plots in all of the trapping periods is shown in Figure 3. The breakdown by species and trapping periods is shown in Figures 4 and 5. Several salient points are evident from these figures. These are: the overwhelming abundance of *Peromyscus leucopus* on all areas, especially the forested ones; the marked reduction in numbers of *P. leuco-*

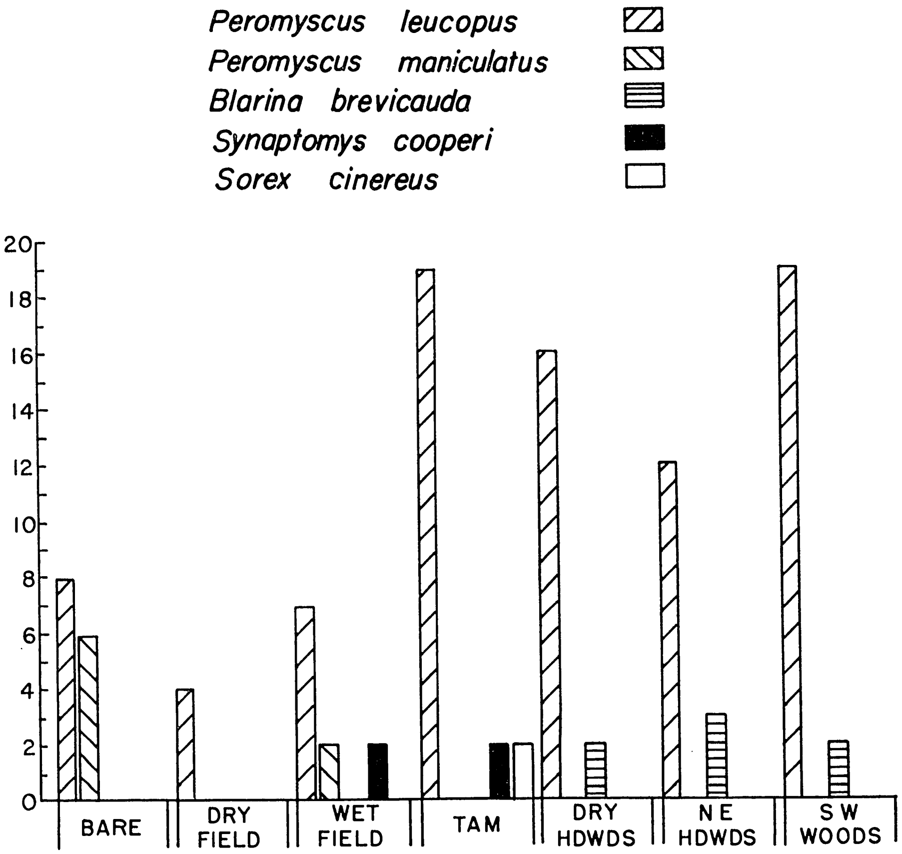

FIG. 3. Total number of small mammals trapped

pus on the open areas as compared with the forested ones; the expected exclusion of *Peromyscus maniculatus* from the forested areas; the unexpected number of *P. maniculatus* found on the Bare area and their apparent seasonal replacement of *P. leucopus* there; the restriction of *Blarina* to the mesic forested areas and its generally low population density; and the appearance of *Synaptomys cooperi* on the Wet Field and Tamarack area.

Peromyscus leucopus was truly ubiquitous on the Reserve at the time of this study. Even in late winter, when all the small mammal populations had shrunk in numbers and area inhabited, this mammal was still occasionally found on the areas with the most severe microclimates. Figure 4 shows the inverse relationship existing between the numbers of *P. leucopus* resident on the open areas and those found on the forested areas. Figure 4 also shows the seasonal abundance and distribution of *P. leucopus*. It will be seen that, with the exception of the Northeast Hardwoods, the more mesic forested areas had a continuous population. The irregularity in the Northeast Hardwoods was undoubtedly caused by outside influences. Raccoons were particularly troublesome on this area; many traps were sprung or torn open either before the mice entered or after they were trapped. The high percentage of "wanderers" (those animals trapped only once) on the Northeast Hardwoods, Tamarack, and field areas is inter-

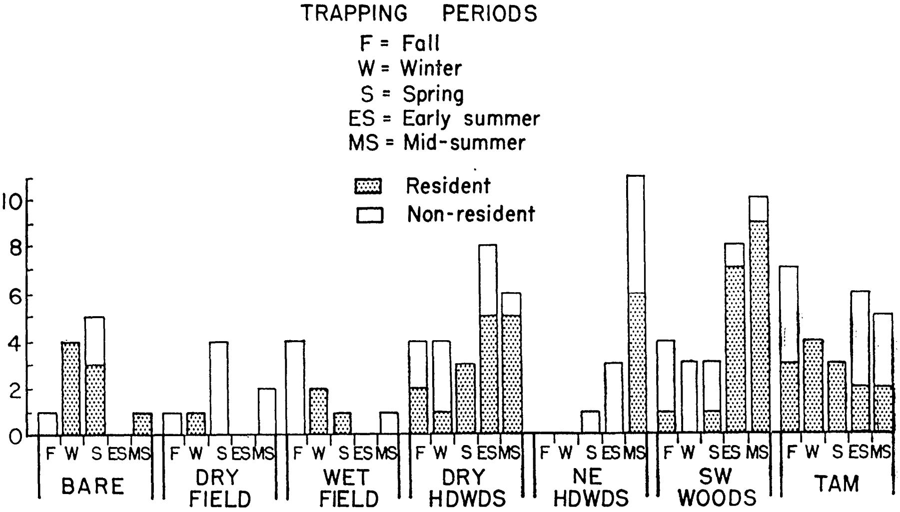

Fig. 4. Seasonal distribution and abundance of *Peromyscus leucopus*. Shaded bars indicate resident animals, unshaded bars indicate non-resident animals.

esting. Two explanations for this come to mind. Either the individual mice have larger home ranges in the fields than in the woods or the young, unsettled individuals gravitate here or are forced by territorial activities of resident animals to move into or through these submarginal habitats. The Southwest Woods animals showed the closest approach to the classical curve of annual fluctuation.

Of interest was the apparent replacement of *P. leucopus* by *P. maniculatus* on the Bare area during the summer. During the fall, winter, and spring trapping periods, only *P. leucopus* had been taken on this area. Then, in the summer trapping periods, only *P. maniculatus* was taken. In this respect it should be noted that the *P. leucopus* population of the Dry Field took a tremendous drop in early summer. Since the conditions on the Dry Field most resembled the Bare area, it is possible that there was an emigration of *P. leucopus* away from the hot, dry areas. This emigration allowed *P. maniculatus,* which apparently can withstand higher temperatures and lower moisture levels than can *P. leucopus,* opportunity to invade the vacated areas. Although this explanation appears to fit the facts, further investigations should be made along these lines. In connection with this subject, it may be noted that there was a shift of individual *P. leucopus* activity from the Dry Field in the fall to the Wet Field in the winter and back again in the spring.

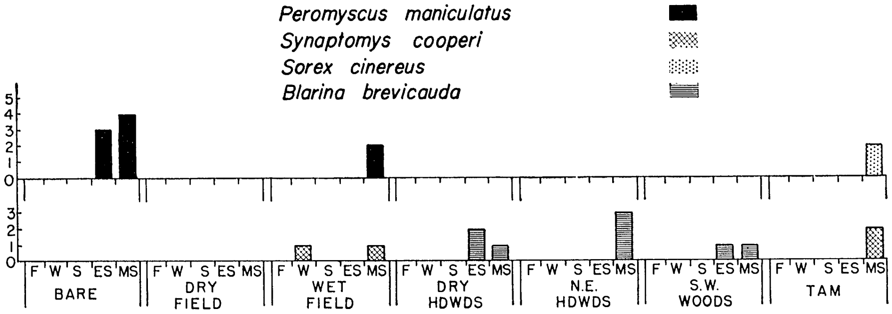

FIG. 5. Seasonal distribution and abundance of small mammals other than *Peromyscus leucopus.*

Undoubtedly, because of the extended drought during 1952, the population of *Blarina,* as well as other small mammals on the Reserve, was very low. While this was unfortunate in some respects, because *Blarina* was restricted to optimum habitats at the time of the study, certain aspects of the problem were thus thrown into sharp focus. One fact that is often overlooked in mammalian ecology is that knowledge of where an animal is *not* present is frequently of equal importance with knowledge of where an animal *is* present. It is significant that when *Blarina* did appear in the live-traps, they showed up on the more mesic, stable areas. Moreover, the only places *Blarina* were taken on the Dry Hardwoods area were in low spots around the edge of the plot, places that were damper than the ridge top where the microclimate station was situated. An important question is, where did *Blarina* find a refuge to survive the double environmental blasts of drought and a nearly snowless winter? Unfortunately the data do not permit this question to be answered completely. I believe that their refugia were in the swamps and bogs, but that the Tamarack area did not satisfy their requirements. Some of the ways in which it may have exceeded the ecological tolerance of *Blarina* were excessive dryness in the fall of 1952, surface soil freezing during the winter, and excess water in the spring and early summer of 1953.

Synaptomys cooperi was taken only on the Wet Field and Tamarack area. This is consistent with what other workers have noted as its habitat. Unidentified microtines were observed to be active on both the Wet Field and Tamarack area long before their presence was indicated by the live-traps. The *Synaptomys* on the Tamarack area were taken only after about 1200 trap-nights extending over a period of some seven months on the area. It is apparent that the use of live-traps alone as a method of sampling is conducive to the collection of inaccurate data.

DISCUSSION

ARTIFICIAL BURROW.—I have long felt that one of the keys to understanding shrew distribution lies in a knowledge of the moisture content of the air in their burrows. Unfortunately, I know of no field instrument that will make continuous recordings of the humidity of the air in a space as small as a shrew burrow. Since it is possible to measure the moisture content of a soil, the following experiment was devised to permit translation of some soil moisture data into terms of humidity of the air in a burrow through this soil.

Since a Serdex Model 201 hygrometer was available, I made a rectangular tube of two layers of screen wire to fit around the instrument. This tube was placed inside a large wooden box (Fig. 6). The space around the screen tube was filled with Hillsdale sandy loam. In the soil around the tube and about 2 inches from it were installed four plaster and four nylon units, plus three thermistors. A hole was cut in one side of the box so that the dial of the hygrometer might be seen. This hole was covered with a piece of glass. The soil was saturated, dried, then wet down again. During this next drying cycle periodic readings of the soil moisture units and of the hygrometer were made. This drying cycle lasted from 25 January through 5 August 1953. At the termination of the drying cycle the moisture units were removed and calibrated at the same time as the units from the field study.

Several facts became evident when these moisture records were plotted. The most important was that the air enclosed in the artificial burrow remained saturated until after the soil moisture units recorded a complete lack of available moisture in the soil. In other words, the enclosed air remained saturated throughout the complete range of soil moisture from 40 per cent through zero. The significance of this fact becomes apparent when one realizes that no study area on the Reserve, at the season when *Blarina* was taken on it, had a moisture level low enough for the enclosed air in a burrow to be anything but saturated. The areas that did not produce any *Blarina* in the fall trapping period, but where the animals appeared later, had moisture levels low enough in the fall for burrow air to be below saturation. The areas that never produced any *Blarina* had, with one exception, these low moisture levels at several periods during the year. Thus, one can state with reasonable surety that *Blarina* was found on the Reserve in only those habitats that allowed the air in its burrows to remain saturated with moisture vapor. The one exception to this general rule was the Wet Field, and we have seen how the temperature regime was more moderate there and how sufficient snow cover would probably prevent extensive soil freezing, thus allowing *Blarina* to inhabit this area, at least at certain periods of the year. This hypothesis agrees with the field evidence gathered by Blair (1940, 1948).

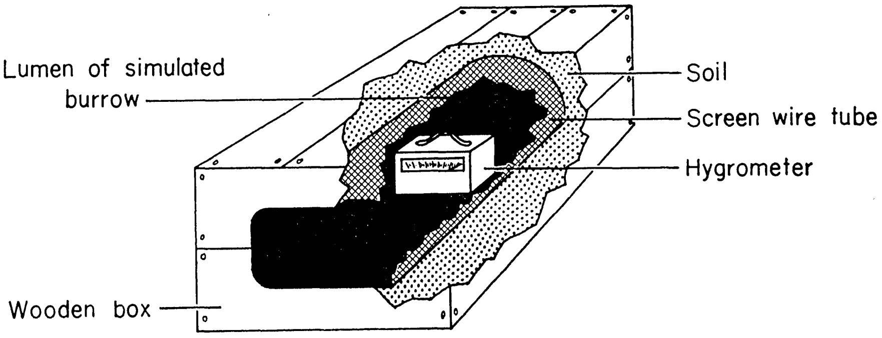

FIG. 6. Details of artificial burrow

I conceive the following picture of the *Blarina* population on the Reserve. The animals are limited in their local distribution to areas having stable soil temperature, enough moisture in the soil to assure that the enclosed air in their burrows remains at or near saturation, and a soil matrix that contains enough leaf litter, leafmold, or grass stems and rootlets to allow tunnels through it to remain intact. If the areas having these requirements do not exceed the upper limits of tolerance for heat in the summer, and if the extent of winter soil freezing does not exclude the animals from enough of their home ranges to prevent foraging for sufficient food, then these areas will be populated by *Blarina* in all seasons of the year. During times of extreme soil heat or extensive soil freezing they will be unable to inhabit the areas so affected. This pattern of distribution is intimately related to the annual and periodic fluctuations in numbers. In the annual oscillation, when the population is reduced by the actions of several agencies, the remnant survives in the most favorable habitat. When the population is increased by the annual increments of new litters, it expands first into those areas which most nearly satisfy the optimum conditions. If, as Formosov (1946) has postulated for several species of Eurasian shrews, snow conditions allow more animals to survive the winter for breeding the next spring, then the resultant increased population expands into areas which, although marginal or submarginal in year-round environmental conditions, are within the animals' limits of tolerance at that particular season. When the seasons progress and tolerance limits are exceeded, these marginal areas become unavailable for occupancy. If snow conditions are particularly favorable, and if the following seasons are also favorable for litter survival, then more individuals are allowed to survive to breed. Thus, the entire population may increase in numbers and in area inhabited. If the expanded population is reduced in size by some factor or factors other than the elemental physical ones (by factors which are differential in their effects on the individual members of the population), then there is nothing to prevent scattered individuals from remaining in the once-marginal areas, but if the population is reduced by the primary or secondary effects of the physical environment, that is if its limits of tolerance are exceeded in any marginal area, then the individuals are excluded from that area and the total population undergoes the process of being restricted to refugia. My experience with *Blarina* indicates that reduction in total size of the population is accompanied almost invariably by restriction in local distribution. This is in agreement with the views expressed by Cantrall (1942), Tinkham (1948), and Andrewartha and Birch (1954).

My data also show the striking seasonal fluctuations that small mammal populations undergo. This concept is logically quite obvious, but it is surprising how many reports there are in the literature that flatly state that the small mammals of a certain region are "down," when actually they were sampled at the yearly ebb. Hamilton (1942) neatly illustrated these fluctuations. For every pair of mammals that survives the unfavorable part of the year, all their offspring (or their equivalent) of the following breeding season *must* be eliminated before the next breeding season if the population is not to undergo marked increase. If two pairs survive this winter where one pair normally survives, then the resulting population next summer will be twice as large as last summer, if other factors such as litter size and survival of young remain equal.

A corollary of this concept is that no animal really inhabits a given environment unless it survives the unfavorable part of the year there. During the favorable part of the year individuals can spread out and invade many environments, but their ability to survive the next unfavorable season is the critical thing. Those that do survive the unfavorable season and breed the next breeding season truly ecize the environment. For much of North America, winter is possibly the unfavorable period, but this period may take the form of an annual dry season, wet season, or season of extreme heat depending upon geography and the particular animal concerned. Those animals that survive this unfavorable period are the ecologically important animals, for they are the progenitors of the ensuing population. The ones that do not survive are also ecologically important, but in another way; they are the building blocks of the food pyramid. Since *Peromyscus leucopus* was the most common animal taken during this study, it may be used to illustrate this principle. Figure 4 shows the seasonal distribution of the resident *P. leucopus* on the different areas. Resident animals were defined as those which had been taken two or more times on an area. Figure 4 also illustrates the shift of activity from one area to another according to season, which sometimes occurred.

DIURNAL PERIODICITY.—Small mammals usually show a nightly cycle of activity (Johnson, 1926), sometimes with two peak periods—one near sunset and one near sunrise (Hamilton, 1939). During the course of the study it became apparent that this bimodal activity cycle did not occur every night. Sometimes one peak or the other or both would be missing. After the field phase was completed and the trapping results were charted, the conditions at the actual time of activity were summarized and added to the charts. Air and soil temperatures, wind, precipitation, type of clouds present, and an estimate of the amount of sky covered (in tenths) had been recorded in the field. Times of moonrise, moonset, and phase were calculated from "The American Ephemeris and Nautical Almanac" for the years 1952 and 1953.

Since the traps had been checked every two or three hours during the nights they were set, it was possible to reconstruct fairly accurately the conditions at the times the animals were active. Each time that an animal was found in a trap was counted as an activity period, and the physical conditions obtaining at each of these periods were analyzed. Some arbitrary decisions regarding cloud cover and moon phase were necessary in order to simplify the records. For example: a .7 cirrus cover with a first quarter moon high in the sky was counted as "moonlight," while the same cloud cover with a first quarter moon near the horizon was counted as "dark." The numbers of activity periods were as follows: dark at time of activity, in forest, 154, in nonforest, 39; moonlight at time of activity, in forest, 27, in nonforest, 10. These results are very crude and much more detailed work of this sort should be done. From these data, however, it appears that of the factors measured, moonlight was the most important in governing activity of the small mammals on the Reserve. The effect of moonlight on the activity of desert mammals is well known (Tappe, 1941). Tappe noted, in the case of *Dipodomys heermanni tularensis* in California that "On nights when the moon is considerably less than full, or when it is partly obscured by clouds, activity usually goes on as it does on nights when the moon is not visible. Evidently light intensity on a clear, full moonlight night is above the maximum tolerated by this mammal for normal emergence from its burrow." He later noted "On nights when a bright moon is absent for only a short time in the early morning hours, activity is concentrated in the period of greatest darkness. If the moon rises late, causing the period of greatest darkness to come in the early part of the night, activity is apparently no more concentrated then than it is in the early parts of nights that are without moonlight at any time." He also noted the effect of rain in restricting surface activity of this mammal. Buss and Harbert (1950) noted that moonlight had the opposite effect on mule deer activity, the occurrence of deer at a salt lick varying from 7 during the dark of the moon to 29 when the moon was full.

SUMMARY AND CONCLUSIONS

1. On a series of seven study areas on the Edwin S. George Reserve in southeastern Michigan, the physical conditions (soil moisture, temperature, freezing, and penetrability) of the environment of *Blarina brevicauda* were recorded and analyzed for a period of 11 consecutive months.

2. This analysis showed that the areas called Bare, Dry Field, Wet Field, Dry Hardwoods, Northeast Hardwoods, Tamaracks, and Southwest Woods stood in that relation to one another in a series with increasing stability of soil temperature. In regard to depth and amount of winter freezing, the relation was Bare, Dry Field, Wet Field, Dry Hardwoods, Northeast Hardwoods, Southwest Woods, and Tamaracks, in decreasing amounts. The latter relationship held true for year-round presence of available soil moisture.

3. Comparison revealed that the microenvironments of small mammals on the E. S. George Reserve had wider extremes of temperature and more fluctuation than did those in northern Michigan which were sampled in a previous study. This difference, I believe, results from permanent winter snow cover on the northern Michigan study plots and intermittent cover, winter rains, and a greater amount of summer insolation on the George Reserve plots. Snow cover, therefore, is probably a factor of major importance in the distribution of some small mammals.

4. Periodic live-trapping of the study areas revealed the following major points of interest. *Peromyscus leucopus* was by far the most common mammal, but with a marked difference in numbers inhabiting the forested and open areas. There was apparently a seasonal replacement of *P. leucopus* by *P. maniculatus* on the area with the most severe microenvironment. *Blarina brevicauda* was taken only on those areas where the soil moisture level at the time of trapping allowed the air in burrows to be saturated. The areas that did not produce any *Blarina* during a particular trapping period, but where the animals appeared later, had moisture levels low enough at the time of trapping for burrow air to be below saturation. With one exception, the areas that never produced any *Blarina* had these low moisture levels at several periods during the year.

5. The daily periodicity of the animals trapped was analyzed and, of the factors measured, moonlight was found to be the most important in regulating the extent of nocturnal activity.

LITERATURE CITED

ANDREWARTHA, H. G., and L. C. BIRCH
1954 The distribution and abundance of animals. Chicago. Univ. Chicago Press: 782 pp.

BLAIR, W. F.
1940 Notes on home ranges and populations of the short-tailed shrew. Ecology, 21: 284–88.
1941 Techniques for the study of mammal populations. Jour. Mamm., 22: 148–57.
1948 Population density, life span, and mortality rates of small mammals in the blue-grass meadow and blue-grass field associations of southern Michigan. Amer. Midl. Nat., 40: 395–419.

BOLE, B. P., JR.
1939 The quadrat method of studying small mammal populations. Sci. Publ. Cleveland Mus. Nat. Hist., 5: 15–77.

BOUYOUCOS, G. J., and M. M. MCCOOL
1916 Further studies on the freezing point lowering of soils. Mich. Agr. Exp. Sta. Tech. Bull., 31: 51 pp.

BURT, W. H.
1940 Territorial behavior and populations of some small mammals in southern Michigan. Misc. Publ. Mus. Zool. Univ. Mich., 45: 58 pp.

Buss, I. O., and F. H. Harbert

1950 Relation of moon phases to the occurrence of mule deer at a Washington salt lick. Jour. Mamm., 31: 426–29.

Cantrall, I. J.

1942 The ecology of the Orthoptera and Dermaptera of the George Reserve, Michigan. Misc. Publ. Mus. Zool. Univ. Mich., 54: 82 pp.

Chew, R. M.

1951 The water exchanges of some small animals. Ecol. Monogr., 21: 215–25.

Crabb, G. A., Jr.

1950 Solar radiation investigations in Michigan. Mich. State College Agr. Exp. Sta. Tech. Bull., 222: 153 pp.

Evans, F. C.

1951 Notes on a population of the striped ground squirrel (*Citellus tridecemlineatus*) in an abandoned field in southern Michigan. Jour. Mamm., 32: 437–49.

Formosov, A. N.

1946 The covering of snow as an integral factor of the environment and its importance in the ecology of mammals and birds. Materials for Fauna and Flora, USSR, Moscow, New Series, Zoology, 5: 152 pp.

Geiger, Rudolph

1930 Mikroklima and Pflanzenklima. Handb. d. Klimat., Berlin: Verlag Gebruder Borntrager. Trans. by U.S. Forest Service, no. 221.

Goodnight, C. J., and E. J. Koestner

1942 Comparison of trapping methods in an Illinois prairie. Jour. Mamm., 23: 435–38.

Hamilton, W. J., Jr.

1939 American mammals. New York, McGraw-Hill Co.: 434 pp.

1942 Winter reduction of small mammal populations and its probable significance. Amer. Nat., 76: 216–18.

Hayne, D. M.

1949 Two methods of estimating populations from trapping records. Jour. Mamm., 30: 399–411.

Johnson, M. S.

1926 Activity and distribution of certain wild mice in relation to biotic communities. *Ibid.*, 7: 245–77.

Murie, Adolph

1936 Following fox trails. Misc. Publ. Mus. Zool. Univ. Mich., 32: 45 pp.

Pearson, O. P.

1947 The rate of metabolism of some small mammals. Ecology, 28: 127–45.

Pruitt, W. O., Jr.

1952 A method of mounting thermistors for field use. Ecology, 33: 550.

1953 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. Misc. Publ. Mus. Zool. Univ. Mich., 79: 39 pp.

Rogers, J. S.

1942 The crane flies (Tipulidae) of the George Reserve, Michigan. Misc. Publ. Mus. Zool. Univ. Mich., 53: 128 pp.

ROWLAND, E. F., L. H. STOLZY, and G. A. CRABB
1955 Frost determination by electrical resistance. Highway Research Board, Bull., 100: 17–21.

SUTTON, G. M.
1949 Studies of the nesting birds of the Edwin S. George Reserve. Part 1. The vireos. Misc. Publ. Mus. Zool. Univ. Mich., 74: 37 pp.

TAPPE, D. T.
1941 A natural history of the Tulare kangaroo rat. Jour. Mamm., 22: 117–48.

TINKHAM, E. R.
1948 Faunistic and ecological studies on the Orthoptera of the Big Bend Region of Trans-Pecos, Texas, with especial reference to the orthopteran zones and faunae of midwestern North America. Amer. Midl. Nat., 40: 521–663, 37 figs.

U. S. DEPARTMENT OF AGRICULTURE
1941 Climate and man. Yearbook of Agriculture. Washington, D. C., 1248 pp.

Submitted 30 January 1956; accepted for publication 6 August 1958

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. (1953) 39 pp., 9 figs.	$0.75
No. 80.	A comparative study of the osteology and myology of the cranial and cervical regions of the shrew, *Blarina brevicauda,* and the mole, *Scalopus aquaticus.* By George R. L. Gaughran. (1954) 82 pp., 67 figs.	$1.00
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