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Animal Activity in Uncontrolled Terrestrial Communities as Determined by a Sand  
Transect Technique

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# ANIMAL ACTIVITY IN UNCONTROLLED TERRESTRIAL COMMUNITIES AS DETERMINED BY A SAND TRANSECT TECHNIQUE<sup>1</sup>

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## INTRODUCTION

Tracking animals by following footprints in dust, mud, sand or snow is probably the oldest known method of identifying animals present in an area, and tracing their movements. Man's early evolution and success depended largely upon an understanding of activity patterns and movements of animals within his immediate environment. Hunting success, which must have influenced the eventual rise of man, de-

pended on being able to assume that an undisturbed animal in his uncontrolled environment follows a known activity and movement pattern.

This paper is a synthesis of temporal and spatial parameters of activity found during the course of comparative community studies using a sand transect technique.

Even very small animals leave trails on the ground. Macro-organisms, including most arthropods, annelids and mollusks, plus all vertebrates, leave locomotory impressions on fine sand. The technique used to determine activity is to note the location and direction of

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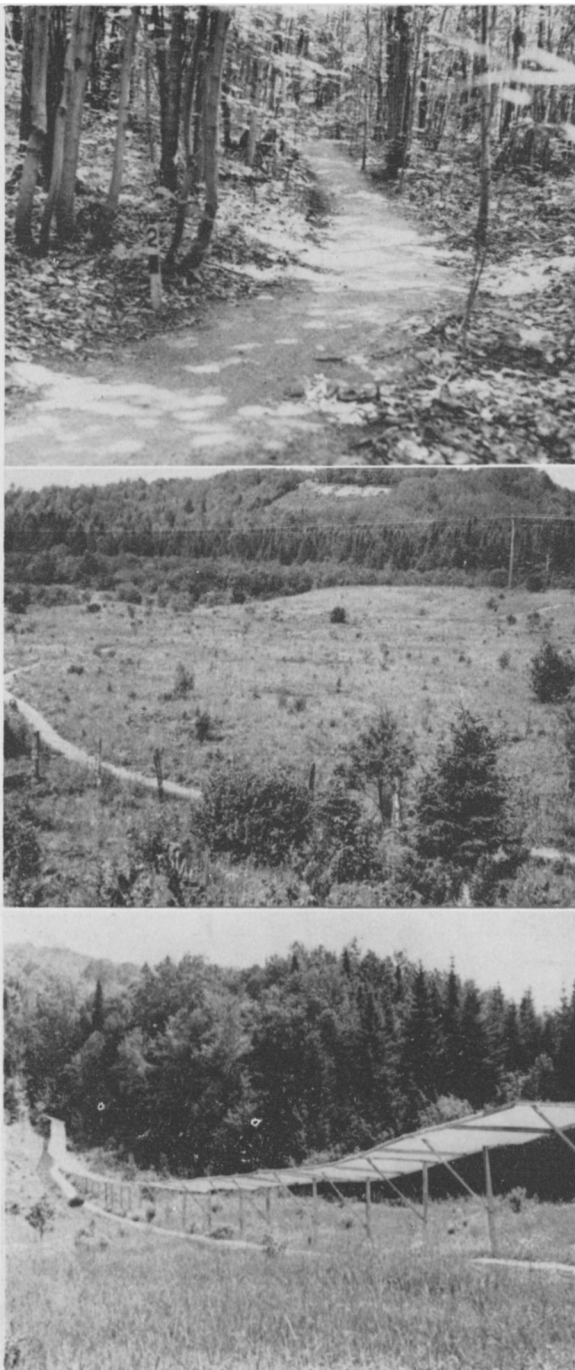


FIG. 1. A portion of each of the 3 transect sites in 1964. Top, woods transect. Center, south half of the circular field transect. Bottom, first 450 ft of the ecotone transect. It extends another 300 ft into the forest.

crossings of individual species across a fine sand transect at regular intervals of time. The location of the transect delimits the scope of the problem.

Three transects were established (Fig. 1); the first, made in 1962, begins in a field and ends inside a forest (ecotone transect). In 1963 a second transect was made in a field (field transect), and a third in

the forest (woods transect). The data presented was gathered over a period of 3 years from 1962 through 1964.

To date several hundred thousand transect crossings, plus meteorological data, have been recorded. From this wealth of data only facets that will assist in dealing with activity data at the species level are presented. Changes in spatial utilization patterns in time will be associated with the general biotic and physical factors which affect activity. Most communities have species from diverse evolutionary groups, so gradients in activity are also viewed from an evolutionary standpoint.

Both the technique and the type of data presented are new. A synthesis of community activity is the objective of this study. This paper opens a new aspect of community ecology and a review of literature at the species level will not be attempted.

#### RELATION OF THIS STUDY TO PREVIOUS STUDIES

When comparing studies, 2 essential premises must be used: 1) the aims of the studies must be the same, at least in part, and 2) the units of measurement must be comparable or have a known relationship. If these requirements are satisfied, the relation of this study to previous studies can be meaningfully assessed by reviewing the types of data produced by other methods.

The most complete descriptive comparison of terrestrial communities was done by Fautin (1946). Although he used the best numerical census methods available at that time, he had to change methods for different species, or groups of species. Possibly because of the work involved, this kind of study has never been repeated. The present study is similar to Fautin's in that it is directed in part toward an elucidation of the structure of terrestrial communities. The system presented here is simpler, less strenuous, and uses a single technique that samples all macro-organisms that move along the ground. It describes possible co-actions in time without having to estimate the number of animals in each population. Obviously a biomass pyramid cannot be drawn from my data, but they show what changes in energy flow might occur through the community in time. For example, it will be shown that red squirrels *Tamiasciurus hudsonicus* suddenly change from a random feeding pattern of maple seeds to restricted straight line movements when they begin to feed on conifer seeds. This demonstrates not only a change in spatial utilization of a habitat, but also a change from one energy source to another. This then is quite a different approach from Fautin's which gave periodic estimates of species abundance. The results of the 2 studies cannot be directly compared because numbers of animals do not equate with transect crossings.

Calhoun (1946) pointed out the great variations in results of various authors who had tried to determine peak periods of activity of *Microtus* in field studies; studies mostly based on time of capture. It was not

until Pearson (1959, 1960) published the results of his traffic surveys using photographic recorders that much sense was made of the variability previously found in activity data. His system yielded data like those presented in this paper, but they came from specific points rather than from a continuous line. My system gives readings at a large number of points but sacrifices precision regarding the exact time and climatological conditions of each crossing. Since variations in climatic conditions near the soil-air interface are pronounced, I question the importance of precision of the measurements except during hours of thermal inversions. One point in favor of the transect system over the photographic recorder is that the former yields data on events outside runways, and gives relatively more data during specific climatological conditions such as showers, thunderstorms, etc.

Other methods that have been used to study the interactions of populations are visual observations, trap recapture methods and activity meters.

Visual observation is more frequently used in studies of birds and reptiles than of mammals. It is also standard practice in determining activity, movements, the delimitation of territories of marked and unmarked diurnal birds. Particularly among diurnal lizards it has been successfully used to demonstrate whether potentially competitive species are active at the same time (Inger 1959) and also in studies of spatial relations (instantaneous position in space) of closely related species (Rand 1964). Visual observation in mammalian studies has been largely restricted to community studies of large diurnal herbivores. Pirlot (1956) describes at some length difficulties in visual censusing on the Luana plains due to the diel and irregular displacements of individuals and herds. Although most visual work has been restricted to diurnal species, Southern, Watson & Chitty (1946) used infrared radiation to observe the nocturnal activity of animals.

The major drawback of visual observation is that the observer must have a clear continuous view. Visual observations of small quadrates on bare ground or rock faces would be possible, but have not been reported. The sand transect produces larger samples and in relatively difficult situations with some restrictions in distinguishing certain smaller species.

To compare sand transect and visual observation studies, measures of activity rates from the latter would be required.

Trap and recapture is by far the most popular method used in mammalian population ecology. Trap sizes and baits used vary from study to study. Results of these studies are not interpretable at the community level because of differences in the efficiency of types and makes of traps (Sealander & James 1958) and the heterogeneity of trap response (Geis 1955). The technique tells little about activity rates and is highly subjective in determining microshifts in spatial utilization. In sand tracking, specific areas of utilization within a habitat, as well as micro-

shifts, can be detected at the population or community levels. Problems which hinge on the symmetry or asymmetry of 24 hr cycles of animal activity in communities as proposed by Park (1941) cannot be determined by normal trapping methods. Usually the worker does not know when, or during which part of its active period, an animal was trapped. Williams (1959), using pitfall traps and special devices to determine the period during which the animals were captured, tried to show the symmetry of activity in evolved communities. Unfortunately the system killed the animals and was only practical for insects and shrews. In my study, the symmetry of activity will be shown to be strongly influenced by weather, a factor which Williams did not consider. Pitfall trapping methods can determine the hours at which animals are active more easily than other trapping methods, but they cannot determine shifts of animal ranges.

Park, Lockett & Myers (1931) and Park (1937, 1938) devised many instruments and systems to measure time of activity. While their work laid essential foundations for the present work on the periodicity of animal activity, it was done largely in sensitive activity cages that could only measure the activity of one individual at a time. In the Panamanian rain forest Park (1935) used the number of calling frogs as an index of animal activity. Park's work is of particular interest because measurements of 6 populations were taken synchronously. Park's approach is complementary in that he measured a vital activity which was not associated to locomotion.

Dyes of urine and feces as used by Kindel (1960) in specific cases permits determination of individual animal movements. Radiotelemetry, like dyes, is a sophisticated method to determine animal movements, but has been limited to single population studies. In spite of the potential of biotelemetry, as described by Adams (1965) and others in the issue of *BioScience* devoted to telemetry, it still seems unlikely that it will ever be entirely practical in studying animal communities. Two problems arise; 1) only animals above a certain size can carry a transmitter, and 2) a large but limited number of animals can be tracked only at great expense. Paths of movement and time of activity can be precisely determined by radiotelemetry, but to understand the function of communities, location in time of any individual must be known in relation to coacting individuals of the same, and other species. Sand tracking tells us both what was and was not at a point during a period.

A smoked paper tracking technique has been used at the population level by Mayer (1957), Justice (1961, 1962) and Sheppe (1965), but these studies are restricted to counts in small areas, from a few square inches to a square yard. These studies have produced point counts in specific situations such as burrows, runways, and feeding stations. Both Justice and Sheppe toe-clipped to recognize individuals.

Sand tracking has been used at the population level for censuring a deer population during migra-

tion (Wright & Swift, 1942) and to study the activity of raccoons (Stains, 1956). Stains reviews the benefits of the tracking system and states that the disadvantages are: 1) the animals are not examined, 2) individuals are not recognized, and 3) rain and freezing impair track counts. Although my tracking system does not overcome the first 2 disadvantages, using a canopy over the track has overcome the latter two.

Recently Odum (1964) pointed out that the concept of ecological levels of organization and the shift from descriptive to functional studies have done much to unify the roots of ecology into a stem. The roots of ecology as defined by Odum are: 1) studies at the species or natural history level, 2) studies bearing on the physical factors of the environment, 3) studies at the population level, 4) community studies, and finally 5) studies of tropho-dynamics, bioenergetics, and biogeochemical cycles. Blair (1964) stated that "no reasonable adequate functional analysis of a natural ecosystem exists." My study is in no way a reasonable functional analysis of the ecosystem, but it is an analysis which considers at least the first 4 roots of ecology and gives us insight into the problems of the fifth root. This study is of particular interest at the community level because it is not restricted to any 1 phylum or class of animals. Platt, *et al.* (1964) state that "ultimate answers can be obtained only in the uncontrolled environments of nature," and "the study of environmental relationships in uncontrolled conditions is extremely difficult." If theories can be developed on the basis of activity data (and I cannot see why not) then this system is an extremely simple way to analyse communities operating on the surface of the ground in uncontrolled conditions. Eventually, a reasonable functional analysis at the ground stratum should give better insight into the analyses of other strata in communities.

#### SITE

The study area is 2 miles north of the village of Lac Carré, Terrebonne County, Québec (latitude 46° 09', longitude 74° 29'), an area of the mid-Laurentian series, approximately 65 miles northwest of Montreal.

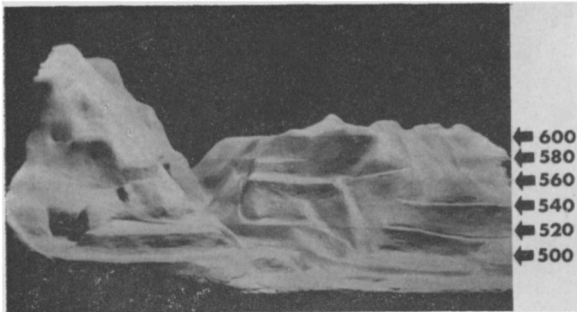


FIG. 2. Lateral view (looking east) of a topographic model of the area showing the relative position of terraces caused by a series of post glacial ice dams. Figures on the right indicate the position of a series of 20 ft contours. The height scale of the model is 8 times the surface scale.

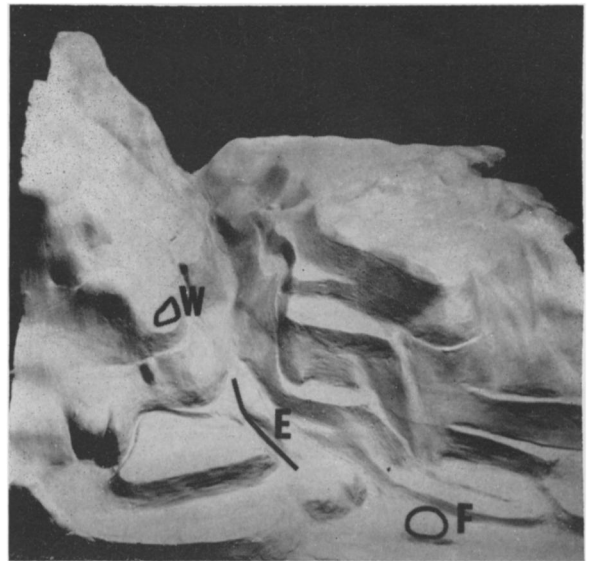


FIG. 3. A 45° angle view of the topographic model used in Fig. 2, with the position of the sand transects indicated F = field transect, E = ecotone transect, W = woods transect.

#### TOPOGRAPHY

The true elevation of the study area ranges from 1000 to 1200 ft. The elevations in figures are accurate relative to one another only. It is estimated that 1000 ft elevation corresponds to a point between the 480-540' contours in the figures. The higher elevations in the southeast section of the area (upper right Figs. 2, 3 & 4) once formed a large basin. Cutting through this and forming a prominent feature of the topography is a small creek from which a 100-ft slope rises to the south and a 200-ft slope to the north. This creek enters a larger south flowing creek in the flat, wide, valley bottom. A main road runs parallel to the larger creek. A significant aspect of the topography is the flat terraces clinging to the sides of the north and south slopes (Figs. 2, 3 & 4). The terraces are postglacial delta-type deposits formed as a result of glacial damming some 2 miles down the main stream (Laverdiere & Courtemanche, 1961). From the 600 ft elevation down, the slopes between terraces are very abrupt in the small creek drainage basin. In the wide valley bottom (lower margin Figs. 3 & 4) deposits were only made in the northeast corner (these are at the 525 ft level) and occur to within 200 ft of the small creek. Finally, at the 510 ft level there is a lower deposit on which the house stands. This deposit is mainly till with alluvium smoothing out some of the minor depressions.

Kettleholes are common in the general area, and the ecotone transect runs through one. This area is shown as a spring flooded area in Fig. 4. The bottoms of these kettleholes have a thick deposit of alluvium which contains little clay, is rather uniform in particle size, and drains in approximately 2 weeks after spring run-off. After heavy rains of 0.75 to

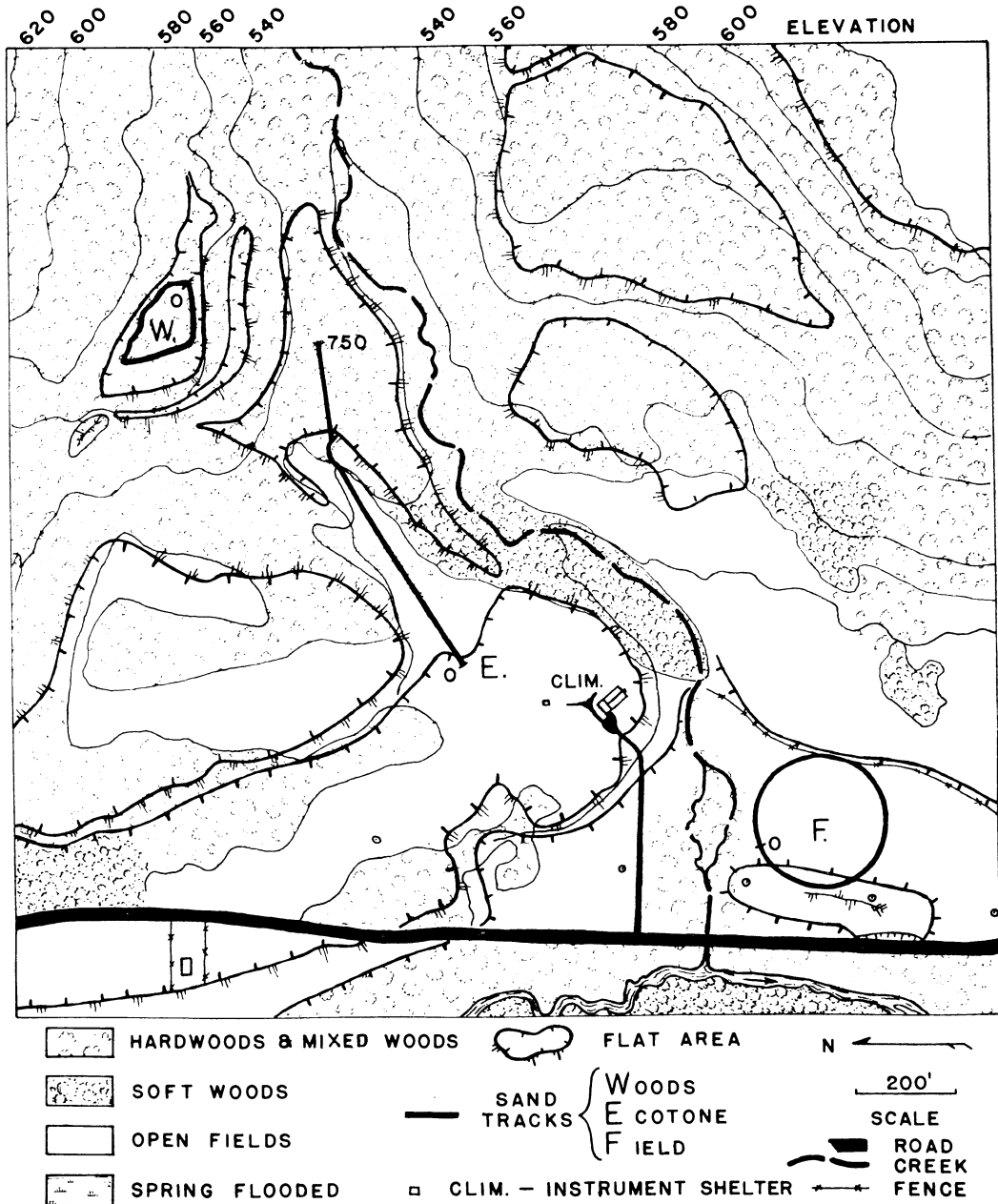


Fig. 4. Map of the area showing the relation of the transects to one another and the larger categories of the vegetation. This figure is oriented as in Fig. 3. The beginning of each transect is indicated by an O.

1.0 inch when the earth is saturated, water accumulates in the hole for a day or two.

SOIL AND ITS RELATION TO DEN AND COVER SITES

Soil structure profiles in this podzolic region are a complex of layers of glacial drift and fine alluvium. There are 3 types of soil beneath the organic strata: 1) bedrock and large boulders are found in the north-

west section of the large valley and on the west slope of the mountain facing this region, and in the area south of the small creek between levels 500 and 520, 2) glacial till, rubble varying from two feet diameter boulders down to fine sand, which is most ubiquitous, is hard packed, contains little silt or clay and is permeable, 3) hard packed alluvial fine sands (mostly 100 and 200 mesh) are found in pockets at the bottoms of kettleholes, or in layers a few inches to several feet thick along the abrupt slopes between

terraces. The fine sand layer of the terraces is usually overlain by glacial rubble along their inner margins. Dens of *Marmota*, *Mephitis* and *Vulpes* are usually found in the fine sands. *Microtus* seem to be pioneer den species and the only animals capable of digging and maintaining dens in the glacial rubble, particularly in areas disturbed by agriculture.

As a secondary result of agriculture, stones have been piled around immovable boulders or thrown down the steep slopes at the edges of terraces in the valley. *Tamias*, *Microtus*, *Sorex*, *Blarina*, *Thomomphs*, *Storeria* and arthropods use rock piles as cover if the structure of adjacent vegetation is suitable.

CLIMATE

The site is in the region which Trewartha classifies as a humid continental climate with cool summers. The coldest month averages below 32° F, the warmest above 50° F but below 71.6° F and precipitation occurs throughout the year (Espenshade 1960). More specific climatic features are drawn from Thomas (1953). Day length varies from 8 hr 36 min to 15

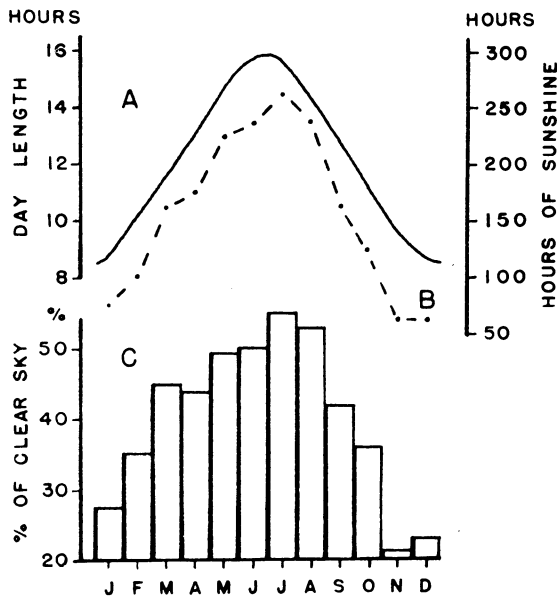


FIG. 5. A—day length, (solid line) computed for latitude 46° 09'. B—mean hours of sunshine per month (broken line). Although curves A and B look similar, June has 5 times as many sunshine hours as December, whereas the day length has only doubled. C—percentage of clear sky based on the mean number of daylight hours which will be cloudless during each month.

hr 57 min. Sunshine hours vary from 62 hr in November and December to 267 hr in July. This represents 21% sunshine in daylight hours for November versus 55% of unclouded sky in July (Fig. 5). Mean annual precipitation is 35 inches, while the rainfall is 25 inches (5 inches in spring, 10 inches in summer and 9 inches in fall). On the average at least 0.1

inches of rain falls every fourth day. The wind is predominantly from the southwest to northwest at a mean velocity of 10 miles per hr. Topography of the site influences the daily wind patterns. Northwest winds funnel in from the west-southwest and cold evening air drifts from the east. The main valley bottom where the field transect is located is susceptible to cold air floods due to a topographic constriction of the valley at the south end. The kettlehole along the ecotone transect is a frost pocket.

VEGETATION

Because the size range of animals studied is large vegetation is described at 3 levels.

The general structures are: maple (*Acer* sp.), yellow birch (*Betula lutea*), and beech (*Fagus grandifolia*) are found particularly on south slopes, while varying amounts of softwoods are interspersed among

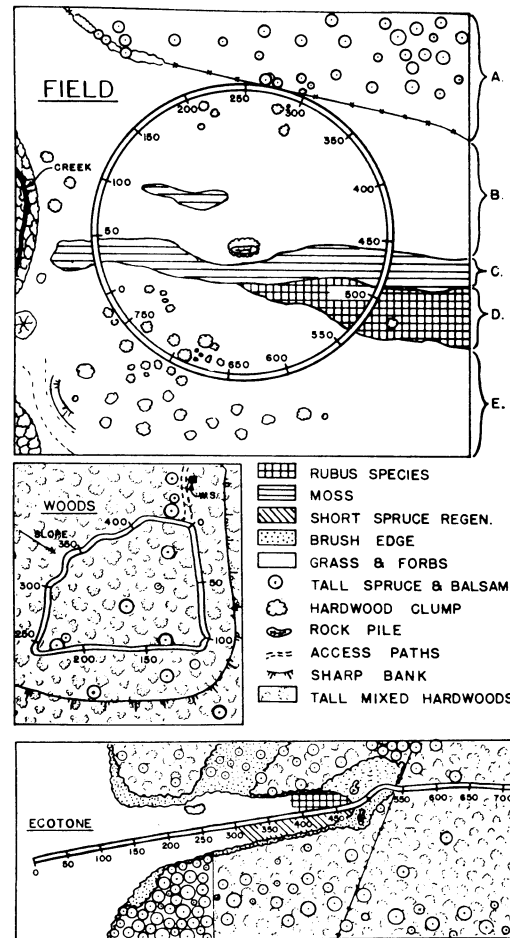


FIG. 6. Detailed maps of areas adjacent to each transect, A—Spruce (*Picea* sp.) savanna. B—Sparse grasses and forbes. C—Predominantly patches of moss and sparse grass. D—Predominantly low blackberry (*Rubus* sp.) bushes but with moss and grass interspersed. E—Dense grass area which includes a small willow (*Salix* sp.) and alder (*Alnus* sp.) savanna.

the hardwoods on north and west slopes; spruce (*Picea* sp.) and balsam (*Abies balsamea*) on the valley bottom. Trembling aspen (*Populus tremuloides*), white birch (*Betula papyrifera*) and spruce are the most common pioneer species. For greater detail see Bider (1961).

The character and position of the vegetation which influence the spatial movements of medium-sized animals are depicted in Fig. 6. In the field the most important features of the surrounding vegetation are: the proximity of the transect to the creek with its alder (*Alnus* sp.) cover; the spruce savanna (top right); and alder-willow (*Salix* sp.) savanna (bottom left), which are diagonally opposite; the position of the fence which includes a broken hedgerow of choke cherries (*Prunus virginiana*); and finally the position of areas where *Rubus* and mosses are dominant. In the woods 3 characters are important. First, the transect is at the end of a terrace (Fig. 3). This constitutes a deadend for animals that move along the terraces. Second, coniferous trees are closer to the track along sections from 400 to 0 and 0 to 250. Third, the section between 250 and 400 runs along the foot of the mountain slope. Because of the importance of the latter 2 characters the transect was divided into 3 sections of 150 ft each in the following manner: section 1 from 400 to 100, section 2 from 100 to 250 and section 3 from 250 to 400. The position of the ecotone transect relative to surrounding vegetation is the most complex. The first 150 ft is typical of a field situation. The variable depths and density of choke cherries and hazelnut (*Corylus cornuta*) along the forest edge is particularly important since the transect runs down the middle of the bay for a distance of about 300 ft. The section between 450 ft and 600 ft is the most variable. The first 25 ft is flat and open. From this point, which coincides with the edge of the woods, the transect climbs abruptly to the 600-ft mark with only one interruption of about 15 ft where it meets the fence-line. Slope, variation in vegetation, and the fence line all influence animal activity. The area adjacent to the last 150 ft of the transect is similar to that of the woods transect, but the terrace on which this section lies is not a deadend, and the slopes down from the terrace are not as abrupt.

Vegetation and site data were recorded by Dansereau's (1958) system (Fig. 7). Section 1 of the ecotone represents the first 150 ft of the transect, section 2 from 150 to 300 ft, section 3 from 300 to 450 ft, section 4 from 450 to 600 ft and section 5 from 600 ft to the end of the transect. Section 1 of the ecotone is similar to the field which is homogeneous except for an occasional bush or small spruce along the edge of the field transect. Section 5 is structurally similar to the woods transect except that the maples along the latter have multiple stems. Vegetation along section 2 of the ecotone, through the kettlehole, is composed of moisture tolerant species. In section 3 young pioneer trees are common in an area shaded during much of the first half of the day.

Section 4 is characteristic of the edge of the woodland with a large diversity in species and size of plants.

Hereafter, numbered sections will be designated as S.1, S.2, S.3, etc.

## METHODS

### CONSTRUCTION OF TRACKS

A Gravely hand tractor with rotary plow was used to break the surface of the ground, and a rotary cultivator was used to pulverize the soil. This was done to a depth of about 6 inches. The rotary cultivator disturbed a 36-inch strip of soil. Soil containing pebbles and organic matter was raked into small piles to dry. Most of the fine soil was then shaken out onto the transect and the remainder scattered into the adjacent area. This procedure was repeated until the transect was free from roots and pebbles. When the soil was wettest the transect was then compacted by running over it several times with the tractor. Rain after compaction tended to smooth out the tire tracks. The last step of the process was to lay down a half-inch layer of fine sand; lumpy sand can usually be rolled with a garden roller after one good drying day. On abrupt topography an empty roller, with one person treading on it was used. After the surface had dried an empty roller, jammed so as not to turn, was dragged over the sand leaving an ideal tracking surface.

Using this process, it took 4 man-weeks to complete 1200 ft of transect. Absence of grass roots in the woods allowed transect construction at 50 ft per man-hour. Under good drying conditions, such as in hardwoods before green-up, 450 ft of transect could be ready in 3 days.

### MAINTENANCE

As the data are being gathered, the transect is erased by dragging an 18-inch soft bristle push broom down the track. Lateral displacement of sand is negligible. Unless the transect is circular, the start loses sand while the end accumulates it, therefore the sand at the starting end must be replenished every 2 to 3 weeks. Seed germination and vegetation encroachment necessitate periodic weeding. When transects were being used periodically, they were sprayed with a herbicide and temporary germination inhibitor (Dowpon) after each tracking session.

When erosion from surface drain-off occurred, accumulated sand deposits on the track were removed. This sand was re-used to fill erosion gulleys if it did not contain organic debris. The most effective method of drying a track after a rainstorm was; a) raking with a garden rake to break the capillary movement of water toward the surface. b) when the surface layer of sand had dried, the track was lightly raked with a soft leaf rake to break lumps and expose the deeper wet sand. The latter procedure was repeated until wet sand was no longer exposed by raking. This procedure dried a saturated transect in one sunny afternoon, instead of several days.

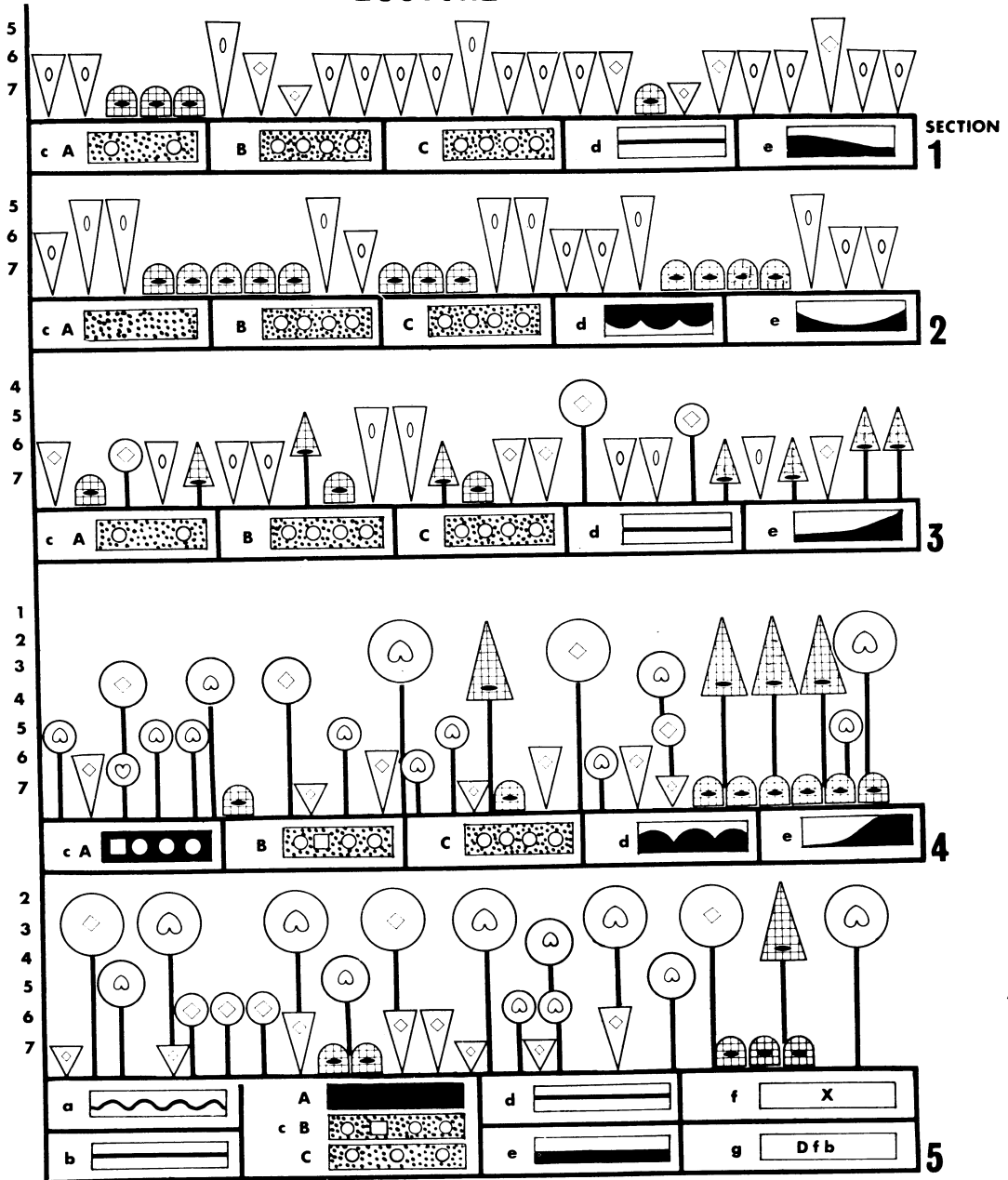


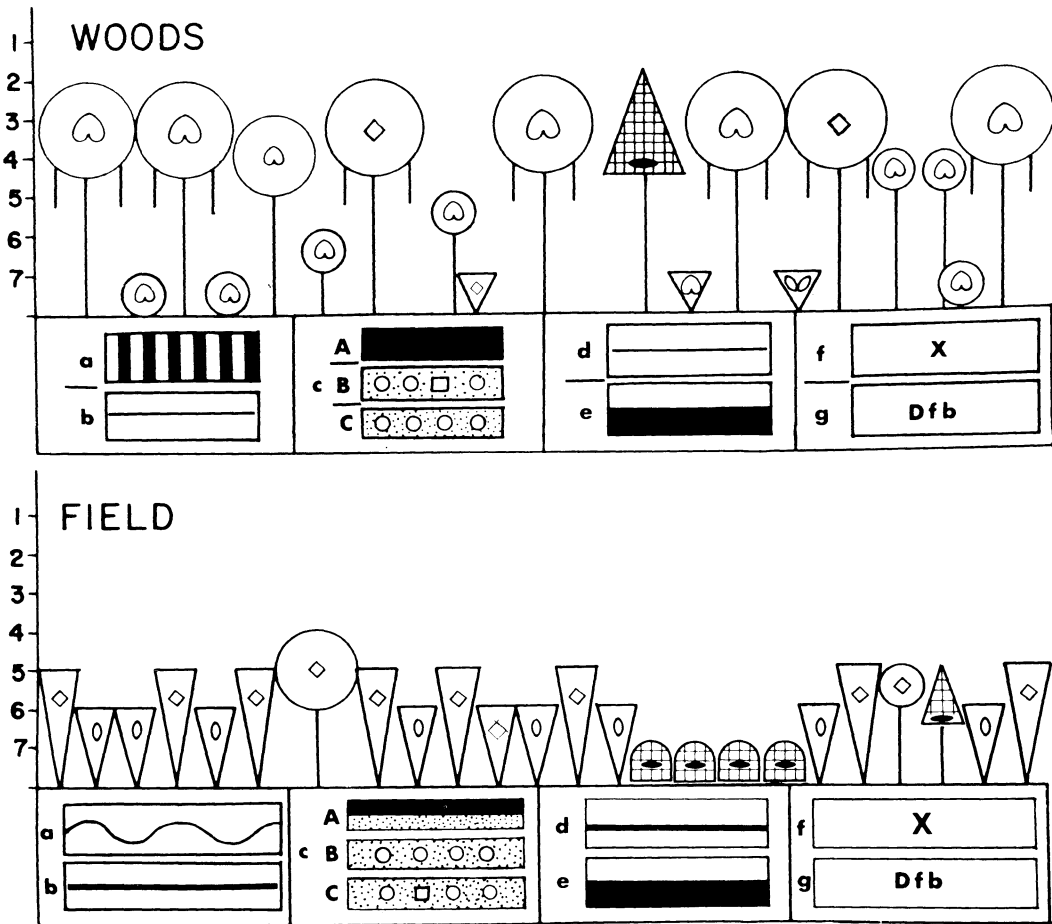
TRACKING SAND

Particle size and depth of sand are the most important factors in the transect technique. Particle sizes of about 0.1 mm. were essential to register small details. A disadvantage is its large surface area making it hard to dry and encouraging capillary movement of subsoil water. Sand moisture is more easily controlled when small and large sand particles are mixed. An ideal mixture of sand (Fig. 8) is shown, but in practice only 3 structures were tried. Both

the nueces sand from Texas (Bider 1962) and a common mixed sand from this study area have worked well for half-inch animals. Laurentian fine sand is too fine to be used alone, but a light sprinkling of this over the coarser common sand produced excellent details of 1/8 inch insects. Movement of sand during transect erasure brings larger particles to the surface so these must be swept off occasionally. Inevitably a considerable amount of colloidal material became mixed into the sand surface, and fresh clean sand

ECOTONE





KEY TO THE SYMBOLS USED

<p><b>LIFE FORM</b></p> <p>○ ERECT WOODY PLANT</p> <p>▽ HERBS</p> <p>◐ BRYOIDS</p> <p><b>STRATIFICATION</b></p> <p>1 &gt; 25 METRES</p> <p>2 10-25 "</p> <p>3 8-10 "</p> <p>4 2-8 "</p> <p>5 0.5-2 "</p> <p>6 0.1-0.5 "</p> <p>7 0.0-0.1 "</p>	<p><b>FUNCTION</b></p> <p>□ DECIDUOUS</p> <p>▣ EVERGREEN</p> <p><b>LEAF SHAPE &amp; SIZE</b></p> <p>◊ NEEDLE</p> <p>◌ GRAMINOID</p> <p>◇ MEDIUM OR SMALL</p> <p>◡ BROAD</p> <p>◕ COMPOUND</p> <p><b>LEAF TEXTURE</b></p> <p>□ MEMBRANOUS</p> <p>■ SCLEROPHYLL</p>	<p><b>a. UTILIZATION</b></p> <p>~ SEMI NATURAL</p> <p>▤ LUMBERED</p> <p><b>b. SOIL STRUCTURE</b></p> <p>— MEDIUM</p> <p><b>c. SOIL TEXTURE</b></p> <p>□ BOULDERS</p> <p>○ PEBBLES</p> <p>▤ SAND</p> <p>■ ORGANIC</p>	<p><b>d. DRAINAGE</b></p> <p>▤ EXCESSIVE</p> <p>— GOOD</p> <p>▤ POOR</p> <p><b>e. RELIEF</b></p> <p>— FLAT</p> <p>▤ DEPRESSED</p> <p>▤ ABRUPT</p> <p><b>f. EXPOSURE</b></p> <p>—</p> <p><b>g. CLIMATE — KÖPEN SYMBOLS</b></p>
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FIG. 7. The vegetation depicted using Dansereau's universal system for recording vegetation. Ecotone—The vegetation along each 150 ft section of the ecotone transect. For each section the soil structure of the 3 horizons are given (c—A, B and C) along with drainage (d) and relief (e). Utilization, soil structure, exposure and climate are common to all sections and shown below section 5. Woods—The mixed forest vegetation of the woods. Additional lines down from trees indicate multiple trunks. Field—The grass and forb vegetation of the field.

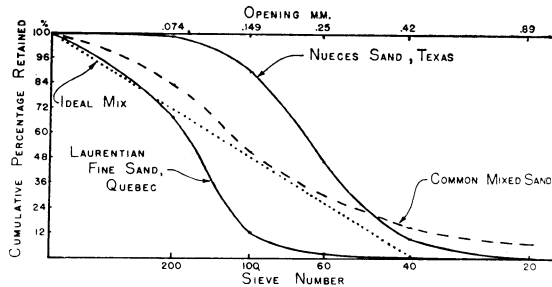


FIG. 8. Particle size structure of sand used for tracking. Cumulative percentage retained is that proportion of the total weight of the sample which is retained by each sieve.

had to be added. The sand used on these transects was predominantly quartz, therefore increased organic content was detected by color alone.

The ideal thickness of the clean dry sand layer was about  $\frac{3}{8}$  of an inch. Thick layers of dry sand were useless because prints, particularly of small animals lost their form. When the sand was too thin, ground water reached the surface during protracted periods of low evaporation. When the sand layer is ideal, the fall of 0.01 inches of dew will result in a shearing away of the wet surface layer, exposing a three-sixteenth inch layer of sand when the transect is erased.

#### THE TRANSECT CANOPY

When tracking under adverse weather conditions, or on calendar schedules, protection against precipitation was accomplished by the use of a suspended polyethylene canopy (Figs. 1 and 9). This proved ideal for continuous tracking and measuring activity during inclement weather, and it inhibited dew fall in open areas. It has withstood gusts of wind up to 35 miles per hr. The sheet iron tie, with a toenail set (the latter is not shown in the diagram), and the bolt construction were combined to allow changes in the angle of the canopy to suit wind and rain conditions. We used about a 1-ft slope in the woods and a little less than 6 inches in the open fields. Temperatures fluctuated between 8° and 90° F. so the polyethylene was put on while temperatures were around 45° F. The film sagged slightly at higher temperatures but this saved restapling during cold snaps. Adjustments in canopy slope were made during the first rainstorm after the installation. Wherever pockets of water formed due to sagging polyethylene, holes were punched with our fingers from above and sloping outwards.

#### THE DATA

Markers were placed at 50 ft intervals along the transects. Data sheets with species columns, and distance unit rows of 10-ft intervals, were used. Because of the thousands of sheets handled, we recorded date and time of the preceding and the present record, track code letter, number of the tracking session,

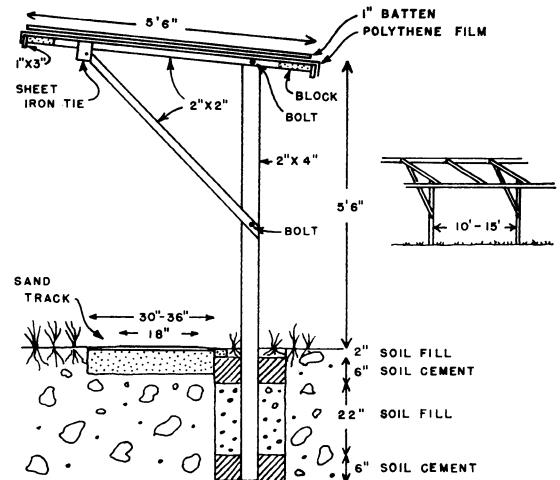


FIG. 9. Cross section and construction details of transect and canopy. Stippled area under transect surface indicates treated sub-surface before sand is spread.

sheet letter (as up to 3 sheets were used for longer transects), and page number. Using this system we had enough built-in checks to avoid errors. Recording was done from the end of the transect toward the beginning so that the orientation of the transect coincided with that of the data sheets. Thus the direction of animal crossings did not have to be recorded in reverse. Night tracking was done by gas lanterns.

#### IDENTIFICATION OF PRINTS

Identifying tracks is a question of practice and experience. Surprisingly, small species are seen so often that familiarity and confidence in identification soon develops, whereas tracks of Carnivora and other medium-sized animals, seen only occasionally, can be confusing. Therefore, my assistants have always circled questionable tracks, noted the time on the sand, and left them to be checked.

All groups or species treated in this paper can be readily distinguished with Murie's (1954) Field Guide to Animal Tracks. Some closely related species are very difficult or even impossible to distinguish, e.g. the Soricidae and Zapodidae. The species in these 2 groups are often found in the same areas of the study site, so they were all fused into their respective families.

*Clethrionomys* and *Microtus* have been analyzed separately because it has been shown from trapping data (Pirlot 1962) that the 2 only overlap to a minor extent along the forest edge at this same site. This ecological separation of the 2 genera has also been shown to exist in Norway by Steven (1955).

According to Murie (1954) the diagnostic characters of the tracks of these 2 animals differed, but this is not the case. The drawings in Fig. 112 of Murie's book are entirely fictitious and were, in fact not Murie's own drawings, which are impeccable. Actually a *Clethrionomys*' print resembles that of a small *Microtus* as depicted in Murie's Fig. 106.

Relatively few Microtine prints were found in the first hundred feet of forest. When they were, the following criteria were used to differentiate the 2 species. First of all a *Clethrionomys* print is a full  $\frac{3}{16}$  inch smaller than that of *Microtus*, making it about the same size as a *Peromyscus* print. *Clethrionomys* weighs between 20-30 g, whereas *Microtus* weighs between 50-60 g and, therefore, *Clethrionomys* does not register as deep a print as does *Microtus* and they are normally clearer. *Microtus* commonly use a walking gait (Fig. 10) and *Clethrionomys* a triangular hopping gait. Confusion might occur between a young *Microtus* and a mature *Clethrionomys*, but fortunately over 80% of *Microtus* activity is confined to runways. Whenever new runways were established I simply postponed my decision until a visual observation of the animal was made. These criteria lower identification error to less than 1%.

The tracks which have given the student assistants

the most trouble were those of some of the Sciurids. Chipmunks, red squirrels, grey squirrels and woodchucks have somewhat similar prints, but the widths of their strides are characteristically larger in ascending order. Stride widths do, however vary with speed of locomotion and confusion may result. In a final analysis the following criteria are used: A wider stride with a small dainty print and a short distance between jumps identifies a chipmunk. A narrow stride with a heavy print and a long distance between jumps identifies a red squirrel. The same criteria are used to differentiate red from grey squirrels, and the latter from woodchucks.

During the summer of 1964, work was begun on a reference collection of prints. Fig. 10 shows pictures of a series of prints from the collection. Each cast consists of the preserved top layer of sand as the animal had left it, set on a reinforced plaster of Paris plate. These casts have been very helpful as teaching and practice aids, and in cases where positive identification would have to be postponed.

#### REFERENCE COLLECTION TECHNIQUE

Two objectives were set in perfecting the cast technique; 1) maximum detail, 2) a form that could be handled. These were attained in the following way: A series of prints crossing the transect were first coated with a thin layer of lacquer from a spray can. This, when done very cautiously, solidified the surface without disturbing the sand. To build up adequate rigidity, commercial lacquer was then sprayed on using a good quality garden hand sprayer. This must be done in dry conditions so the lacquer does not soak into the sand and form a thick brittle mass. For moisture control, a photoflood lamp powered by a portable generator was used. When the lacquer hardened so the prints could be sheered from the sand, sheet iron was slid beneath the print, lifted, and taken to the lab. A mould of appropriate size was made with  $\frac{3}{4}$  inch wood strips nailed to a plywood platform, the surface of which was covered with wax paper or polyethelene. A piece of  $\frac{3}{4}$  inch galvanized wire screening cut to the dimensions of the mould was placed on the bottom. A mixture of approximately 2 parts of water to 1 part by volume of plaster of Paris was poured into the mould. Bubbles were rapidly brought toward the center and finally the sand track was slipped onto a plaster and pressed down very lightly. When the cast was completely dry, in 1 to 2 weeks, additional light coats of lacquer were added to prevent damage in handling and to help keep it clean.

#### CONSTITUENTS OF THE COMMUNITY

Species which have crossed the transects are listed in Table 1. The number of species which crossed the ecotone transect was twice that of either the woods or field transects. When the ecotone track was roofed and continuous data were gathered another 9 species were recorded.

The adequacy of the transect lengths for determin-

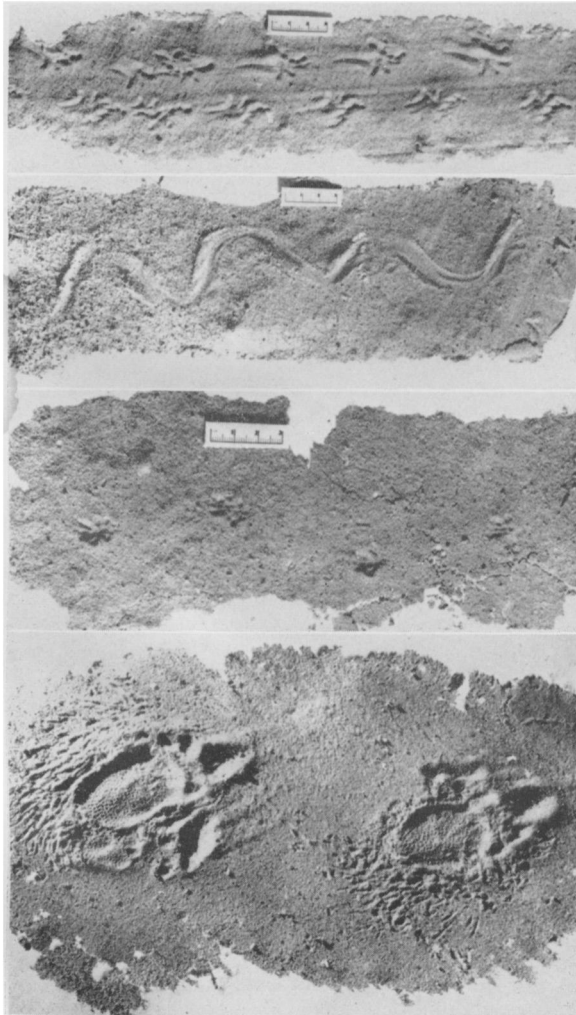


FIG. 10. Pictures of casts in descending order: *Bufo americanus* going left, *Storeria occipitomaculata* going right, *Microtus pennsylvanicus* going left and *Erethizon dorsatum* going right. Both mammals depicted were registering their hind feet over their forefeet.

TABLE 1. The constituents of the community.

TROPIC LEVEL	Major Categories	Sub Categories <sup>1</sup>	Tracks on which they were found			
			F	E	Ec	W <sup>2</sup>
HERBIVORES	Porcupine	<i>Erethizon dorsatum</i>		x <sup>3</sup>	x	x
	Deer	<i>Odocoileus virginianus</i>		x	x	x
	Moose	<i>Alces alces</i>		x		
	Hare	<i>Lepus americanus</i>	x	x	x	x
	Flying Squirrel	<i>Glaucomys sabrinus</i>		x	x	x
	Grey Squirrel	<i>Sciurus carolinensis</i>		x	x	x
	Red Squirrel	<i>Tamiasciurus hudsonicus</i>		x	x	x
	Chipmunk	<i>Tamias striatus</i>	x	x	x	x
	Deer Mouse	<i>Peromyscus maniculatus</i>	x	x	x	x
	Jumping Mouse	Zapodidae	x	x	x	x
		Eastern, <i>Zapus hudsonius</i>				
		Woodland, <i>Napaeozapus insignis</i>				
	Red Backed Vole	<i>Clethrionomys gapperi</i>		x	x	x
	Meadow Vole	<i>Microtus pennsylvanicus</i>	x	x	x	
	Woodchuck	<i>Marmota monax</i>	x	x	x	x
	Rat	<i>Rattus norvegicus</i>		-	x	
	Muskrat	<i>Ondatra zibethicus</i>		-	x	
	Ruffed Grouse	<i>Bonasa umbellus</i>		x	x	x
	Sparrows	Fringillidae				
		Chipping, <i>Spizella passerina</i>	1	2		
		White-Throat, <i>Zonotrichia albicollis</i>	2	1		
		Savannah, <i>Passerculus sandwichensis</i>	1	1		
		Song, <i>Melospiza melodia</i>	1	1		
		Chickadee, <i>Parus atricapillus</i>		1		1
	Invertebrates	Invertebrata	x	x	x	x
		A catch-all with the exception of the following three groups:				
	Earthworms	Annelida, Oligochaeta, Opisthophora	x	x	x	x
Snails	Mollusca, Gastropoda, Pulmonata	x	x	x	x	
Roundworms	Nematoda and Nematomorpha	x	x	x	x	
INSECTIVORES	Toad	<i>Bufo americanus</i>	x	x	x	x
	Frogs	Ranidae & Hyliidae				
		Green, <i>Rana clamitans</i>	2	1		3
		Leopard, <i>Rana pipiens</i>	1	2		
		Wood, <i>Rana sylvatica</i>		2		1
		Pickereel, <i>Rana palustris</i>	0	0		
		Bull, <i>Rana catesbeiana</i>		0		
		Spring Peeper, <i>Hyla crucifer</i>		0		
		Grey Tree, <i>Hyla versicolor</i>	0			
	Salamanders	Urodela				
		<i>Eurycea bislineata</i>		-	x	
		<i>Ambystoma jeffersonianum</i>		0	0	
	Red Bellied Snake	<i>Storeria occipitomaculata</i>	1	2	x	
		Ring Neck Snake, <i>Diadophis punctatus</i>		0	x	
		Green Snake, <i>Opheodrys vernalis</i>	0	0	x	
	Garter Snake	<i>Thamnophis sirtalis</i>	x	x	x	x
	Birds in general	Aves gen.				
		Blue jay, <i>Cyanocitta cristata</i>		1	x	1
		Robin, <i>Turdus migratorius</i>	1	1	x	
		Starling, <i>Sturnus vulgaris</i>	1	1	x	
		Veery, <i>Hylocichla fuscescens</i>		1	x	1
		Thrush, <i>Hylocichla sp.</i>		1	x	1
		Ovenbird, <i>Seiurus aurocapillus</i>		1	x	1
		Cowbird, <i>Molothrus ater</i>	1	2	x	
	Woodcock	<i>Philohela minor</i>	x	-	x	
	Flicker	Picidae, <i>Colaptes auratus</i>	x	x	x	
	Crow	Corvidae, <i>Corvus brachyrhynchos</i>	x	x	x	
Shrews	Soricidae					
	Shrews, <i>Sorex sp.</i>	x	x	x	x	
	Short tailed, <i>Blarina brevicauda</i>		x	x	x	
Mole	Talpidae					
	Star-nosed, <i>Condylura cristata</i>		x	x	x	
CARNIVORES	Skunk	<i>Mephitis mephitis</i>	x	x	x	x
	Raccoon	<i>Procyon lotor</i>	x	x	x	x

TABLE 1 (continued)

TROPIC LEVEL	Major Categories	Sub Categories <sup>1</sup>	Tracks on which they were found			
			F	E	Ec	W <sup>2</sup>
	Lynx.....	<i>Lynx canadensis</i>		-	x	
	Fox.....	<i>Vulpes fulva</i>	x	x		
	Weasel.....	<i>Mustela erminea</i>		x	x	
	Mink.....	<i>Mustela vison</i>		-	x	
	Otter.....	<i>Lutra canadensis</i>		-	x	
	Cat.....	<i>Felis domestica</i>		x	x	
	Mountain Lion.....	<i>Felis concolor</i>		-	x	
	Bear.....	<i>Ursus americanus</i>		-	x	
		Number of species found on each track	32	51	59	30
		Total possible - 62				

<sup>1</sup>Subcategories indicate species which were either seen or recognized as having been on the track but which were grouped together under one major category.

<sup>2</sup>F - Field track, E - Ecotone track, Ec - Ecotone track with canopy, W - Woods track

1 - Dominant, 2 - Sub-dominant, 3 - Common, O - Occasional, x = present, - = not found on ecotone track before the canopy was installed. Blanks indicate that the species was never found to be active along or near the particular track.

ing the species composition of the communities can be shown as follows: species recorded on the first and last 150-ft sections of the ecotone included all those recorded on the 783-ft field and 450-ft woods transects respectively.

In 1965, both *Alces* and *Lynx rufus* crossed under the canopy and *Vulpes* crossed in 1966 and 1967. Although *Plethodon cinereus* is found on the site, it has never been seen crossing a transect. *Martes americana*, *Martes pennanti*, *Mustela frenata*, and *Canis lupus*, all said to be trapped in similar habitats in the area, have not been recorded. Granted, these animals are rare, but then so are the felids, and yet both species of *Lynx* and a *Felis concolor* crossed, the latter being a record for the region. *Eurycea* was recorded only under the canopy because they move during or shortly after rain.

To summarize: 1) in similar habitats as many species will cross a 150-ft section as they will a 783-ft transect. 2) the ecotone track constitutes a reliable transect, representative of both field and wood communities. 3) there is no evidence that a canopy inhibits the passage of any species. 4) continuous tracking under varying weather conditions enhances the possibility of detecting a) species which only frequent the area occasionally, and b) those that are only active during or shortly after rain.

SPATIAL UTILIZATION

The data for each species were compiled on a basis of the daily number of crossings per 150-ft sections except the last section of the field which was 183 ft. This produced a total of 13 sections; field (S.1-5), ecotone (S.6-10), woods (S.11-13).

The data were gathered in 4 discrete periods in 1963; 1) 2 single days plus 5 consecutive days ending June 30th, 2) 7 consecutive days in late July, 3) 7 consecutive days in late August and early September, and 4) 3 days and 4 nights in mid-October.

The single variable of classification variance test with different numbers of categories, described by

Dixon & Massey (1957) was used to test the differences between the means of the different groups of sections or periods and to establish activity levels. Activity levels are determined using repeated applications of one-way analysis of variance. First, the mean number of crossings of all sections are tested. Where a significant difference among these is noted, sections with excessively high or low means are successively eliminated from the analysis. Thus several sets of sections are obtained whose means do not test significantly different among themselves. Such sets of sections form "activity levels." The activity levels of the dominant forms are presented in Fig. 11. Statistical analyses were run on all groups which occurred in the area during the study, and the results are included in pertinent sections of this paper.

TOTAL SPATIAL UTILIZATION OF WOODED AREAS

The most important facet of woodland spatial utilization is that the majority of forms eventually utilize the entire area at random during their active season. Table 2 shows that 16 out of 20 species utilized S. 10-13 equally. Six of the 20 species were significantly more active at the forest edge, S. 9. Eleven of 20 species were less active in S. 10, and more active in S. 9 than the mean activity of S. 11-13. This distribution of activity in the first 300 ft of forest versus that of the deeper forest indicates that the forest edge might act as an absorbent barrier rather than an elastic one. An absorbent barrier could be called a biological barrier as opposed to an elastic physical barrier such as that formed by a container enclosing molecules in motion. When animals encounter a biological barrier they probably tend to move parallel to the barrier for some distance. The result of this would be that all animals whose home ranges are delimited by barriers would tend to be more active along the barrier, thus creating an activity vacuum at some distance away from the barrier. This edge and vacuum effect fits the woodland data presented, and might be of significant importance in problems of intra- and interspecific com-



TABLE 2. A summary of the distribution of total activity in terms of activity levels in the fields and woods. Sections included in each bracket constitute an activity level (means of activity not significantly different). These are arranged in an order of decreasing magnitude from left to right.

	WOODS		FIELDS
ERETHIZON	(9-13)		
LEPUS	(9-13)	x <sup>1</sup>	(1-8)
GLAUCOMYS	(9-13)		
TAMIASCIURUS	(9) (10-13)	x	
TAMIAS	(9) (10-13)	x	
PEROMYSCUS	(9,12) (10,11,13)		(1-8)
ZAPODIDAE	(9-13)	x	(7,8) (1-6)
CLETHRIONOMYS	(9-13)		
MICROTUS			(1,4) (2,5) (3,6) (7,8)
MARMOTA	(9-13)		(1-8)
BONASA	(9-13)	x	
INVERTEBRATA	(9) (10-13)	x	(3-6) (1,2,7,8)
BUFO	(9-13)		(1-5) (6-8)
RANA	(9-13)	x	(1-8)
COLUBRIDAE	(9,13) (10,11,12)	x	(2,5) (1,3,4,6-8)
AVES	(9) (10-13)	x	(2,5) (1,3,4) (6-8)
CORVUS			(1-7) (8)
PHILOHELA			(1-5) (6-8)
SORICIDAE	(9) (10-13)	x	(4) (1,5,8) (2,3,6,7)
TALPIDAE	(9,11) (10,12,13)		
MEPHITIS	(9-13)		(1-8)
VULPES			(1-8)
MUSTELA	(9) (10-13)	x	(1-8)
PROCYON	(9,10) (11,12,13)		(1-8)

<sup>1</sup>X denotes examples wherein Section 9 was higher and Section 10 was lower than the mean of Sections 11 to 13.

and the specific pattern of utilization of an individual or family of mice. These animals are very directional, that is, they tend to move from homesites to specific feeding areas using specific paths. Occasionally they change both homesite and feeding area. To demonstrate how directional they are, see the activity of *Peromyscus* in Periods 2 and 3 on the woods track, Fig. 12. During these periods visual observation indicated that the animal's homesite was a log near the 230-ft mark. If the animal utilized the area around its homesite at random, then we might expect the histogram to form a normal activity curve with the mode in the segment closest to the site. This, however, was not the case, for the feeding area was at a distant point along the track and this produced a skewed activity distribution. The closer the feeding station is to the homesite the more leptokurtic the curve will be (Fig. 12 P.3). If the feeding station is at some distance across the plot, then 2 curves are produced, one broader skewed curve close to the homesite and a second sharp-peaked curve (resembling curves produced by any of the tunnel-dwelling animals (Fig. 12 P.1 and 4.). The same figure shows that there were several changes of homesites and feeding areas. The following winter there was only 1 active homesite on the whole flat, a vertical hollow poplar stub near the 350-ft marker, that had been occupied in the preceding June.

Higher activity of *Peromyscus* in section 12 can be attributed to homesites being located near that section during three of the four periods. Over a whole

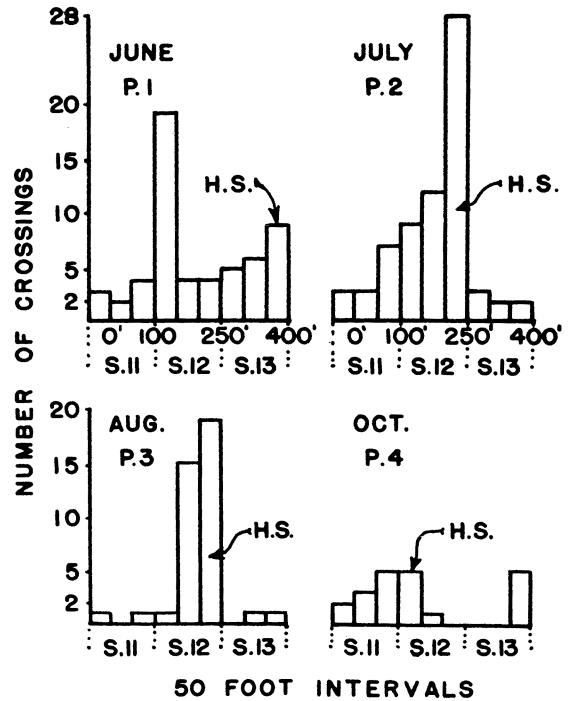


FIG. 12. A detailed record of the distribution of *Peromyscus* activity around its home site on the woods transect during the four periods of 1963. P—period. S—section. H.S.—indicates that the *Peromyscus* home site was closest to this 50 ft interval.

summer, or when *Peromyscus* populations are higher, this preferential utilization in time might not be as apparent as in this sample.

The Colubridae, in this case *Thamnophis*, were more active in S.9 and 13. The high level was due to fall activity (Fig. 11, P.4), and the terrain. S.9 rises abruptly into the woods and S.13 runs along the edge of the terrace nearest the mountainside. Gravid females and young snakes were found only in the fields. Only mature snakes were found in the woods and some came out of hibernation above the woods transect as early as mid-April when the terrace was still covered with snow. It seems that female *Thamnophis* migrate down to the field to bear their young during early August. Later they seek suitable hibernacula in the woods, or at higher elevations. In this area all higher elevations are wooded. This speculation is based on activity in P.1, 2 and 3 woods, which was always lower, or statistically as low as the lowest sections of the fields and ecotone whereas S.9 and S.13 P.4 were as high as the highest field sections (Fig. 11). Also the October mean daily snake activity in the woods equaled that of P.3 in the fields and was twice as high as that found on the ecotone and woods in P.1, 2 and 3 or the field in P.1 and 2. Furthermore unpublished mark recapture data from 1967 tend to confirm that some migration does take place.

Assuming that there is a fall migration toward the woods, and since snakes have difficulty climbing



slopes where leverage points are few and far between, it is not surprising to find high activity on S.9 and 13. To get up the incline parallel to S.9, snakes move obliquely along the slope producing an artificially high activity. S.13, where the track is parallel to the foot of the slope, is different. Here half of the tracks were located in the last 50 ft of the section, the area where the slope of the mountain was least abrupt. In S.13, there were 26 crossings, of which 11 were uphill, 11 downhill, and 4 were uncompleted uphill attempts. However, in the next 50 ft there were 3 crossings, all directed away from the fields, making a total gain of 3 *Thamnophis* into the deep woods.

*Parascalops* was found on another transect in 1966, thus confirming by tunnel size, that the Talpidae referred to in this paper are *Condylura*. Obviously moles have very specific crossings and the significance of the means between sections is determined by the number of tunnels intercepted by the transect in each section and by their utilization. For each tunnel, we could detect only 1 crossing per 2 hr period and thus our counts are probably low. There were 4 consistent mole crossings under the woods track; 2 in S.11, a less active one in S.12, and a more active one in S.13. Under the ecotone, there was 1 tunnel in each section. The one at the edge of the woods in S.9 was very active. Areas of preference cannot be determined from these results because a starting point and section lengths were arbitrarily chosen, but it is clear that the *Condylura* are dispersed in discrete pockets leaving large areas unutilized.

The only other animal to show preferential utilization of a section other than S.9 was *Procyon*. A 3 year study of *Procyon*, using continuous data from 1964-1966 (Bider, Thibeault & Sarrazin, 1968), shows that the deeper sections of the woods in this area are sparingly utilized as compared with the first 300 ft. Probably the wood's edge acts as a security route particularly during the months of June and July when the animals are merely moving from cover to feeding stations. *Procyon*, a fairly large carnivore (broader ecological tolerance) should be expected to show high activity along a biological barrier, and this would extend to a greater ecotonal depth than with smaller animals.

To sum up, the general total spatial activity pattern of the woodland community is one of random utilization (18-20 species) with the possible exception of *Peromyscus* and *Condylura*. Preferential utilization by *Thamnophis* seems to be artificial and based on locomotory problems. In the first 150 ft of the forest edge there is a general tendency toward greater activity (significantly higher in 40% of the cases), while the next 150 ft seems to be a vacuum area where activity is usually a little lower than the mean activity of the deeper woods. The most important biological significance of these findings is, a) that the woods are being used very nearly to their spatial maximums, and b) that interspecific co-actions must be decreased by one or more of the following: 1)

through specific phenological utilization of areas (intense utilization of specific areas at specific times of the year), 2) by having specific non-conflicting circadian rhythms, or 3) by being active in different areas during specific climatic conditions.

When each species in a community utilizes all the available space in a random fashion, and when interspecific co-actions must be decreased by mechanisms other than spatial parameters, this would show a degree of community evolution or maturity, especially when compared with a situation in which species are segregated through specific utilization of discrete areas throughout their active period. The utilization of field areas seems to fit the second situation wherein total utilization is much more segregated into pockets of activity.

#### TOTAL SPATIAL UTILIZATION OF FIELD AREAS

In the fields (S.1-5 of the field transect and S.6-8 of the ecotone transect) 9 of 17 species had more than 1 level of activity among the sections and 8 species utilized the area at random. Of the 8 species which utilized the fields at random, 4 were carnivores and would be expected to utilize an area this small at random because of their broad ecological tolerances. Therefore, the area tested is probably too small to note specific utilization. Random utilization by *Rana* was the result of 2 equally active species, but in 2 discrete areas. *R. pipiens* was dominant in the field, and *R. clamitans* on the ecotone. Among the species which had more than 1 activity level in the fields, the Zapodidae should be commented upon. By live trapping and observation over a period of 10 years, it has been found that *Napaeozapus* are restricted to the woods and *Zapus* to the fields except in S.7, 8 and 9 of the ecotone transect where both are found. In P.2, Zapodidae activity in the woods was more than twice as high as that of P.1 and 3. The higher level of activity in S.7 and 8 was caused by activity occurring only in P.2. It seems that higher Zapodidae activity in the field along S.7 and 8 was due to a range expansion of *Napaeozapus* and that *Zapus* activity is random.

Considering the foregoing, we can add 2 species to the list in Table 2 (1 *Rana* and 1 Zapodidae) for a total of 19 species or forms, and of these 8 utilized the area at random (i.e. 42%). If the carnivores are then excluded, for reasons mentioned above, only 4 of 15 forms utilized the area at random (i.e. 27%). Whether or not the carnivores are included has little effect on the hypothesis that the general utilization of woodland areas is random whereas areas of the fields are more often utilized at different levels of activity.

For the 8 species tested for areas of preferential utilization S.7 and 8 were in the level of lowest activity 7 times, S.6, 5 times, S.4 once and S.1, 2 and 3, twice each. Section 5 was in the highest level, 5 times, S.1, 2 and 4, 4 times, S.3, 3 times, S.6 twice and S.7 once. This indicates that unlike the woodland edge, where activity is greatest, field edge ac-

tivity is lowest for most species and, conversely, sections away from the edge effect are utilized at different levels of activity by different species in a random fashion.

It is well to remember at this point that the 2 low activity sections 7 and 8 of the ecotone are in a bay formed by an intrusion of the field into the woods (see Figs. 4 and 6). It is probable, therefore, that the lower activity at the forest edge might normally be apparent only in the first 100-150 ft from the margin of the woods.

#### PERIODIC SPATIAL SHIFTS IN THE FOREST

This section deals with the seasonal patterns of spatial utilization in a system where for the most part all space will eventually be utilized at random. Four of the 20 species did not utilize the forest area (S.10-13) at random and their spatial utilization was discussed earlier. The data (Fig. 11) show 2 ways by which species can utilize a total area at random without continuously repeating their spatial pattern throughout the season.

*Lepus* has a pattern whereby intensity of utilization changes during the summer. An analysis of variance between periods shows that *Lepus* had 3 levels of activity, high in P.1, moderate in P.2 and P.3, and very low in P.4. The change in intensity is not as important as the shift which occurred. In P.1, the number of crossings in S.9-13 were respectively: 31, 27, 48, 36, 46. In P.2; 28, 9, 10, 11, 17. In P.3; 29, 8, 8, 3, 11. In P.4; 3, 9, 0, 0, 0. These figures show a gradual shift from activity in the deep woods in the early summer toward the edge of the woods in the fall. Functionally, this spatial pattern relates well to the available food supply. In early summer, the masses of spring flowers still persist in the deep, dark woods. Full leaf does not occur until the first 2 weeks of June. As the ground vegetation dries up or dies back, *Lepus* move down toward the forest edge and, as will be seen later, into the open fields.

Further variance tests between periods showed that:

- 1) *Tamiasciurus* were more active in the deep woods during P.3 and 4 than they had been during P.1 and 2.
- 2) *Napaeozapus* was more active in all these woodland sections during P.2.
- 3) *Clethrionomys* was more active on the last 2 sections of the ecotone in P.2.
- 4) *Bonasa* was more active along the woods transect in P.3.
- 5) The invertebrates were more active on the woods transect in P.1 and 2 than in P.3 and 4.
- 6) *Bufo* had 3 levels of activity, P.1 and 2, P.3 and finally P.4 in decreasing order.
- 7) Birds had 3 levels, P.2, P.1, P.3 and 4 in decreasing order.

*Tamias* and *Tamiasciurus* may compete for food, therefore, these 2 species will be discussed later. In general, we would expect that all populations should be at their highest in the fall, before vegetation and

climate begin to affect a normal fall-winter mortality. In relation to the periods tested, one could expect increasing populations from P.1 to P.3, then possibly a decline in P.4. Similarly, if there are no spatial shifts or phenological changes in rates of activity, we could expect them to follow the same pattern as that of population growth and decline. For all species, except *Tamiasciurus* and *Bonasa*, activity was highest in P.2 or P.1 and 2. This indicates that, like *Lepus*, *Napaeozapus*, *Clethrionomys*, Invertebrates, *Bufo* and Birds utilize these woodland areas more intensely, while food at the ground level is still available, or at least before it gets too sparse, due to decomposition, drying out or germination. The insectivores, *Bufo* and birds follow the invertebrates. Unlike *Lepus*, the mechanisms involved are not known, because shifts to specific sections, or areas of utilization during any single period were not detected except for the invertebrates in P.3 (Fig. 11). Higher invertebrate activity along S.11 and 13 is probably due to myriapod activity.

It will be demonstrated later that there are phenological changes in activity rates that could produce such patterns, but spatial shifts into areas with different vegetation, climatic or edaphic conditions at other times are not to be discounted.

Along the woods transect, both *Tamias* and *Tamiasciurus* were more active in specific sections in P.3. *Tamias* was most active in S.11 while *Tamiasciurus* was twice as active in S.12 than in S.11 or 13 (32, 60, 29). The latter was not significant using an analysis of variance, which was not surprising, as the squirrel activity had been very sporadic (27 crossings to and from one tree on the first day). A chi-square test, however, showed that the 3 sections were not equal to a theoretical 1:1:1 ratio. The squirrels, or squirrel, had been observed carrying cones from a spruce tree while a chipmunk had been observed on many occasions carrying leaves to a hole within the transect. During this period of high total activity of the 2 species, the greater part of their activity had been in 2 discrete sections. In P.4 squirrel activity was again at random, and higher than in P.3 but the chipmunks were inactive.

It seems that the possibility of random encounter and "biofriction," if not competition, may be decreased by the timing of the concentration of activity toward specific patterns of utilization. *Tamias* and *Tamiasciurus* are often active at the same time, and both will eat the same food. The dominant seeds eaten by these 2 species in this area are those of the maple and the conifers. Conifers are sparse (Figs. 6 & 7), but more numerous along the edge of the transect in S.13. This arrangement, therefore, permits the isolation of conifer seed gathering activity. Even though S.12, P.1, is in an activity level of its own (Fig. 11), the total red squirrel activity during this period was very low (6, 15, 2 per section). During P.2 activity increased a little, but not significantly. In P.3 and 4 a significantly higher level was attained. Meanwhile *Tamias* activity followed the same pattern

as that of the squirrels in the first 3 periods but they were inactive by mid-October. In June and July, when activity was low, there were no preferential areas of utilization except *Tamiasciurus* S.12, P.1. This one minor deviation was caused by a squirrel, occasionally seen feeding on an old cache of cones within the transect. Otherwise feeding activity of both species consisted of scratching around for maple samaras and other unidentified food items, which produced a pattern of random utilization. In P.3 when activity of both species was at its peak an important segregation of the area of utilization occurred. *Tamias* was significantly more active.

*Bonasa* activity in the woods was significantly higher in P.3 than in P.1, 2 or 4. These, like squirrels and chipmunks, scratch around for tree seeds, and at this time of the year, maple seeds at least are numerous and ubiquitous. Unlike the preceding species, these three are far more dependent on the tree seed crop which is produced late in the season, and the high activity of P.3 in the upper woods is simply a spatial shift attuned to production.

The spatial utilization of the woodland area by all species is normally complete, and the rate of utilization in time seems closely related to food production. Very few, if any, shifts seem to arise due to interspecific biofriction.

#### SPATIAL UTILIZATION OF THE FIELDS

The three dominant primary consumers in the fields are the invertebrates, *Microtus* and the sparrows. Unfortunately, the birds were not broken down into granivores and insectivores, but by visual observation it was clear that any distinctly high levels of activity in specific sections would be due to white-throated or chipping sparrows.

The total activity of birds produce 3 levels of activity in the fields. The highest was found in S.2 and 5. The activity of S.2 can be attributed to white-throated sparrows, while that of S.5 to chipping sparrows. The differences of levels of total activity are essentially due to activity which occurred in P.1 and 2 (the nesting season). There was always bird activity around the bases of the trees (Fig. 6) and therefore the high activity in the 2 sections was due more to the density of trees adjacent to the track than to the production of food. The utilization of a potential resource was limited by cover, nesting or perching sites.

Invertebrates were consistently more active in S.3, 4 and 5 of the field and S.6 of the ecotone, with one exception (S.5, P.2). An ecotonal effect might explain this distribution. One-third of S.1 is approximately 50 ft from the forest edge, while  $\frac{1}{3}$  of S.2 runs parallel to the fence line which separates the field from the spruce savanna (Fig. 6). Higher activity in S.3, 4 and 5 does not relate to vegetation, because S.1, 2 and 3 supported sparser vegetation than S.5, and half of S.4 runs through a moss and *Rubus* patch. Otherwise the activity in S.4 might have been as high as that of S.6 on the ecotone.

Nonetheless invertebrate activity is consistently highest in the sections farthest away from the forest edge, and the amount of activity is not proportional to the amount of vegetation produced.

*Microtus* was most active in S.1, P.1, S.1, 3 and 4, P.2 and S.1 and 4, P.3. The mode of activity in the 4 periods shifted from S.1 to S.4 to S.1 to S.4 with the final result that the total activity in S.1 and S.4 was equal and formed the highest level. S.5 had the highest level in P.2 and P.4 and the second highest in P.1 and 3, but in total it ended with the same activity level as S.2, in which activity increased throughout the season. *Microtus*, like the invertebrates and the birds, do not utilize the field at random. Their areas or pockets of activity are not limited to, nor do they completely utilize, any specific form of vegetation. Microtopography might be an important factor in the establishment of runs and areas of highest activity, but this in itself would not explain the total activity distribution.

*Sorex* feed on invertebrates, but their spatial utilization in the fields depends on where *Microtus* form their runways. There were 10 major *Microtus* runways in the field (major runway—more than 10 crossings at 1 point per period). At other points there were never more than 2 crossings per period. Allowing 3 ft in width for each passage, the length of track normally utilized by *Microtus* and *Sorex* constituted less than 4% of the total track length, or 1 crossing per 84 ft of track length. 82% of the *Microtus* crossings and 83% of the *Sorex* crossings were at major runways. The number of major runways per section were 2, 1, 0, 4, 3. If the number of crossings per section was related to the number of runways per section then we should consistently have had 5 activity levels. This was not true. Some runways were more active than others. *Microtus* and *Sorex* activity levels were always lowest in S.3 where major runways were absent. The highest *Sorex* activity level in the field, for each period was in the section which combined the highest number of *Microtus* runways with the highest invertebrate activity level, except during P.1.

The mode of *Microtus* activity on the ecotone always occurred in S.6. *Sorex* activity is highest inside, or closest to, the woods along both the field and ecotone transects in the spring. Along the ecotone the mode of activity shifted slowly away from the forest edge toward the area with the best combination of food and cover (i.e. invertebrates and *Microtus* runways) returning suddenly to the forest edge in the fall.

*Thamnophis* and *Storeria* combined were always most active along S.5. In P.4, S.2 was as active as S.5, and total activity over the summer was equal in S.2 and 5. Although invertebrate activity was low in S.5 during P.2, snakes established themselves there at that time and remained until the end of the season. It would seem that the preferential area of utilization could have been chosen for some reason other than food supply, most probably climatic conditions.

S.5 is on the knoll, therefore the nocturnal temperatures are slightly warmer and more basking sites are available than elsewhere. S.6 (ecotone), where invertebrate activity always dominated, was a poor area for snake activity. If some of the *Thamnophis* migrate as postulated in the description of woodland activity, the high activity along S.2, P.4 would be expected because this area is closest to the woods. High activity in S.5, P.4 might also indicate that negative geotaxis is the basic homing mechanism utilized in finding suitable hibernacula.

*Rana pipiens* were the dominant field species while *R. clamitans* were the dominant species on the ecotone. This separation was probably related to physical factors and not food supply. *Bufo* was the only species which had 1 level of activity in the field transect and another, higher level, on the ecotone. In the first 2 periods, the range of activity in the field was 16-59, whereas along the ecotone it was 193-498. In P.3 the field range was 44-61, while that of the ecotone was 4-114, and differences between sections were not significant. S.6 of the ecotone had the highest activity of all 13 sections (woods included). It is evident that food was not the limiting factor for toad distribution, as invertebrate activity was as high in S.3, 4 and 5 of the field as S.6 of the ecotone. The limiting factor for *Bufo* in spatial utilization seems to be soil moisture. The ecotone transect runs through a kettlehole, which is often damper than the field, but just about as cool since it is a frost pocket. After prolonged periods of drought, and usually towards the end of August, this kettlehole dries out considerably, but the soil still remains damp. As a result *Bufo* can profit by an abundant supply of insects in S.6.

In summary, the distribution of activity of field species is more often limited by physical than by biotic factors. There seems to be a lack of "phenological pursuit" (i.e. species utilizing an area when phenological events make food items available). It is strongly suspected that this situation is abnormal, and a result of the peculiar vegetation structure. In the mixed forest zones there are no natural vegetation structures comparable to an old field community such as this. In other words, unlike the woodland community described in the previous sections, this community has not evolved to a point where it can make the best use of the productivity available.

CHANGES IN THE DAILY PEAK OF ACTIVITY THROUGH TIME

If high activity of one species inhibits that of its competitors or predators, then peak periods of activity in the community should not overlap.

The data presented are from 1963 when activity during rain was not recorded. The weather during the 4 periods was a sequence of sunny days ending in cloudy weather. Only complete activity days for either nocturnal or diurnal animals were used.

During 1962 and 1963 continuous climatological data were recorded on film. The photographic system was a flash-synchronized Bolex H 16, with wide angle lens, activated by a home-made time-lapse clock and

solenoid mechanism. A picture was taken every hour. The data collected were; barometric pressure (Taylor naval barometer), wind velocity and direction (Taylor instruments), relative humidity (Serdex membrane hygrometer) and 5 temperatures (Taylor indoor-outdoor thermometers). Thermometers recorded temperatures 1 inch below the soil in the sun and in the shade, 1 inch above the soil in the sun and shade, and 6 inches above the soil in the shade. General daily records such as precipitation, cloud cover and dew were recorded separately.

In this study a weather system is assumed to start and end with the clearing weather of 2 consecutive cold fronts. The lowest minimum temperature occurs on the first night, and highest maximum should occur on the last sunny afternoon of each weather system. Conversely, the lowest maximum will occur during the first afternoon, while the highest maximum will occur on the night preceding or during frontal activity. Maximum temperatures above 95° F, and minimum temperatures well below 50° F, which are often threshold temperatures (see sections on the effect of climate) occurred while this data was gathered, but when they did they were normal for the time of year involved. In this section only changes in time of peak activity throughout the summer in relation to the number of active forms in the different habitats are compared.

The activity of *Lepus* and Aves in the woods in June (Fig. 13) was calculated by taking half of the activity of the sum of an even 2-hr interval (e.g., if 21 crossings had occurred between 22.00 and 24.00 hours and 41 crossings between 23.00 and 01.00 hours, the 23.00 and 24.00 hour interval would have  $(0.5 \times 2) + (0.5 \times 41) = 31$  crossings). The *Lepus* curve is a typical unimodal peaked curve. Animals having over 30% of their daily activity in a 1-hr interval usually have a unimodal curve. In flattened curves, such as that of Aves, activity for a 1-hr interval never rises above 15%. Peak activity was 9.4%

% OF TOTAL ACTIVITY ON 24 HOUR TIME SCALE

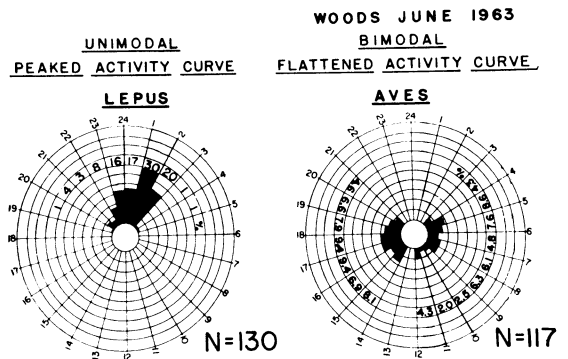


FIG. 13. Examples of 2 general types of diel activity, *Lepus* unimodal peaked activity and Aves bimodal flattened activity. The figures in the arcs are percent of total activity. N is the number of crossings.

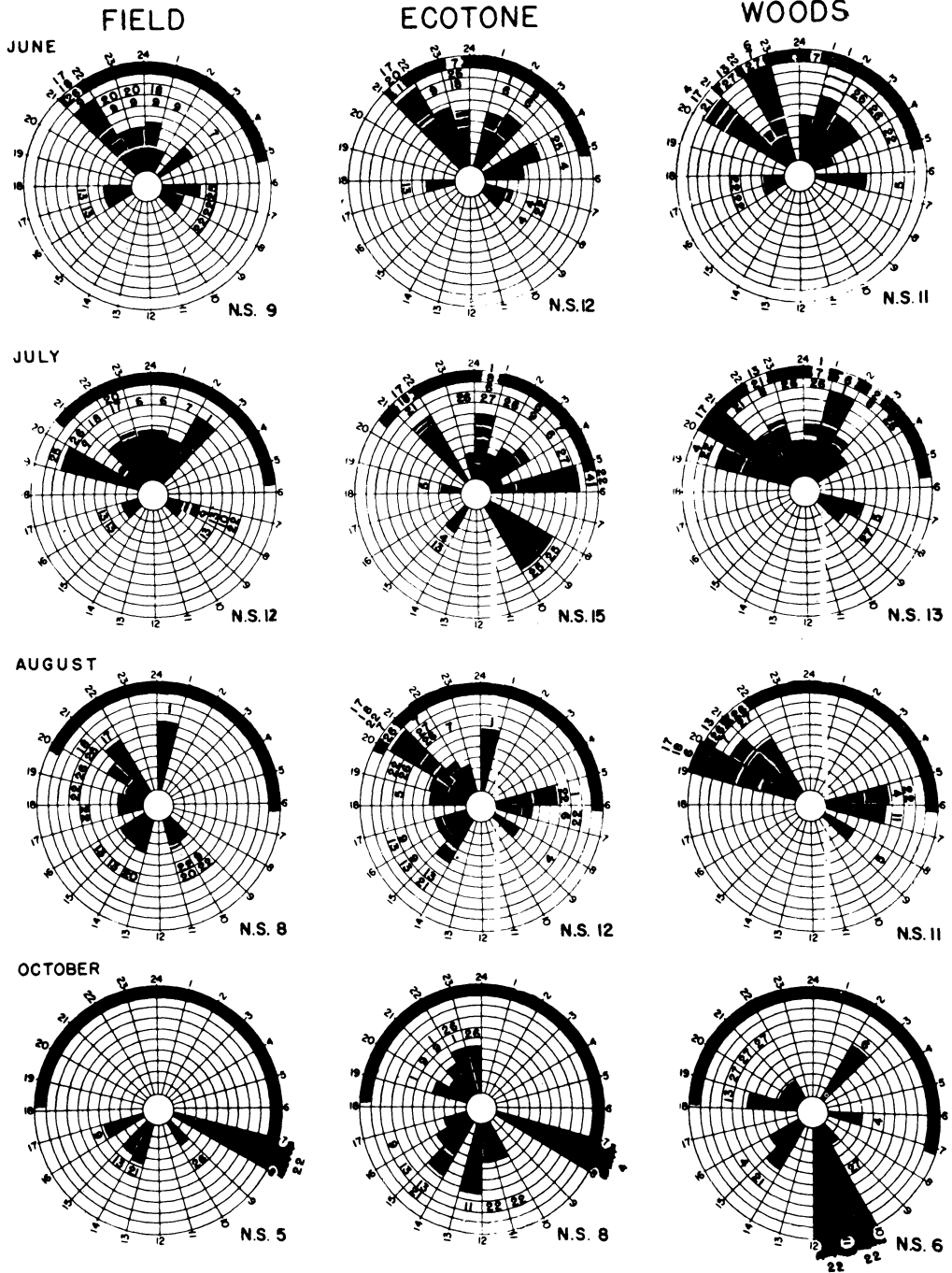


FIG. 14. A comparison of the time of peak activity (the mode of circadian activity) of all forms over the 4 periods. Each polar graph is divided into 24 hr periods. NS is the number of species which crossed the

but, for the sake of clarity, those intervals which fall within 10% of the highest peak are included as peak hours. Thus, if an animal has 2 or more reasonably important peaks of activity, this will show as bimodal (e.g. Fig. 14, *Sorex* and birds, October ecotone), or multimodal (e.g. Fig. 14, *Microtus*, October ecotone) activity.

Fig. 14 shows the peaks of activity of all species which crossed the respective tracks more than 3 times per day in each period. This arbitrary cutoff was made specifically to leave out any animals which might walk only through the area to or from a feeding area, and those whose numbers were so low at any one time that their apparent peak of activity might be unreliable.

In June, sundown and sunrise occur at 21.00 and 5.00 hours respectively, whereas they occur at 18.00 and 7.00 hours in October. This represents an increase of 5 nocturnal hours between P.1 and P.4 (Fig. 5 and black bands Fig. 14). June nights are shortest but, due to the annual temperature lag, they are not warmest. July has longer nights, but minimum temperatures are higher. From the end of August to mid-October the nights become longer and progressively colder to a point where there are freezing temperatures every clear night. The coldest October temperature recorded was 8° F in the field.

The relation between length of night and temperature, with respect to the time of peak activity in each form, is most strongly reflected in the dispersion of field activity modes. In June, the activity peaks of nocturnal species are compressed into a short period right after dusk. In July, when nocturnal temperatures are warmer, nocturnal modes are more evenly spread over the night. By October, *Microtus*, snakes, and *Sorex*, all arrhythmic, shift from nocturnal to diurnal activity. The strictly nocturnal species revert to early-evening activity peaks in August and, finally, become inactive or almost inactive in October. For diurnal forms, which are usually most active close to dawn and dusk in the early part of the season, activity modes shift closer to midday.

In the woods, the forest canopy and the higher elevation relative to the field produces slower and less marked declines in nocturnal temperature. As a result there is a wide dispersion of modes in both June and July. In late August and early September many trees begin to shed their leaves, and the thermal insulation of the canopy decreases. This compresses the modes of nocturnal activity into a relatively short period. In October, when all the leaves have fallen, only a few nocturnal species remain active. The low light intensity in the woods is a second factor which permits better segregation of modes. Nocturnal activity begins almost 1 hr earlier in the woods than in the field (Fig. 14, *Bufo* (No. 17) in both fields and woods in each period).

The ecotone presents a unique situation in which

the animals seem to take advantage of alternatives. The wooded area of the ecotone is 2-3° F cooler than the upper woods, but the field sections are 5-10° F warmer than the lower fields during the nights of stable weather. This, therefore, decreases the restrictions imposed by temperatures in the field without affecting the activity along the sections in the woods.

The greatest segregation of modes occurred when vertebrate activity was highest (10,547 crossings in July). In August, during the period of high compression of modes, there were only 5,046 crossings compared with 7,201 in June. In October, when many species had already become inactive, there were only the equivalent of 1,156 crossings for a 7-day period.

During each period, the greater the number of nocturnal species the greater the number of hours during which peaks occurred (July; 8.3 species in 7.3 hr, June; 7 species in 6 hr, August; 5.3 species in 4 hr, October; 1.6 species in 2.3 hr). The best dispersion of peak hours in relation to the length of night occurred in July when all species peaked during 81% of the night hours. In other periods the relation was; June 75%, August 37%, October 15%.

In summary, under seasonal conditions without precipitation, the time of peak activity for each species tends to change throughout the summer. Diel activity peaks in the community tend to segregate when minimum temperatures are highest, and they contract toward the warmest part of the day or night as temperatures decrease. Diurnal animals tend to have activity peaks at dawn and dusk during long days, but toward mid-day as the days shorten. Arrhythmic species shift their peaks of activity from night to day as nocturnal temperatures cool. When nocturnal temperatures consistently compress activity into a few hours after dusk, non-hibernating mammals and amphibians become inactive. Finally, the best dispersions of activity peaks occur when total activity is highest, and there is a positive relation between the number of active nocturnal species and the number of hours during which peaks occur.

#### CONTINUOUS TRACKING

During the summer and fall of 1964 data were collected on the covered ecotone track every 2 hr from June 1st to September 10th and at least twice a day up to November 15th. More detailed meteorological data than were taken by photography in 1962-63 were recorded by observers concurrently with the continuous tracking data. When tracking was done less frequently due to my absence, my wife took meteorological readings at predetermined hours between tracking sessions.

#### CHANGES AND ADDITIONS IN METEOROLOGICAL INSTRUMENTATION

Normal minor changes and replacements of instrumentation were made and the Taylor windspeed and

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track more than 3 times per day, and each mode is expressed as the percentage of total activity for the period. Each division equals 5%. The numbers in the polar graphs refer to the species listed at the bottom of the figure. The black band around the top outside each graph indicates darkness.

direction system was changed for a Nassau windmaster, an instrument with a lower starting speed. Rainfall was measured in an 8-inch rain and snow gauge, and Duvdevani type dew gauges were put into use. A 50 junction Eppley pyrliometer linked to a chart recorder was also added to the instrumentation. Data from the latter is not shown, however, it was used to establish, with much more precision, factors such as type and time of cloud cover, sunrise and sunset, and as a control on our meteorological data.

#### MISSING DATA

Three partial breaks in the data occurred over the 165 day period, 2 quite close to one another in July and 1 in October.

Shortly after midnight on July 19th, 0.93 inches of rain fell in less than 2 hr. The rain, accompanied by 15-20 mph winds from the northwest, obliterated parts of the track and eroded the side of the track from the 475 ft to the 600 ft mark. Complete counts of frog, toad and mouse activity became impossible, but birds and larger mammals, including chipmunks, registered throughout the next day. By dusk of the same day the track was completely in operation.

Again, shortly before noon July 29th, 0.80 inches of rain fell within 20 min with the same results as the storm of the 19th. Full operation resumed July 30th at 8.00 hours.

From October 5th to 7th a third lapse was caused by a relatively light but continuous oblique rainfall. 0.13 inches of rain fell on the 5th and 0.18 inches of snow and rain fell on the 6th and 7th. The track was operable by dusk of the 7th and the first reading after the storm was taken before dawn of the 8th.

Three inches of drifting snow on November 15th ended all hope of continuing the tracking session. By mid-November, insolation is so low (Fig. 5) that evaporation at the sand surface is practically non-existent.

Equivalent amounts of rain or wet snow without driving winds, did not affect the continuity of the tracking session. On October 3rd, 0.96 inches of rain in a 5-hr period, and 0.48 inches of snow and rain on the night of October 29th did not affect tracking conditions.

#### TABULATION

The number of crossings for each species during each tracking interval was superimposed on meteorological tables covering periods of 16 days (Fig. 15, A & B). Fig. 16 is the key to these figures. The data in this synoptic form produced the first good indication of the effect of climate on animal activity.

The 1963 work compared activity during 4 discrete periods of normal clear weather in different seasons. Considerable variation in activity occurred from 1 period to the next. This suggested that phenological events influence activity to a greater extent than climate.

### PHENOLOGY OF ACTIVITY

A series of histograms (Fig. 17, A—F) represents daily activity of each species or group over the entire study period. These figures demonstrate the differences in constancy of daily activity between species and help interpret periodic variations.

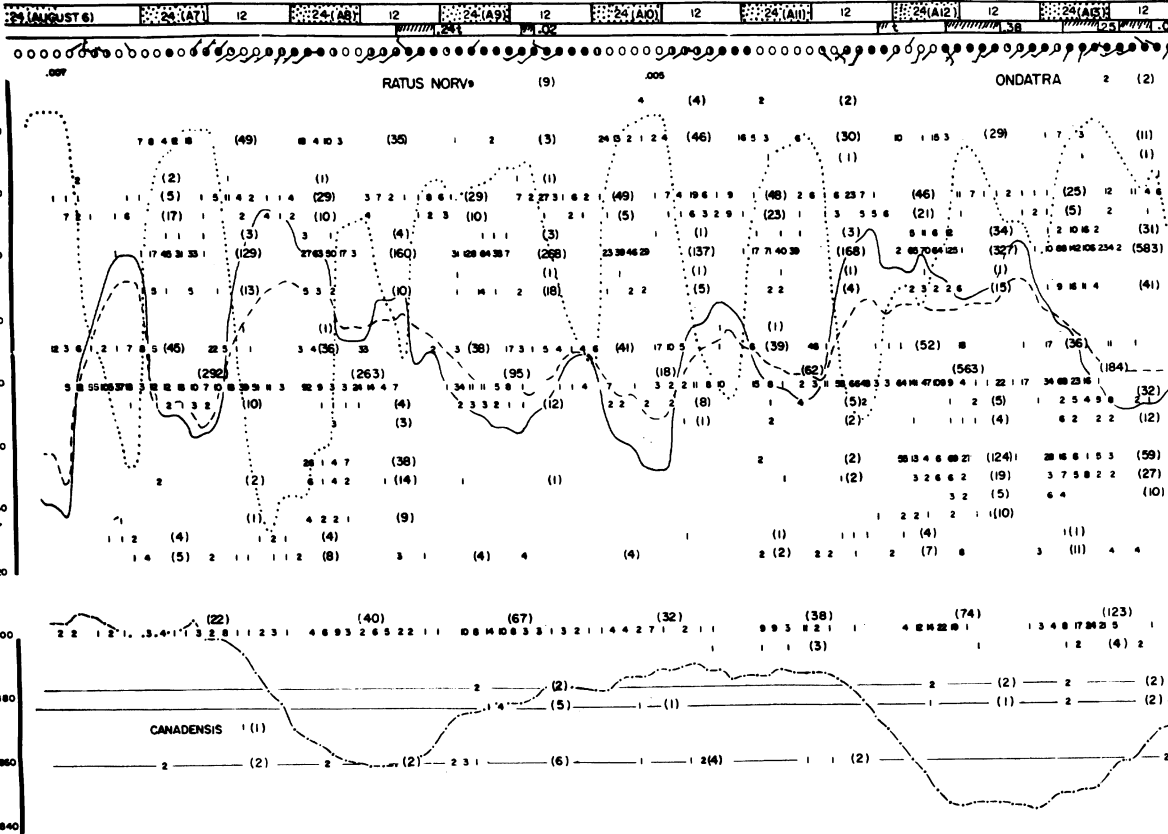
#### ONSET OF ACTIVITY

Snow depth in February and March was practically constant at 26 inches in the open fields. By April 15th snow in the field and on the south slopes had melted, but patches remained on the forested flats, such as the woods sections of the ecotone and woods transects. A *Thamnophis* was observed coming out of hibernation on the south slope above the woods transect and one active chipmunk was seen in a rock pile south of the creek. Frozen soil 1 inch below the surface was common in the woods. *Hyla crucifer* choruses had begun on May 6th, but on May 8th a female *Hyla* was unearthed in the woods. Chipmunks were active at this time. Tracking was carried out on May 15th until May 19th, but data are not presented because of the long lapse between May 19th and June 1st. Activity of all species was low except that of *Lepus* and the invertebrates, which were as high as during the first 16 days of June. June 1st did not represent the onset of activity, but we can assume that there was a gradual increase of activity up to the level attained by the first week of June. The activity of birds and hibernating mammals probably started around April 15th and that of reptiles and amphibians around May 1st. These general observations have subsequently been substantiated by data gathered in May of 1965-67.

#### A THEORETICAL APPROACH TO THE INFLUENCE OF POPULATION GROWTH ON ACTIVITY

Two characteristics of populations in boreal regions are; 1) Populations are lowest in spring when mating begins and, 2) Breeding seasons are usually well defined. These characteristics could have a subtle effect on the phenology of summer activity. With an abrupt onset of breeding we can expect a sharp rise in activity as new recruits disperse, but subsequent litters will not have the same effect. The initial rise in the rate of activity each season will be influenced by litter size (Fig. 18). If, for instance, first litters average 4-5 young, the population activity should increase by 225% when the new recruits disperse. The dispersion of the second and third litters would only increase activity by 68 and 41% respectively. Furthermore, even though there is an increase of 250% due to the first litter of animals having litter sizes of 1-6, activity increases due to subsequent litters of the same size range decreases to 42, 18, 10 and 6% respectively. This discussion appears here because the phenological histograms show periods of increased activity, which might be misconstrued as resulting from increased population size. After the first litter, mean activity should never double, and yet there are many examples in which both abnormal increases and decreases in

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PRECIPITATION



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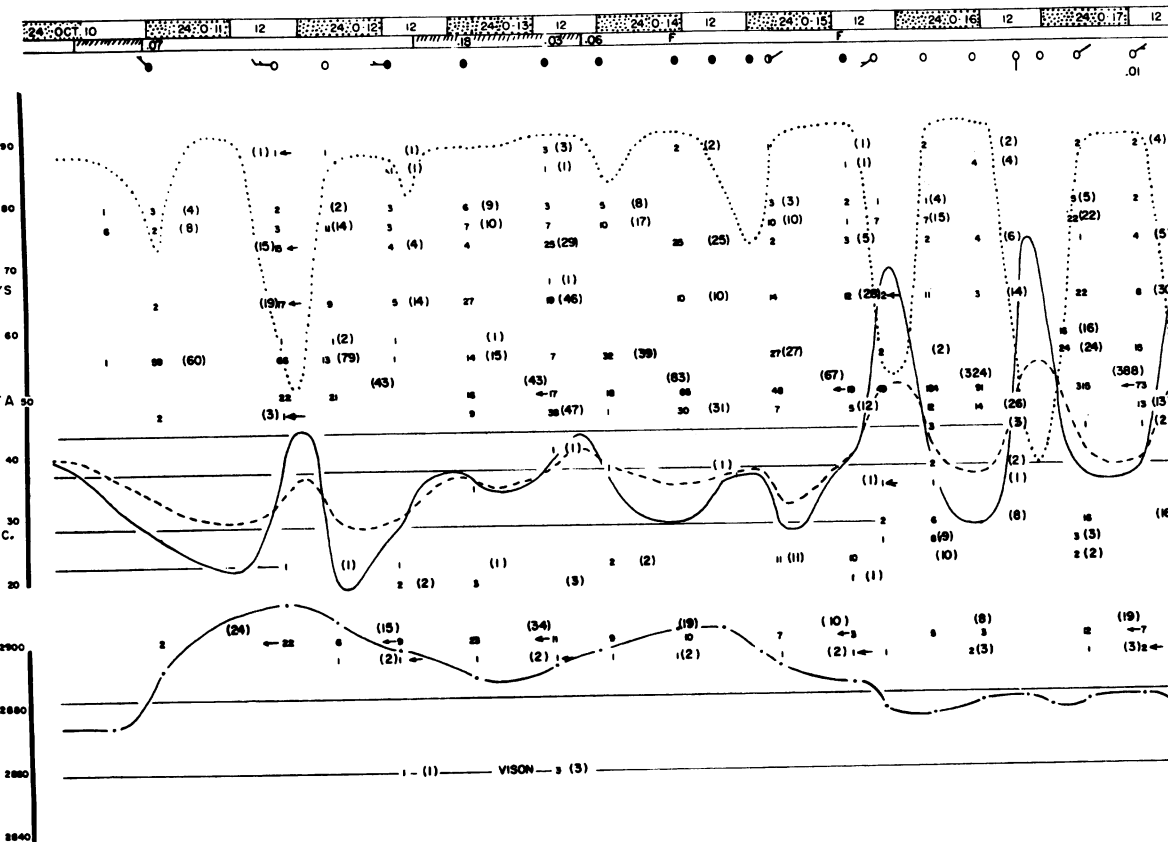
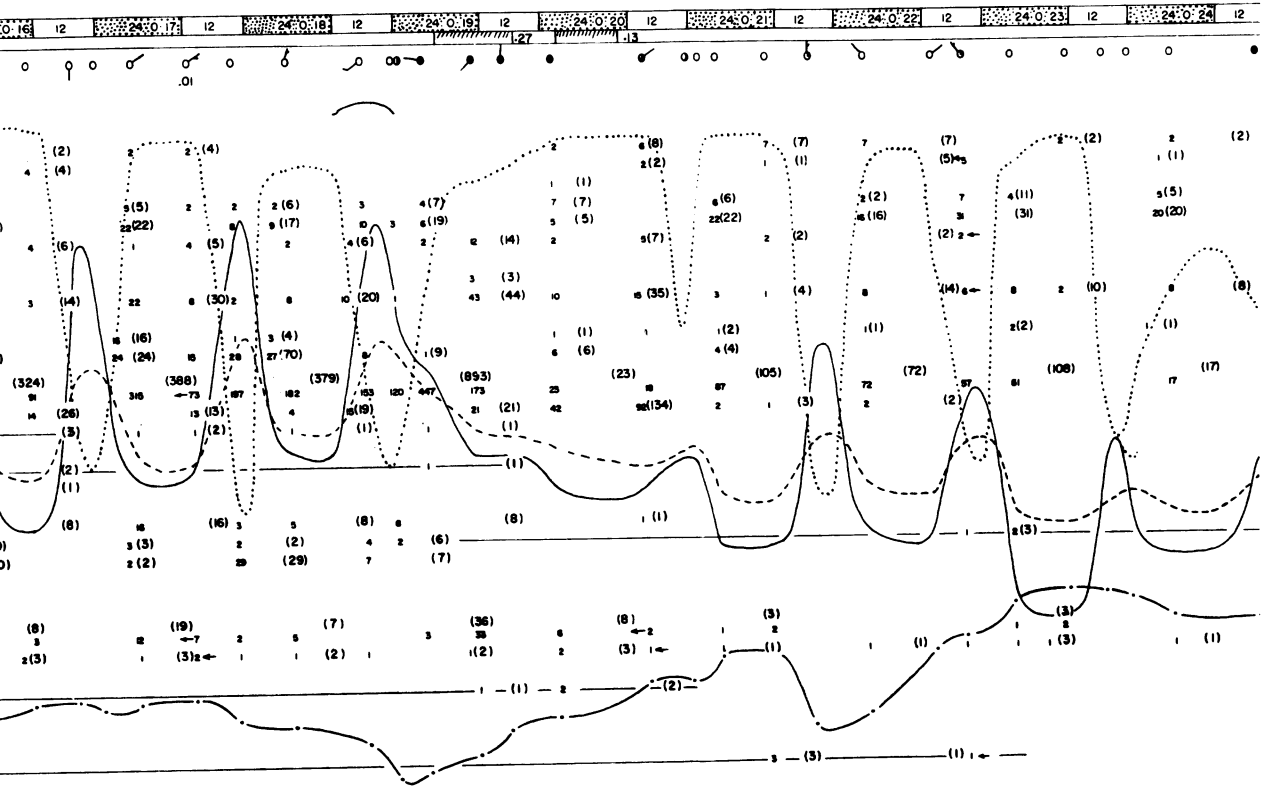
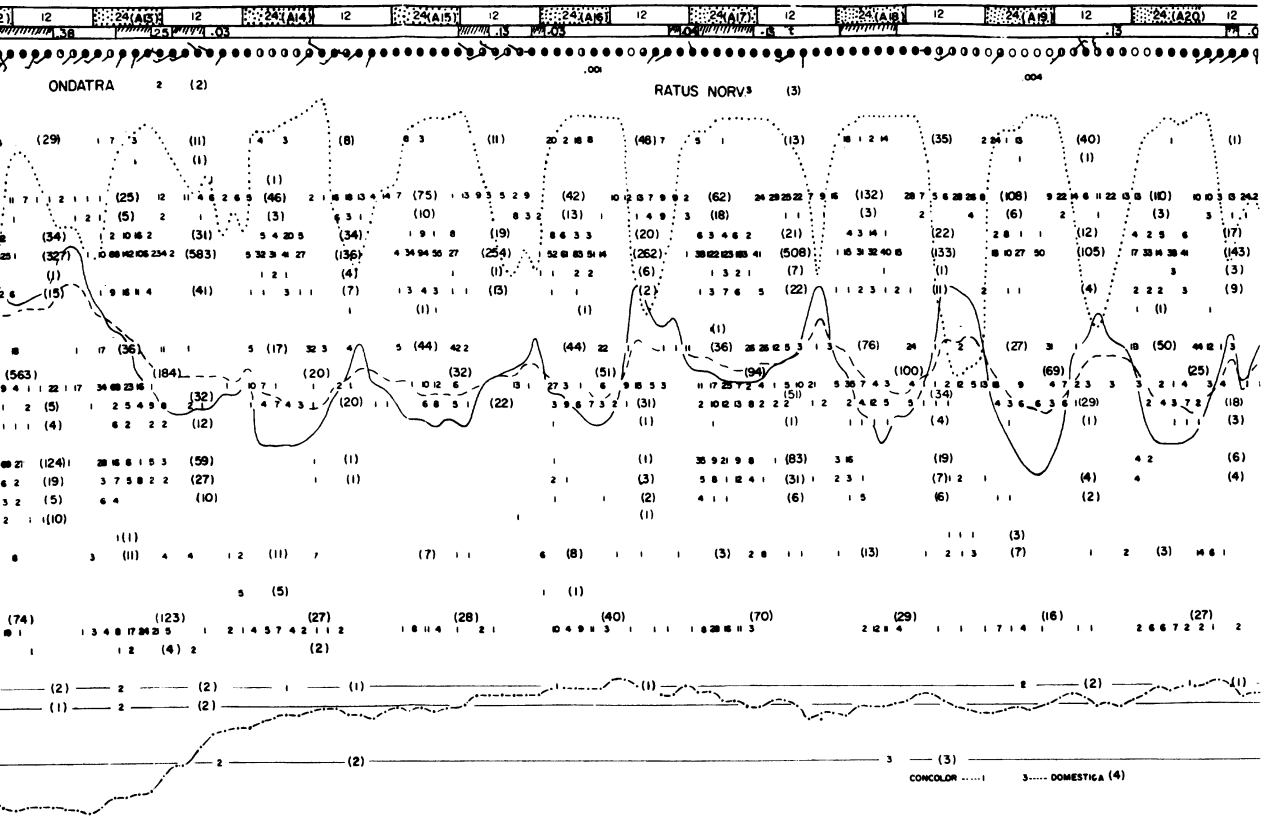


FIG. 15 A & B. 56 days of compiled data on activity charts which show at a glance some of the relations between community activity and climate. The key to the figure is Fig. 16. The June series depicts the variations in activity found during fairly normal weather. The July series shows the effect of a stationary front on activity. Under such climatic conditions an analysis of the effect of climate on activity can be made

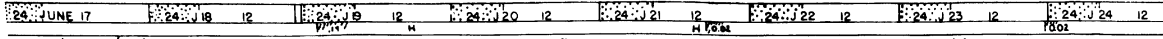
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shows  
effect



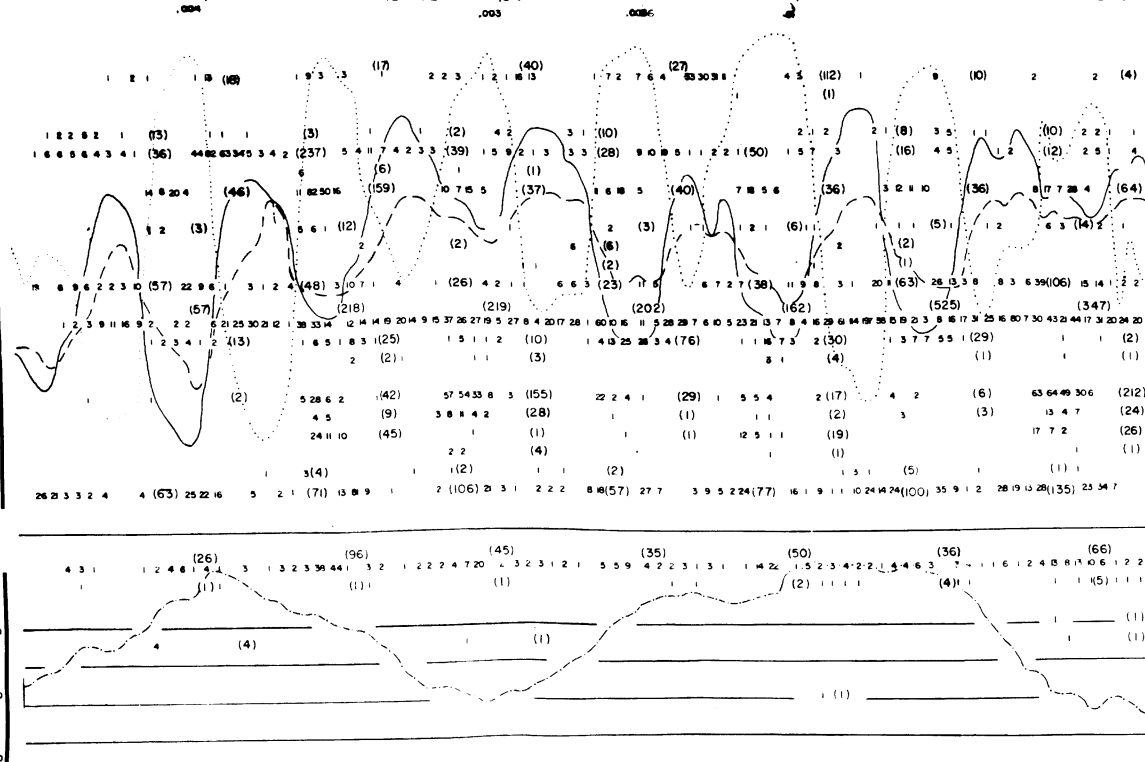


more easily than is possible under conditions such as those depicted in the other 3 charts. In August each weather system produces several consecutive nights with temperatures under the amphibian threshold. This shows in the charts as large blank areas. The October graph, an example of fall activity, also shows the effect of an Indian summer. In October the track was read only a few times a day (see Text).

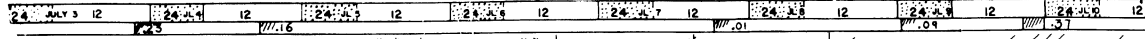
DATE & TIME  
PRECIPITATION



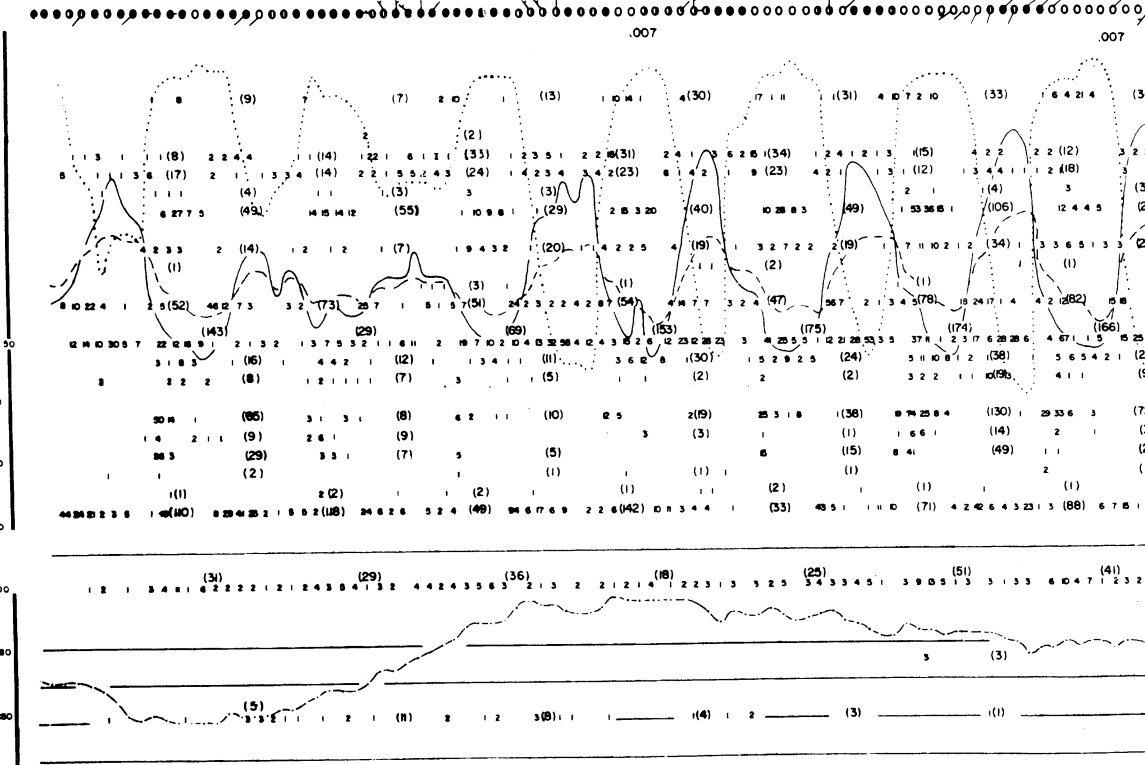
ERETHIZON  
ODOCOILEUS  
LEPUS  
GLAUCOMYS  
SCIURUS  
TAMIASCIURUS  
TAMIAS  
PEROMYSCUS  
ZAPODIDAE  
CLETHRIONOMYS  
MICROTUS  
MARMOTA  
BONASA  
FRINGILLIDAE  
INVERTEBRATA  
ANNELIDA  
MOLLUSCA  
NEMATODA  
BUFONIDAE  
RANIDAE  
URODELA  
STORERIA ETC.  
THAMNOPHIS  
AVES GEN.  
PHILOHELA  
PICIDAE  
CORVIDAE  
SORICIDAE  
TALPIDAE  
MEPHITIS  
PROCYON  
LYNX  
VULPES  
MUSTELA  
FELIS  
URSUS

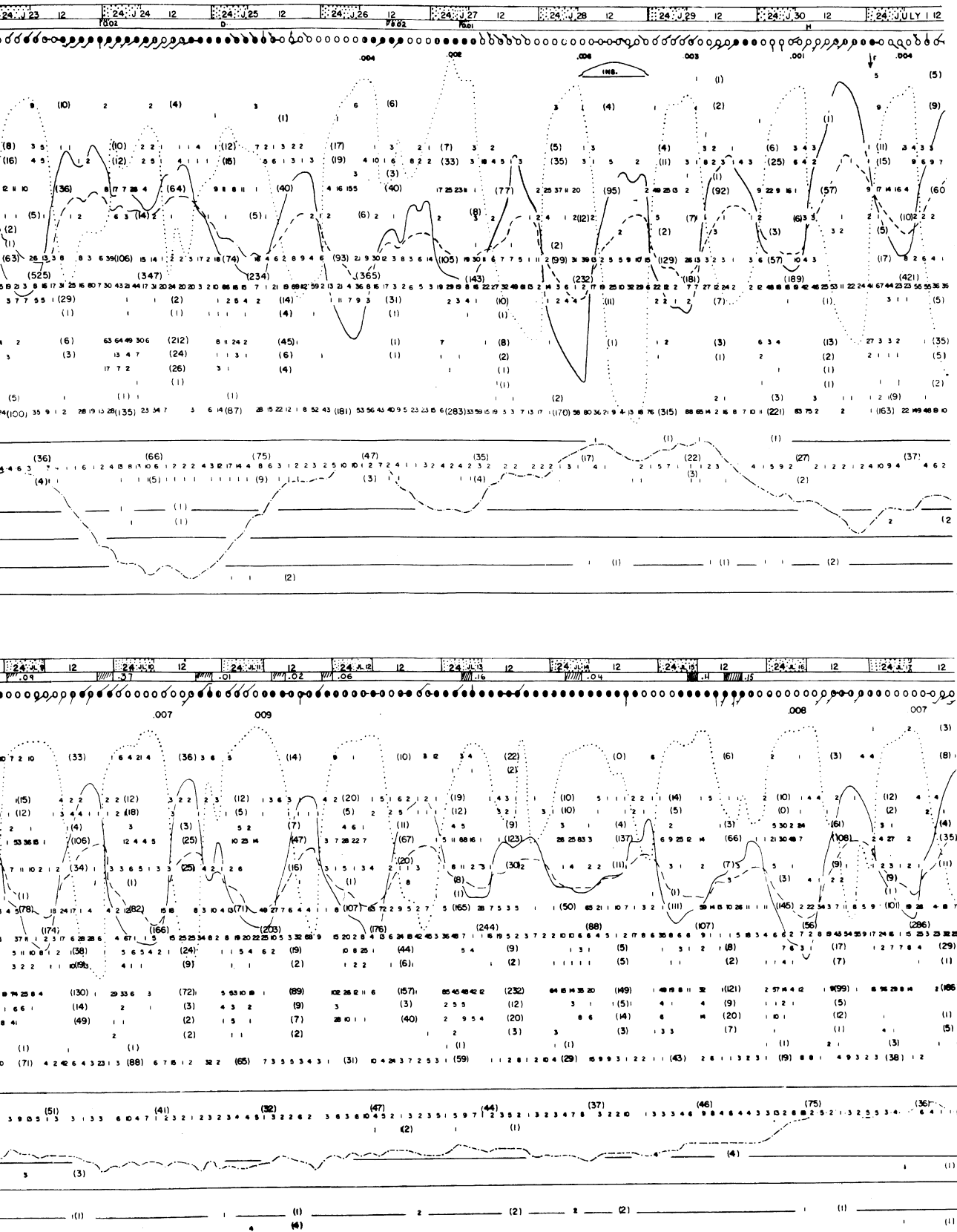


DATE & TIME  
PRECIPITATION



ERETHIZON  
ODOCOILEUS  
LEPUS  
GLAUCOMYS  
SCIURUS  
TAMIASCIURUS  
TAMIAS  
PEROMYSCUS  
ZAPODIDAE  
CLETHRIONOMYS  
MICROTUS  
MARMOTA  
BONASA  
FRINGILLIDAE  
INVERTEBRATA  
ANNELIDA  
MOLLUSCA  
NEMATODA  
BUFONIDAE  
RANIDAE  
URODELA  
STORERIA ETC.  
THAMNOPHIS  
AVES GEN.  
PHILOHELA  
PICIDAE  
CORVIDAE  
SORICIDAE  
TALPIDAE  
MEPHITIS  
PROCYON  
LYNX  
VULPES  
MUSTELA  
FELIS  
URSUS





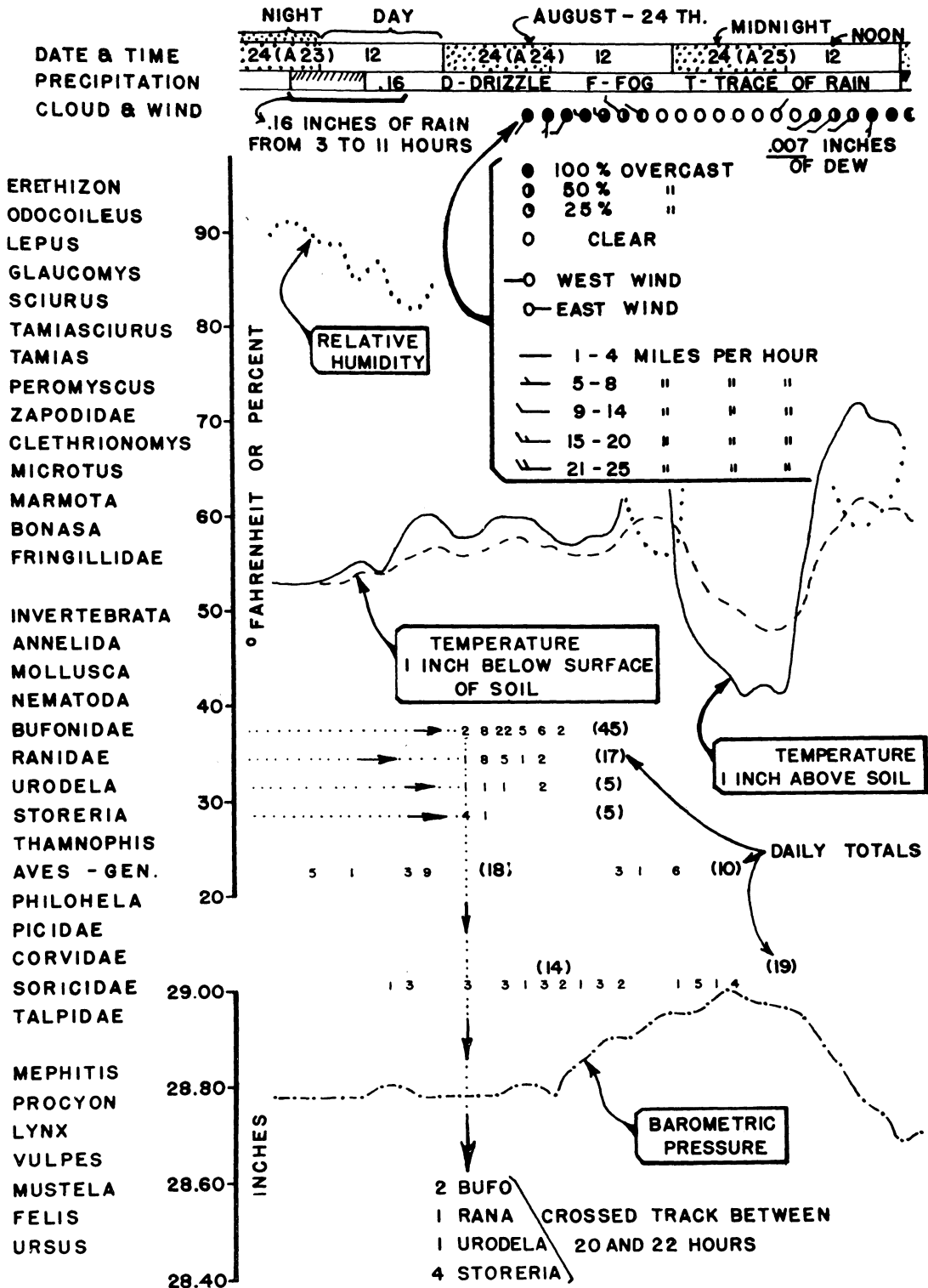


FIG. 16. Generalized key to Figs. 15 A & B. Examples of how to read activity data; Bufonidae (in center of species column) crossed the track twice between 20.00 and 22.00 hr in the subsequent 2 hr intervals (read across). They crossed 8, 22, 5, 6, 2, 0 times etc., or a total of 45 times between 12 hr August 23 and 12 hr August 24. In the interval 20.00-22.00 hr there were also 1 Rana, 1 Urodela, 4 Storeria, 3 Soricidae (these are lined up vertically). Daily totals for nocturnal animals are at 12.00 hrs. (Bufo) for diurnal animals at 24.00 hr (Aves gen.) and for arrhythmic animals at 6.00 hr (Soricidae).

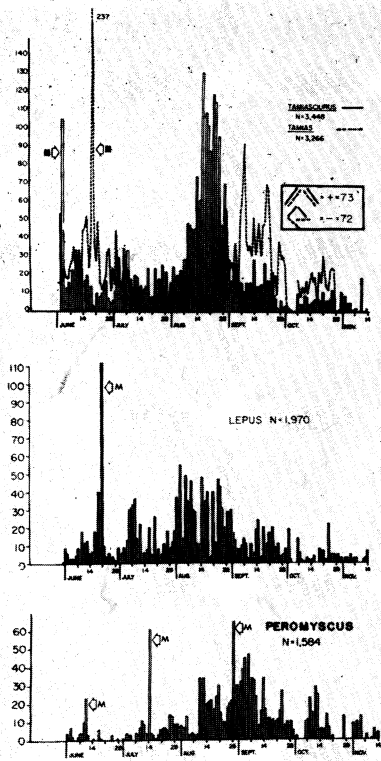


FIG. 17 A

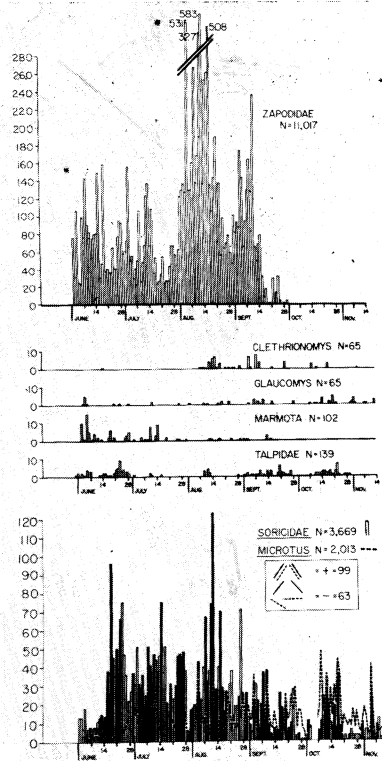


FIG. 17 B

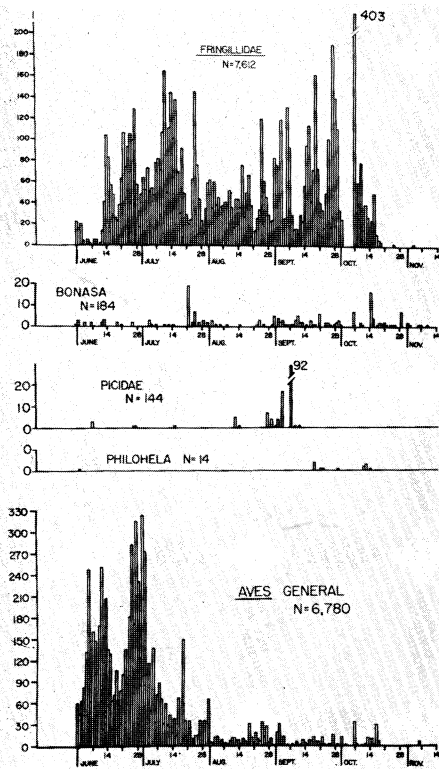


FIG. 17 C

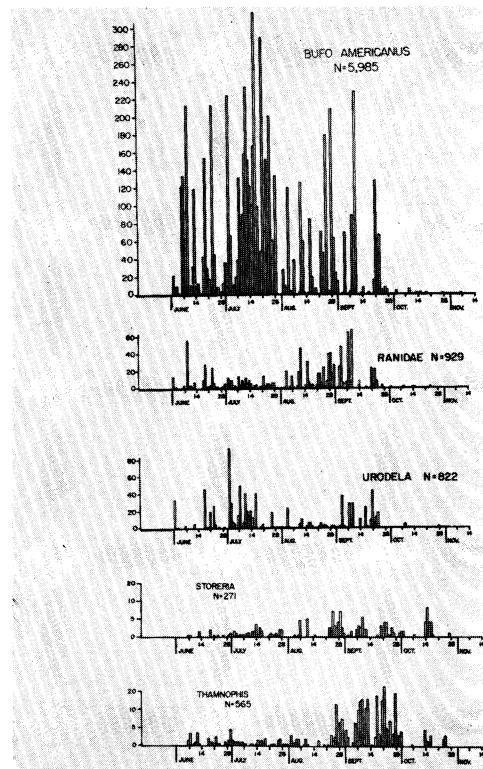


FIG. 17 D

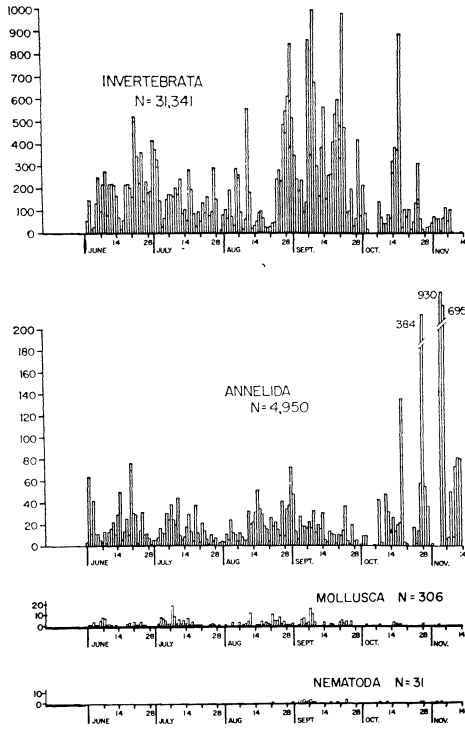


FIG. 17 E

activity occurred. Although activity seemed to increase rather slowly in the spring, many different patterns occurred in the fall towards the end of the active season. Activity of non-hibernating forms such as *Tamiasciurus*, *Lepus*, *Peromyscus*, *Sorex* and *Microtus* tapered off in the fall, whereas *Tamias*, Zapodidae, anurans, urodels, reptiles, invertebrates, annelids and birds had high peaks of activity just before the end of their active period. Species which had last minute flutters of activity were those which change locality for overwintering or hibernation.

CESSATION OF ACTIVITY

By September 15th, the last *Marmota* and *Picidae* activity had been recorded. Because of the normally small numbers of *Marmota* crossings, this date might not be representative; however, activity away from the burrows had ceased. A large group of flickers fed in the area on September 8th and this probably represented their last large migratory flight out of the area. This increased activity was not correlated with any particular weather system or strong winds.

By the end of September many species had become inactive. Among these were all the amphibians which had their last major activity period between September 21st and 25th. Temperatures on these nights were in the fifties but after this date temperature at sundown was rarely over 50° F. Zapodidae activity slowly decreased from mid-September to the end of the

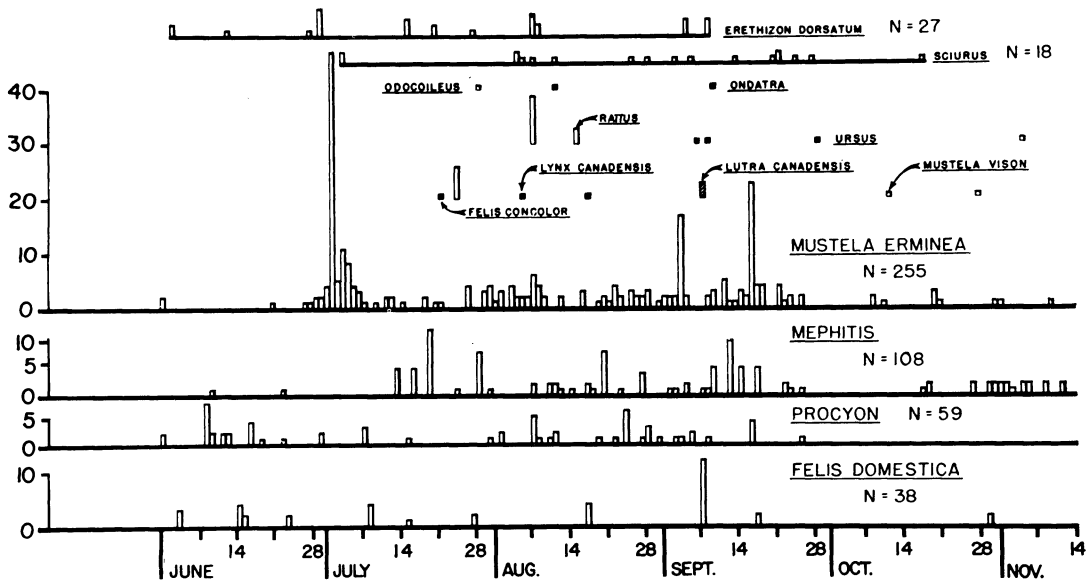


FIG. 17 F

FIG. 17. Phenology of activity of the forms found in the community. The ordinate represents the number of crossings, the abscissa represents the date. M = mating peak, N = number in sample. Boxed legends indicate the number of times both species increased or decreased their activity simultaneously (+), or the 2 species did not change their rates of activity in the same way from that of the preceding day (-). Fig. 17 A Herbivorous mammals. Fig. 17 B. Herbivorous mammals continued and insectivorous mammals. Fig. 17 C. Birds. Fig. 17 D. Amphibians and reptiles. Fig. 17 E. Invertebrates. Fig. 17 F. Carnivores and incidental mammals.

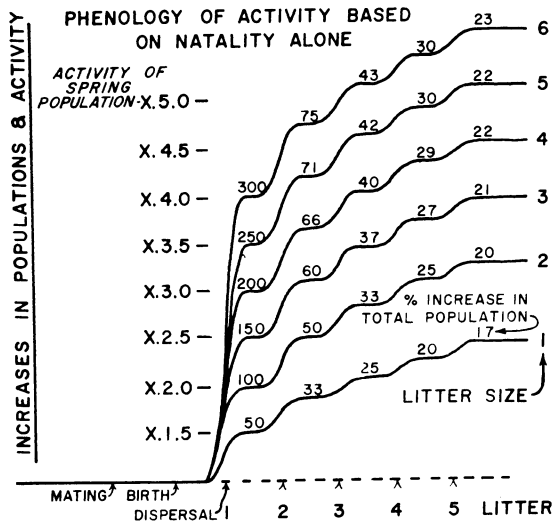


FIG. 18. A theoretical model showing to what extent mean activity should increase due to the dispersal of new recruits in populations having 1-5 litters and 1-6 young per litter.

month with 2 minor increases which were synchronous with the last 2 anuran peaks. *Procyon* was never observed after September 25th.

Between the middle and end of October the last flights of migrating birds occurred and the snakes ended their active period. Snake activity in the fall was relatively high when afternoon temperatures reached into the sixties. This rarely happens in the area after the first of November. *Tamias* activity ended abruptly on November 1st. This was surprising as their activity had been increasing slowly after the stormy period of October 5th, 6th and 7th. Possibly hibernation had not completely set in when the dens were damaged by rain, and this damage might have reinitiated a period of food gathering and/or nest repair.

The only other hibernating mammal dealt with was *Mephitis* and it is assumed that their activity stopped around mid-November. *Mephitis* tracks have never been seen after permanent snow covers the area and this usually occurs around the third week of November.

#### HYPERACTIVITY

Hyperactivity, excessive activity on a single day, produces sharp peaks of activity twice as high as, and sometimes several times higher than, activity on the preceding or following days.

Two extremes in hyperactivity are *Tamiasciurus*, with 1 peak, and *Bufo* with more than 15. It will be shown that these peaks may be due to different factors.

#### INTERPRETATION OF PHENOLOGICAL HISTOGRAMS MAMMALIAN, HERBIVORES AND INSECTIVORES (FIG. 17 A & B)

*Tamiasciurus*, *Tamias*, *Peromyscus*, Talpidae, Sori-

cidae and *Microtus* were all activated by the storm conditions of October 5, 6 and 7. This was probably due to stores or burrow damage, and not directly correlated with the climate because the result was an increased activity period and not a hyperactive peak.

All the histograms show periods in which activity as a whole is higher (e.g. *Tamiasciurus* August 10-30, *Tamias* August 5-September 30, *Lepus* August, Zapodidae August 1 to September 14 etc.). These active periods represent the growth, storage, and winter nest building activity.

Prior to growth and storage low activity is interspersed with days of hyperactivity. The lows correspond well to periods of gestation and the hyperactive peaks, at least for *Tamiasciurus*, *Tamias* and *Lepus*, result from mating activity. Although *Peromyscus* mating was not observed, it would seem from the time elapsed between hyperactive peaks, that these arose from mating activity. Assuming that the 3 first species had successfully mated at the first opportunity, dates of the mating peaks shown in the histograms would represent sexual activity related to the conception of the second litter. The time lapse between *Tamiasciurus* and *Tamias* curves and the date for *Tamias*' second conception (June 20) correlates well with the onset of activity. Why did the sciurid mating peaks occur on single days? On the date of the *Tamias* mating peak, activity was seen all along about a quarter of a mile of forest edge. It seemed that all the chipmunks had chain-reacted into a frenzy and were absolutely unaware of danger. The *Lepus* behaved in similar but even more pronounced fashion;—these nocturnal animals were chasing in daylight. While collecting data on the ecotone track during the late morning, 5 hares were counted at 1 time gamboling in the field along the forest edge. Hyperactivity of hares could have been caused by 4 or more males chasing 1 female. Males have been shown to gather within a female's home range while she is lactating (Bider 1962), and quite possibly she instigates a chase which involved all the courting males at one time.

Zapodidae did not produce well defined mating peaks. All the high peaks above 170 in August were nights during which rain occurred. Similarly, the high peaks of June 2, 19 and July 3, 9, 13 and 14 corresponded to nights in which rain occurred. The peaks of June 4, 9 and 16 did not coincide with either rain or warm temperatures. In fact nocturnal temperatures for the first 2 dates, were in the upper forties, while that of June 16 was in the low thirties. The climate for these hyperactive days was similar to many others in the 16-day period. Therefore, hyperactivity during the latter 3 nights discussed may have arisen from mating activity of a portion of the population.

*Sorex*, like Zapodidae, responded consistently to rain. With 27 hyperactive peaks of which only 3 occurred when there was no rain. The dates of the 3 rainless hyperactive peaks were August 27 (71), October 16 (19) (Fig. 18B) and 31 (10). The latter

2 were probably not significant but that of August 27 could have been a mating peak. *Microtus* had only 2 hyperactivity peaks up to August 5 (Fig. 17A, June 18 & 23), but from then on they doubled their activity on 19 occasions, and all peaks were associated with rain. In general *Sorex* activity was higher at the beginning of the season with *Microtus* generally more active toward the end. Since both species seemed to respond similarly to climatic conditions, a test was run to verify this. When the activity of both populations increased or decreased from that of the previous day, the day was assigned a plus (blacked columns *Sorex*, Fig. 17B). If one population's activity increased while the other decreased the day was assigned a minus sign. Totals of 99 plus, and 63 minus signs were recorded with the latter including 10 days in which one species' activity did not change. This means that 66% of the time *Microtus* and *Sorex* activity followed the same pattern. The same test on *Tamias* and *Tamiasciurus*, which are taxonomically and ecologically more similar, yielded as many plus days as minus days (73 and 72). Since *Microtus* activity was very low when that of *Sorex* was very high and vice versa, and since their increases and decreases in activity were fairly synchronous, it appears that the phenology of the increased activity periods might be very important in decreasing biofriction, particularly where the two species use the same runways.

#### BIRDS

Sparrows were very static in their daily activity up to mid-July. From then on only a few ill-defined peaks and 1 good peak (October 8) occurred. Sparrow activity is peculiar in that it normally builds to a peak and then decreases gradually over a period of a few days. These increases in activity seem to have no direct relation to weather. The hyperactive peak (October 8) might have been due to the feeding of a band of migrants, but it occurred immediately after the protracted storm of early October and bird activity had been suppressed by the snow, sleet and temperatures ranging 15° to 33° F over a 3-day period.

*Bonasa* activity was irregular. There were many inactive days up to July 21 followed by 3 weeks of fairly continuous activity from August 21 up to the end of the tracking period. The high peak of activity in June was due to a group of at least five grouse which crossed the track from north to south between 9.00 and 11.00 hours then moved back and forth between 11.00 and 13.00 hours. The additional crossings were by birds that entered and exited from the same side of the track and one crossing from north to south. All this activity occurred on the crest of the hill in the woods around the 600 ft marker. Unless all the birds flew back from south to north after the initial movement, which is unlikely, the data indicate that this hyperactivity was a family migration. The high peak in October consisted of 5 north-south, and 5 south-north tracks plus 4 entries and exits from the same side. This time however, the crossings

were spread all along the transect making it difficult to tell actually how many individuals were responsible.

Feeding activity of flickers had been building up in the area but ended abruptly on September 9. The 92 crossings occurred during the last four hours of the afternoon.

This particular valley is a feeding area for migrating woodcock, and the small amount of woodcock activity during late September and early October correlates well with their migratory period. All this activity took place between the 400 and 600 ft markers at night. Only then were woodcocks active in the woods. Normally in summer they were active in the dry open fields.

Larger birds, particularly starlings, redwings, cowbirds and robins were very active up to the end of the first week in July. After this, robins, veerys, thrushes, and occasional groups of jays were responsible for low, but constant, activity. Over the years mid-July has been the period when the greatest number of species is sighted. By August the Icteridae and starlings, which were the most common birds in June and early July, are seen only in large flights.

Broad peaks of activity up to July 21 for sparrows, and to July 7 for other birds, are probably related to reproduction. After this a protracted period of maintenance and growth occurs for larger species while this activity is replaced by more sporadic periods of feeding for the smaller seed eaters.

#### AMPHIBIANS

This group is obviously very erratic in its daily activity. A detailed analysis in the section dealing with weather systems will show the climatological events which produce activity and hyperactivity, the latter being common. What is notable here is that high activity only occurred during a restricted period of the season and that 3 genera did not reach their respective maximum activity periods at the same time.

*Bufo* had their high activity period from July 8-28. The dispersion of activity both before and after this period was drawn out with protracted periods of low counts separated by high, but restricted, periods of activity. *Bufo* calling had finished about the third week of May, so the data represent feeding and growth and not migration.

The *Rana* group consists of several species including the two Hylids. *Hyla crucifer* and *R. sylvatica* had both returned from the breeding ponds when tracking began. *R. pipiens* was still in the ponds and *R. palustris*, *R. clamitans* and *Hyla versicolor* had not yet started calling on June 1. There were 4 hyperactivity peaks in June, but none in July. Hyperactivity increased through August, culminating in the second week of September. A last suppressed spurt of activity occurred during a warm, cloudy and wet period at the end of September. August-September activity is mainly caused by a greater activity potential due to the larger number of both young and



mature *R. clamitans* and *R. pipiens* in the area. In both June and September there were many linear tracks (animals following the transect). In June a *R. palustris* was seen hopping along the transect. It had entered at the 750 ft mark and did not exit before the 150 ft mark. In September, innumerable juvenile *R. pipiens* and *R. clamitans* were seen but only the latter seemed to be generally heading toward the woods; hopping along several hundred feet of transect before leaving it. Therefore, only the activity of July and August was essentially feeding activity. The rest was mainly migration.

Urodela, mainly *Eurycea bislineata*, increased their hyperactivity to a maximum on July 3 when 93 (10% of the total) crossed the transect on a single night. After this their activity declined through July, remained low in August, and reached a second peak in September.

Major activity periods of the amphibians did not overlap, although it will be shown that these animals are hyperactivated by identical climatic conditions. *Rana* activity was lowest when *Bufo* activity was highest, and Urodela activity decreased while *Bufo* activity increased in July and, finally, a second activity period for Urodela occurred in September when the total activity of *Rana* and *Bufo* was decreasing.

#### REPTILES

Both groups of snakes had the same phenological activity pattern, although the *Thamnophis* had relatively higher fall activity than the *Storeria*. As had been noted previously, the general fall increase in snake activity is related to the increased numbers of active animals due to young born in the fields in late August.

The accentuated activity of *Thamnophis* at this time is related to their migration back to the woods. By definition hyperactivity among the *Storeria* was restricted to 2 peaks in the second week of August, but the numbers are so low that it seems improbable that they are valid. Seemingly valid hyperactive peaks in the *Thamnophis* histograms are the 4 high days in the last week of September. These sunny warm days generally activate diurnal poikilotherms. These days caused hyperactivity because potential days of activity are fewer at this time of the year. Secondly, when conditions favour activity, migration takes place. The total pattern of snake activity is identical to that of the invertebrates, but about one-fiftieth in size. The slight lags of 1 to 2 days in phenological histograms (Fig. 17) are essentially due to; 1) the relative importance of nocturnal insect activity at different times of the year, and 2) invertebrate activity days ended at 24.00 hours whereas *Thamnophis* days ended at 06.00 hours.

#### INVERTEBRATES

The Invertebrata curve represents activity of both diurnal and nocturnal species. During the first 16 days of June 40% of invertebrate activity was nocturnal. By August 5 it had dropped to 30%. Be-

tween August 5 and August 23 50% of the activity was nocturnal. From then to September 8 nocturnalism had dropped back to 30% of the total activity. From September to the end of the season diurnal orthopterans were the dominant species, so in all probability 70% of all activity after the first week of September was diurnal.

In general, activity doubled in the latter part of June, decreased to a low point around the third week of August, and then stayed relatively high for about a month before the final decrease. During periods in which diurnal activity is dominant, particularly from late August onward, all the high peaks, which include 500 or more crossings, were days with maximum temperatures in the seventies or eighties and nocturnal temperatures over 50° F.

Four days of high activity in mid-October were typical Indian summer weather (Fig. 15B). For the first 3 the temperatures were 67-28, 74-36, 78-38° F. On the 4th the maximum was 78° F, but cloud came in at sundown and retarded the drop in temperature which eventually reached 38° F. Since the temperature remained above 50° F until midnight nocturnal insects had about 6 hr of activity, compared with about 2 hr on the previous nights. This additional period of nocturnal activity produced the hyperactive peak, 600 of 900 crossings after dark compared with about 200 on the previous night.

Later, on October 26, a sunny warm day with a maximum of 68° F there were 325 crossings. However, 2 practically identical days, November 3 and 4, produced only 64 each.

In general the most active peaks, earlier in the season before population declines take place, are all on the last clear day before a weather front comes in. Hyperactive peaks occur when the sky clouds up during the afternoon or just before dusk. This was true for August 10 and 31, September 8-10 and 23. If conditions favouring hyperactivity occur while a warming trend is in progress, heightened activity will occur. Examples of this occurred on August 28, 29, 30 and September 1, 20 and 21. These are usually caused by minor fronts within a large air mass.

The weather on the days of June 23 and July 1, 13, 17 and 28 was similar to that which caused hyperactivity in August and September. On July 11 and July 18 the same conditions occurred, but rain fell as soon as the cloud moved in during the afternoon and this moderated the activity.

All the inactive periods were caused by very cold, cloud-covered days, particularly during the first few days after passage of a front, when the skies are slow in clearing.

The annelid activity peak on June 2 occurred on a rainy night but after this, and up to mid-October, no hyperactivity occurred. After October 14 hyperactivity, characteristically, occurred on the coldest, wettest days of the tracking session. October 19, 29, November 6 and 7 were all days in which rain occurred most of the day and all night while the temperatures remained in the thirties. On November

6 when there were 930 annelid crossings, over 800 worms were actually picked off the track, and many along the edge of the track were active under a sheath of ice produced by sleet.

After September 7, every peak night, or night with more than 30 crossings, coincided with rain between midnight and dawn. This relation never existed prior to this date. This activity was all in the field and most pronounced around the lowest areas. Therefore, it was probably a local phenomenon in that these animals were emigrating from saturated soil, caused by low evaporation and incessant precipitation.

The active period of the mollusca is quite similar to that of the amphibia with the exception that there are no well defined peak periods of activity or periods of hyperactivity. They were only active when the grass or litter was wet, but they did not always respond to these conditions.

Nematoda, which were for the most part Nematomorpha, left their host orthopterans in early September. After this only a few were found on the transect in wet weather.

#### CARNIVORES AND INCIDENTALS

*Mustela erminea* was the most important carnivore in the area during 1964. Their activity was fairly consistent over a 3-month period starting in the third week of June. The 3 hyperactive peaks were probably due to mating activity.

A weasel and tracks were observed throughout the day and evening of July 2. Although the weasel was not seen on September 4 and 18, on both these dates his total number of crossings was made in 2 discrete periods separated by several hours. These were the only times weasels had crossed the track more than twice over a 2-hour period. In this case they had crossed 7 and 10 times on the 4th, 11 and 12 times on the 18th. Moreover, these tracks were for the most part a crouched gait unlike the normal hopping gait. When running down prey, such as *Microtus*, they use a third gait, which resembles that of a squirrel or chipmunk. The three occasions on which hyperactivity occurred would correspond to the extreme limits of the weasel mating season.

The larger carnivores *Mephitis* and *Procyon* sometimes hunted along the track, but most of the time they crossed it in specific areas. For the *Felis* the inverse was more often the case. All single and double crossings were movements through the area, whereas all higher peaks indicated foraging. Skunks did not forage along the track in October and November. Late season activity was probably that of a single skunk.

In 1962 numerous dead shrews, moles and voles were found on the track, all killed by cats (*F. domestica*), and it was felt that although this might be normal in some areas it did not enhance this project. Shooting every cat seen in 1963, 1964 and 1965 has not eliminated the population, but, since the program began, *Felis* hunting activity was detected only once in 1964 (see September).

All the species depicted in the top section of the graph probably did not play a role in the metabolism of the community. This activity was exploration and dispersion. Since a crossing is completed each time an animal leaves the track, species such as *Erethizon* and *Rattus* give a high count, particularly if they move along the whole track in one period. *Rattus* activity correlates well with the closing of a dump a half-mile away at the end of July. Otter activity was produced by 3 tracks together and moving in the same direction. All movements of the larger carnivores and omnivores (*Lynx* sp., *F. concolor*, *Lutra* and *Ursus*), during all tracking sessions including this one, were from south to north away from the creek, with only one exception, that of *Ursus* towards the end of September.

#### FACTORS AFFECTING ACTIVITY RATES

Phenology of activity gives a general background for a more detailed discussion of the hierarchy of factors affecting rates of activity. This section will lay the groundwork for future studies on the function of species, using this sand transect technique. Rates of activity can be controlled by factors at 4 levels; annual, seasonal, meteorological, and, finally, the climatic level.

#### ANNUAL—SIZES OF POPULATIONS

To determine the effect of a biotic or physical factor on the activity of a particular species, the researcher often feels that several years of data are needed. While this of course is possible, pitfalls may be encountered.

Population densities, particularly in northern latitudes, can fluctuate enormously from year to year. Therefore, the effect of any factor should only be analyzed in view of changes in rates of activity within each year. For example, 2 or 3 years of *Bufo* activity data cannot be pooled to study the relation between temperature and activity. This procedure might be very tempting when it is realized that examples of certain physical events, such as dry fronts, hail, lightning, eclipses or flooding, only occur on rare occasions and, samples of even the most common climatic factors such as temperatures must include only short periods of time because there are periodical changes in rates of activity caused by phenological events.

A second pitfall can be caused by a fusion or masking of phenological events and population increases. If high mortality of new recruits keeps a population from expanding in June or July, then the first increase in activity rate in August might reflect either the dispersal of a complete litter, or a phenological event such as winter food gathering. The rise of *Lepus* activity in August (Fig. 17) was partly due to 2 recruits to the area. Being the first young recruits of the season they produced a perceptible increase in mean activity. With relatively large animals, Lagomorphs or carnivores, young recruits can easily be detected, but with insectivores and rodents

it is usually difficult to distinguish adults from juveniles unless both are found together. When tracks of juveniles are found with those of adults, the difference in area encompassed by the digits of the 2 age groups is easily seen, but the difference in diameter or toe length is not readily measurable.

Thirdly, relative spatial utilization of different areas might also be affected by low population densities. When a population decreases toward a low, small areas or islands of adequate habitat within marginal habitat might continue to be utilized. This would be most likely to happen where density-dependent factors operate to disseminate a population. In this situation isolates would be most likely to survive, and would continue to use their adequate home range simply because they know it best and are therefore safe in it. It was indicated earlier that *Lepus* utilized all sections at the same level of activity (total 4 periods 1963). However, the utilization of the field might have been saturated, whereas the woodland populations might have been low. Mean *Lepus* activity on the ecotone in 1963 was 6.5 crossings per day, versus 12 in 1964. If activity in the field remained constant between 1963 and 1964 total utilization by *Lepus* would not have been equal in all sections in 1964.

Finally, if a population is high, maximum activity rates might be underestimated. During July 1963, when Zapodidae activity was excessively high, activity 300 ft out into the field was as high as that inside the woods. If in this case Zapodidae activity were only measured in the woods peak activity would have been underestimated.

#### SEASONAL—PHENOLOGICAL EVENTS

When activity data from a single year are examined, certain patterns of change in rates are obvious. At this level the term "phenological activity" is applied, because different rates of activity are related to recurring natural phenomena.

The basic activity rate can be defined as that necessary for the maintenance of an overwintering population. In early spring we can expect low and constant maintenance activity. Later we can also expect a series of changes in activity due to (1) mating, (2) population growth, and (3) food gathering. If a population changes areas of utilization for reproduction, growth, or overwintering, then we would also expect a change in activity rates due to migration. Examples of all these changes in activity rates have been described in the previous section, but this interpretation was based on known activities of only a few populations.

A discussion of the basis for the interpretation follows. First, we would expect population growth and weather to change activity rates. Fig. 18 shows the theoretical percentage increase in population, and therefore activity, if there is a direct relation between the two, and if no other factors intervened. Obviously none of the phenological histograms (Fig. 15) other than those of *Clethrionomys*, *Glaucomys*,

*Bonasa*, *Storeria* and *Thamnophis* could be interpreted as following the theoretical population growth-activity pattern. The weather affects rates of activity, but these changes can only be superimposed on the larger changes due to phenological phenomena, with possibly one exception. Mid-July to August is the warmest part of the year, and during this period there is a slight drop in activity of at least a few species (e.g., *Tamias*, *Tamiasciurus*, *Lepus*, *Zapus* and the Carnivores). The lower activity might be real but, at least in the case of *Tamias*, *Tamiasciurus*, *Napaeozapus* and *Procyon*, this decrease does not occur in cooler areas, such as the stream bed for the first 3 species or the fields for *Procyon* (Thibeault, 1968; Bider *et al.*, 1968). From this then it can be concluded that, even within a restricted area which presents a heterogeneous environment, animal phenology can change with a horizontal distance of 200 ft or with a 30 ft difference in elevation.

Even though the phenology of activity on the ecotone transect applies specifically to this particular site, these data can be used to define the characteristic activity patterns produced during each phenological event. The times during which the events take place are rather approximate and would be expected to vary slightly at different sites within the area.

Maintenance activity can be described as low and constant. The only late breeders in this area are the snakes, and their activity up to the third week of August is the only example of spring maintenance activity. In the fall many non-hibernating residents show this same pattern (*Tamiasciurus* Sept. 21 and Nov. 15, *Lepus* Oct. and Nov. 15, *Peromyscus* mid-Oct., *Microtus* and *Sorex* late Oct., *Mustela erminea* late Sept.). Even during late fall maintenance activity there are occasional days of hyperactivity, characteristically these are caused by a climatic release from suppressed activity, and if the resurgence of activity is too high, the next day will have low activity whether or not the weather is favorable (e.g. Fig. 17A, *Lepus* from Sept. 24-30 had a mean number of crossings of 6.7, and on Oct. 1 and 2 9.5 crossings. Nocturnal minimum temperatures increase from 38 to 43° F but activity decreases to 2 on Oct. 3 with the mean for Oct. 1, 2 and 3 = 7). This same pattern also works for *Tamiasciurus* (on Oct. 8 and 9 mean activity = 4, for Oct. 10 and 11 mean activity = 5.5), (Oct. 12-19 = 5.8, Oct. 20 and 21 = 6.5), (Oct. 22-25 = 7, 26 and 27 = 7), (Oct. 28-31 = 4), (Nov. 1 and 2 = 5), (Nov. 3-5 = 4.7), (Nov. 6-11 = 3.7). In over a month of continuous tracking the mean activity was calculated for 10 weather series and these means ranged from 3.7 to 7, which for *Tamiasciurus* is both low and constant. This technique can be applied, with caution, to other species. For example *Lepus* Fig. 15B, Oct. 18 and 19 no activity, and on Oct. 20 there were only 8 crossings. On the first 2 nights minimum temperatures reached their maximum for this period (Indian summer) and it is possible that the hares moved to cooler sites thus not actually showing the characteristic increase in activity after

suppression on this transect. The period of maintenance activity for most species occurs between mid-September and early May, with the exception of a few late breeders such as the snakes.

#### ACTIVITY RELATED TO REPRODUCTION

From field observations on *Lepus*, *Tamiasciurus*, *Tamias*, and *Mustela erminea*, it seemed that courting behavior produced the high peaks of activity in June and early July. For all these species part or all of the activity was diurnal and could be observed. Mating activity of nocturnal species was never observed directly but, if known mating peaks can be recognized, then there is a possibility that they could be determined for other populations of mammals. The histograms all show a peak in activity far in excess of peaks in the preceding or following 2 weeks of activity. This peak is also associated with a few days of higher than normal activity for the same period. On the basis of excessively high peaks alone, the *Peromyscus* data were interpreted as including 3 mating peaks (Fig. 15A). *Zapodidae*, *Microtus* and *Sorex* all have many hyperactive nights, but they respond positively and spectacularly to rain, whereas other species are relatively independent of climatic conditions. Careful analysis of the *Zapodidae* and *Sorex* data isolated a few nights of hyperactivity that are not related to rain. Examples: *Zapodidae*, June 4, 9 and 16; *Sorex* August 27. Other than these, nights of high activity such as *Zapodidae*, June 27 and 28, which by definition do not represent a hyperactive state, still might represent mating activity. Both these nights were clear and cold, the former being the last night of spring freezing. This is simply speculation, but these peaks occurred on nights in which climatic conditions normally produce low activity. There is, of course, no reason to suppose that rain-activated animals do not mate in the rain. However, if the response to the rain of June 18 (*Sorex*, 96) is compared with the response to the lighter rain and drizzle of the nights of June 23 and 24 (66 and 75), it certainly does not seem likely that superposition of mating and climatic activity occurred on the 18th. On the same basis of analysis no mating peaks were found in the *Microtus* data. Total activity of other mammalian species studied was too small to do a reliable interpretation of activity related to mating. It seems that with reasonably large samples mating peaks stand out in the activity patterns of those animals whose activity is less affected by climatic conditions. Mating activity might be masked by activity related to climate, but this seems unlikely. The characteristic pattern ascribed to mating activity is not found in the phenological histograms of forms other than mammals. Presumably, the mammalian pattern would occur in studies encompassing an avian mating arena.

#### STORAGE ACTIVITY

Storage activity patterns are found in the histograms of *Tamiasciurus*, *Tamias* and *Zapodidae*. Their

harvesting and nest-building activity was observed visually. Characteristically, it is a period of high and constant activity. The high activity of *Peromyscus* (Aug. 10-Sept. 10) and *Lepus* (Aug.) might also have been due to storage and growth but, as was pointed out earlier, *Lepus* activity in this period might have been simply a response to population increase either due to juvenile recruits or a migration into the area from the deeper woods.

This same pattern (high and constant) appears in the bird graphs, but in June and July instead of toward the end of the season. The activity at this time is very intense and might be related to recovery from migration along with the added burden of feeding nestlings. Fringilid activity is highest during the strawberry and raspberry season, and as both fruits have clumped distribution and are found along the ecotone transect, activity might reflect a concentrated feeding area. In late July and August low activity on the ecotone might reflect a movement toward the ubiquitous grass seed supply in the field. The same reasoning cannot apply to the insectivorous birds, at least not at the local level, for they really do become less active during July. This is surprising because insect activity as a whole increases toward the end of August, and it might have been reasonable to anticipate that, with increased movement of prey species, the efficiency of the predator could remain constant with lower activity.

#### MIGRATION ACTIVITY

The groups that best demonstrate migratory activity are the amphibians, reptiles and birds. This activity is characterized by short periods of high activity. This pattern can best be explained if we keep in mind that (1) migrations occur during marginal weather conditions, and (2) the migrators are usually highly motivated to move. The result is that weather usually suppresses activity for a few days with a fresh upsurge occurring as soon as the weather is favorable. This type of activity can be further verified by direction and location of movement. The *R. clamitans*, *Eurycea* and *Thamnophis* were all found to be migrants having observable spring and fall migrations. Only a few fall migrations of birds were detected, e.g., Fringillidae, Picidae and *Philohela*, but closer observation and better differentiation among species might have shown that all the high peaks after mid-August were caused by migrators. Spring bird migration was largely completed by the time tracking was started.

Fall migratory peaks would normally be expected to be larger than those of the spring. The sole exception was *Eurycea*, for they overwinter and breed in the stream and only adults migrate up past the ecotone transect in the spring. The 2 small peaks on July 26 and Aug. 4 are probably due to newly metamorphosed individuals migrating from the stream, but by and large the young never get as far as the ecotone during their first summer.

The dispersion of activity peaks in the *Bufo* and

*Storeria* histograms differ from those of the migrators in that they form single blocks of activity, i.e. *Bufo* between June 5 and Sept. 28, *Storeria* Aug. 7 to Oct. 21. Like other heterotherms, activity is released at a climatic threshold, but their peaks are more or less equal in height. The heterotherm migrators, on the other hand, respond to the same climatic conditions with a level of activity proportional to their drive. When the drive to migrate begins and activity is released by climate, these animals respond sharply (see the June peaks for *Rana* and *Eurycea*).

The first 2 peaks of *Rana* activity correspond to favorable climatic conditions for movement, as do the first five hyperactive peaks of the Urodela. However, after this period there were attempts to migrate every dusk, except on the nights of July 6 and 13 (Fig. 17D), and every time rain fell during dusk or early evening there was a surge in activity. On July 22 there were only 4 *Eurycea* crossings, yet 0.01 inches of rain fell at midnight. Obviously the spring migration was over, at least across the ecotone transect.

#### DISPERSAL

The phenological histograms (Fig. 17G) include species which are only detected occasionally. These include erratic, occasional and discontinuous activity of individuals dispersing from summer habitat and looking for new home ranges or overwintering sites. The annual number of crossings for species recorded as transients during the dispersal phase might be a good index of the populations success in rearing young because unlike so much of the other activity, this is more likely to be spatially at random.

#### WEATHER SYSTEMS

In the study area there is an average of 7 days of precipitation per month (over 0.1 inches), i.e., rain every 4th day (see climate). The weather systems are not cyclic, but within each system there is a pattern which is characterized by clearing sky cover, clear sky, clouding, and finally rain. Concurrent with sky conditions, temperatures fall and rise (Fig. 15A, July 16-19, July 20-23, July 24-26, July 27-30, Fig. 15B, Aug. 9-12, Aug. 13-17 and Oct. 14-19). Most poikilotherms have a threshold temperature around 50° F, and many of the diurnal forms have behavioral adaptations which permit them to use radiant energy to increase their metabolism and become active. Based on these known biological characteristics and the fact that the march of temperatures and isolation during each system normally encompass many combinations of these physical conditions in a somewhat regular pattern, it should be expected that a rhythm of total activity should occur through each weather system (Fig. 19). The extent and sequence of the variations are shown as "meteorological activity rhythms." Both diurnal and nocturnal activity curves are composed of the sum of 4 components.

Diurnal activity was divided to show graphically the contributions of invertebrates, reptiles, birds and mammals to the general rhythm of activity. The 2

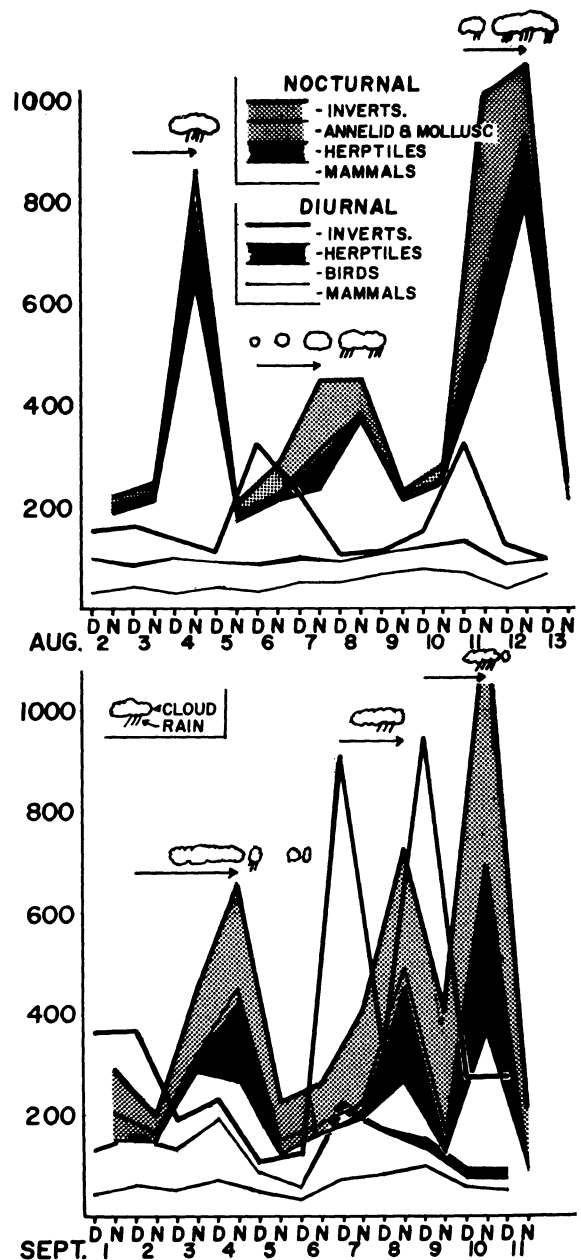


FIG. 19. Meteorological activity rhythm. Abscissa is the total daily number of crossings for diurnal species and nocturnal species. The arrow indicates the time lag between peak diurnal activity and peak nocturnal activity within each weather system. Points of inflection for the two groups correspond to the Ds. for diurnal species and Ns. for the nocturnal species.

samples (Aug. and Sept.) were chosen because in the first invertebrate activity would not be too dominant, whereas in the second it would. In the August sample the mean activity rates of mammals, birds, and invertebrates were 51, 48, 68 crossings per day versus 63, 66 and 235 in August. By scoring a plus if the

total daily activity increased, and a minus if it decreased, and then comparing these pluses and minuses with those of each group, the extent to which each major group contributed to the total pattern of variation was determined. Mammalian activity, including most of the sciurids, diurnal *Sorex*, and *Microtus* was synchronous with total activity 62% of the time, birds 71%, reptiles and amphibians 91%, and invertebrates 86%. Both mammals and birds were more synchronous in September (70% and 80%). The results indicate that the diurnal meteorological rhythm is not a simple reflection of poikilotherm activity, but that endotherms are also affected particularly during periods of maintenance activity.

Nocturnal activity is dominated by the mammals. In the August sample there were 3988 mammal crossings, 939 invertebrates, 504 reptiles and amphibians, 155 annelids and mollusks. In September there were 2202 mammals, 1886 invertebrates, 695 reptiles and amphibians, and 260 annelids and mollusks. In these samples synchrony of the 4 groups to the total activity was mammals 95%, reptiles and amphibians 71%, annelids and mollusks 62%, and invertebrates 91%. The total meteorological rhythm could be expected from exotherm activity alone, however, it is obvious that in these examples, mammals, because of their dominance, could easily have established an isostatic situation wherein total activity would have been rather constant or independent of the weather. The principal climatic factor which affects peak mammalian activity is rain, whereas temperature alone affects most invertebrates exclusive of annelids and mollusks, and finally, both temperatures and rain affect amphibian activity. When both rain and warm nocturnal temperatures occur together as on Aug. 4 and Sept. 10, a sharp rise in activity can be expected, but when temperatures rise without nocturnal rain the peaks are not as great (see Aug. 4 and 8). When temperature rises on a cloudy night rain occurs on the next night, as temperature falls a plateau of high activity is created by the compensatory differences in rates of activity between the exotherms and endotherms.

There should exist a relation between energy flow and activity and periods of high activity should relate to periods of production rather than maintenance. If these assumptions are true, then we could assume that success of diurnal populations is related to the number of warm sunny afternoons, and that of nocturnal populations to the number of nights with cloud cover and/or rain during the summer. This aspect might also be an important criterion in determining the zoogeographical limits of populations. This is particularly important where rain is concerned. The time of rainfall can be very important (day or night) but the quantity is much less so. To take one extreme, if all rain fell during the day, and all nights were clear, certainly activity would be low, and possibly only high enough to allow maintenance feeding. Thus a large portion of each population might not survive the winter. Similarly, the number of days during

which threshold temperatures are reached is more important than the maximum, minimum, or mean temperatures.

#### ACTIVITY INFLUENCED BY THE TIME OF CLIMATIC EVENTS

It has been shown that total animal activity fluctuates in a pattern which relates well to the different stages of each weather system. Although a good many of the species involved contributed to the activity pattern, only a few played a dominant role. It is from among these few, whose activity fluctuates dramatically under different meteorological conditions, that examples will be drawn to show the possible types of responses to the time at which climatic events occur. The species drawn upon will be Zapodidae, *Microtus*, *Sorex*, Invertebrata, *Bufo* and *Thamnophis*.

Reactions to daytime rain were referred to in the interpretation of the phenological histograms. At that time it was pointed out that invertebrate activity was suppressed during rainy days, while both *Microtus* and *Sorex* were stimulated. To demonstrate the effect of the rainfall alone on these, the percentage of total activity was determined for the following sub-periods; 2-4 hr and 0-2 hr before the rain, the 2-hr period following the onset of rain and 2-4 hr period after the onset of rain. The following results were obtained: Invertebrates 36, 30, 9 and 24%, *Sorex* 23, 18, 27 and 32% and *Microtus* 2, 2, 53 and 42%. These results clearly indicate suppressions of invertebrate activity by rain, no effect on *Sorex*, and acceleration of *Microtus* activity. The different reactions of the latter 2 is interesting because these 2 species utilize common runways in the fields, and both have similar responses to meteorological conditions (i.e. increased activity on cloudy and rainy days).

The effect on invertebrates of the time during which cloud cover occurs during the day is shown by graphs A, B and C (Fig. 20). Clear days produce a fairly symmetrical distribution of activity over the daylight hours, but activity decreases during that part of the day which is cloudy. On clear days *Thamnophis* activity is bimodal, but a unimodal curve is produced when there is cloud in the AM or PM. The mode occurs in the sunny part of the day. Exceptions to this rule occur on very warm and cloudy days (e.g. around 70° F.) when snakes are continuously active.

It must be pointed out here that the number of days of each type used to construct the graphs of both Figs. 20 and 21 was very variable. Only clear-cut examples were used, and as a result only 50% of all days could be used. This then brings up the point that any diel activity pattern which is affected by a climatic condition is only as important as its probability of occurrence. Therefore, though the situations depicted only occurred in approximately 4-20% of the cases, and might have little influence on community function or the evolution of the species, there is an academic interest in determining the operative mechanisms involved in shifting activity patterns.

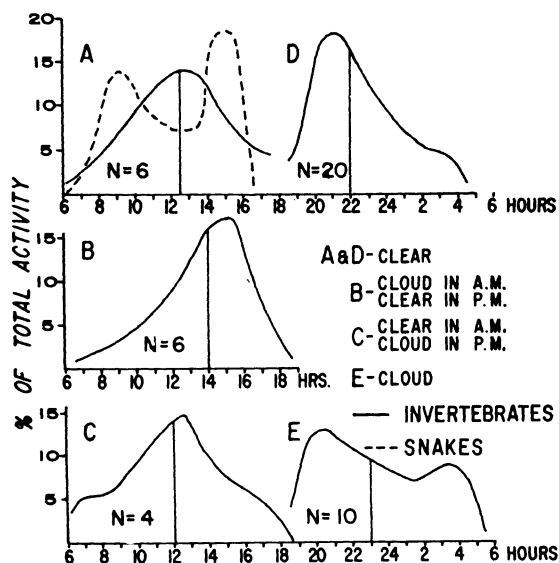


FIG. 20. Circadian rhythm curves of invertebrate and snake activity under various cloud conditions. Curves are based on the means of the hourly percentages of total daily activity. N is the number of days in each sample. The vertical line under each curve is the time at which 50% of the total activity has occurred.

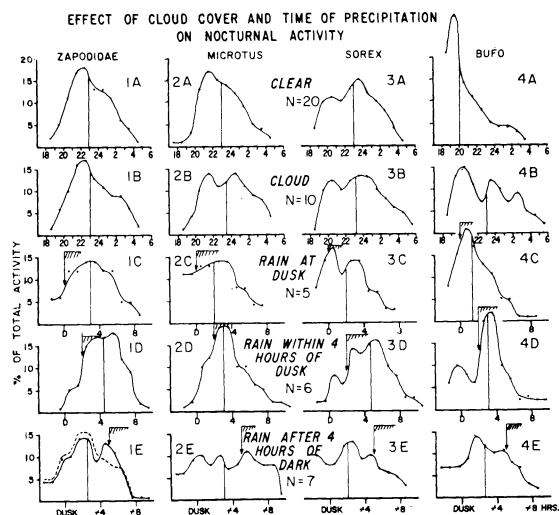


FIG. 21. Modifications of circadian rhythms due to cloud cover and time of precipitation. Curves were calculated in the way described in the caption of Fig. 20.

The distribution of the percentage of hourly activity under different nocturnal climatic conditions is variable for the groups analyzed. Both Figs. 20 and 21 show the distributions of activity on clear and cloudy nights. On cloudy nights without rain, invertebrates, *Microtus*, *Sorex* and *Bufo* curves become bimodal, or in the latter case, trimodal with a considerable shift of activity toward the later part of the night. This represents curves formed under neither restricted nor accelerating climatic conditions.

These curves also represent the closest approximation possible, under uncontrolled conditions, to situations under which animals usually find themselves in controlled laboratory experiments. It is noteworthy that these conditions would probably occur once in every 10 nights in this region. Fig. 21 shows a dramatic change in the activity pattern of *Microtus*. This occurs because they are arrhythmic and have already responded to the rain regardless of the dark. Zapodidae, *Sorex* and *Bufo* on the other hand respond as the light intensity decreases and the latter remains more active later in the night than they do under clear conditions. This reaction to rain at dusk causes 50% of the *Microtus*, *Sorex* and *Bufo* activity to occur in a period which includes predusk and two hours of dark. Because rain initiates a micromigration of *Napaeozapus*, it is understandable that the reaction to rain would not necessarily shift the intensity of activity toward either the beginning or end of the night, but it would rather flatten the curve to produce a more homogeneous distribution.

Rain within 4 hr of dusk, in all examples, affects a surge of activity. It is interesting to note that the initial increase in nocturnal activity remains apparent in all cases, but is more pronounced in the more primitive species.

Later rain, 4 hr after dusk, has little effect in stimulating Zapodidae, *Sorex* and *Bufo* activity, with one exception. This occurred on the night of July 22 at 24.00-2.00 hours when *Napaeozapus* reacted to the rain. *Microtus* reacted to late hour rains, not so much by producing an excessive activity peak, but more by a prolongation of relatively high activity. If there were no reaction at all, then these curves should have the same form as those under cloudy conditions, but they do not. Possibly the relative humidity, barometric pressure or temperature differences which might occur under these specific conditions might be responsible for these differences.

#### COMPARISON OF ACTIVITY BETWEEN THE DISCRETE DATA 1963 & CONTINUOUS DATA 1964

Trends of the 1964 daily-activity curves were compared to the 1963 ecotone data.

*Tamiasciurus* activity at the end of June, July, August and mid-October followed the same pattern over the 2 years. There was only a weak increase at the end of August, but this represented only the end of food storage period. The *Tamias* curve does not indicate a higher period of activity toward the end of the season, but again storage might not have begun in late August. The largest discrepancy was in the October activity. Where there had been virtually no activity in mid-October 1963, there was as much in October 1964 as there had been at the end of June, July and August.

*Lepus* activity did not conform, but this is not surprising in that a good portion of the activity which occurred during the peak period of August 1964 was caused by 2 young hare which were born near the transect.

*Peromyscus* at the end of June 1963 had a run of three active days in which the activity had gone from 2-11 for the first 4 days and up to 50, 68 and 33 during the last 3 days. This certainly could have been due to mating activity, and this could have shifted the low periods of activity which normally follow mating activity. The activity at the end of July ranged from 2-24 with no hyperactive peak days. In P.3 and P.4, 1963, *Peromyscus* activity was relatively much lower than that in 1964.

The Zapodidae activity trends were similar over the 2 years, but as in the case of the sciurids, the discrete P.2 occurred just at the start of the Zapodidae's most active period.

*Clethrionomys*, although trappable from early spring to late fall, seem to travel over the litter for only a short period of the year. This phenomena reoccurred in 1964 but about 2 weeks later.

Both the *Microtus* and *Sorex* trends compare very well over the two years, although *Microtus* activity could have been a little higher in P.3, 1963.

Among the mammalian species with small numbers, comparisons should not be drawn, but certainly the Talpidae trend did not conform and might have been reversed.

Among the birds, Fringillidae and Picidae were fused in the 1963 data, the fit is good. *Bonasa* fits well and no *Philohela* would have been expected on the dates in which the 1963 data were taken, with the exception of October.

The invertebrates, amphibians and reptiles all conformed rigidly in their phenological activity trends over the two years.

In total, this indicates that the phenological events of amphibians, reptiles, birds and invertebrates are well established periodical events, whereas in the mammals only high activity periods due to storage reoccur at approximately the same date every year. The time at which modifications in rates of activity due to reproduction occur, are variable. As a result, short sampling periods are less reliable for mammals and if the periods are not closely enough spaced, major events might be entirely missed. Sampling, during the course of a summer at one month intervals, seems extreme and risky.

#### THE NUMBER OF SPECIES IN TIME

Normally when a field problem is undertaken, determination of a minimum sample area is of the greatest importance. In community ecology where some animals have extremely large ranges, a new approach must be envisaged. Minimum sample size can be arrived at by use of species-area curves (Kendeigh, 1961). These imply instantaneous counts, and are therefore only practical for sedentary species such as plants and some very small animals. When using this tracking method we can introduce the concept of time. Fig. 22 is a species-time curve derived from the 1964 continuous data. The base number 20 includes general categories, such as birds, invertebrata, *Rana*, etc., rather than species. This does not affect

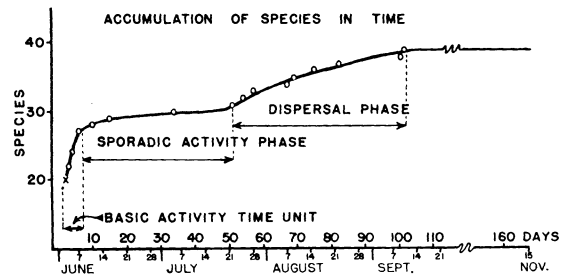


FIG. 22. Number of species in time curve. The x at 20 denotes the total of all species recorded on the first day. In this study the 20 included all the complex groups. The o's represent additional species which crossed the track at later dates. This curve only represents the active season.

the thesis, as the data start well after spring immigration has occurred. The remaining points represent new species crossing the transect. The curve demonstrates the following:

(1) In the first 7 days there was an accelerated increase in new species. The species represented are the basic units of the community. The climatological cycle for the 7 days included rain, a dry spell, warming temperatures and finally a second rainstorm. This period, therefore, gave all resident populations which are influenced by climatological conditions an opportunity to become active.

(2) From the 7th to the 50th day there was a decline in the rate of accumulation of new species. These additions were skunks, grey squirrels and flickers, all of which were sporadic in using the area during the early part of the summer.

(3) Finally, the additions between the 50th day and 100th day were all forms which were recorded once or only on a few isolated occasions. This 3rd period represents an exploratory and/or dispersal phase. I would expect that the first 2 phases should apply as a general rule whereas the 3rd would depend largely on the position and type of area being studied.

From this it can be concluded that the shortest period required to determine the resident community would be approximately 2 weeks, assuming this period included at least 1 complete weather cycle.

#### CONSIDERATIONS CONCERNING THE ANALYSIS OF DAILY ACTIVITY

The activity data of a single day are worthless. There are, aside from differences due to chance alone, many factors which influence animal activity. The climate in relation to the weather system, the precise time at which cloud cover or rain occurs, the speed of the fronts, all have important bearing on the rate of animal activity in time. For those species which are influenced by weather and particularly those becoming hyperactive due to climatological events, diel time analysis of activity can be very biased. Hyperactive surges in activity due to rain might produce a second peak of activity in a single day which is several times that of the activity prior to the rain.



The activity over a weather cycle is more reliable, but again the higher hyperactivity of the last day of a cycle could still bias the information from preceding days particularly during higher periods of activity. Inadvertently the analysis of the modes of activity presented earlier was an ideal situation because each period was represented by a few days midway through a weather cycle, thus eliminating the possibility of incorporating biased hyperactivity due to climate. Days of exceptionally high activity due to mating could not be circumvented.

One of the main points of this section is that studies of activity must be approached from a new point of view. Activity must be analysed by: 1) grouping similar days of different weather systems, 2) using only examples of weather systems from within a biophenological event and 3) comparing the relative levels of activity from one year to the next.

### SUMMARY OF CONCLUSIONS

Throughout the text sub-summaries and conclusions were indicated within each section. However, the work on this project was carried out in what might be called mechanical stages. For this reason a brief summary must be made, not in the order presented thus far, but rather in the light of the hierarchy of activity parameters.

Qualitatively the location of the transect with respect to the structure of the vegetation is of greatest importance. The greater the variability of the vegetational structures the greater the number of species. The ecotone in this case was extreme. A subordinate factor which also contributed to the diversity of species was the location of the transect in relation to the general topography. The ecotone was quite close to a stream and obviously intercepted a thoroughfare along which animals moved parallel to the creek bed and the open fields. The woods transect was on a terrace which constituted a deadend, with the result that even during the dispersal phase no large animals, other than deer, crossed it. Likewise, a few of the species active on the field transect were there simply because of the proximity of the creek or the riparian vegetation and the surrounding savannas.

A second major division relating to the qualitative aspect of communities, is time. The transect is fixed and animals move, therefore, it is only a question of time before all species which inhabit the area, cross it. The minimum period of time needed to detect all the basic species within a phenological phase of the community is one full weather system. During the summer 2 activity phases are evident. The first, called sporadic, is the period during which new species accumulate at a relatively slow rate. These utilize the area frequently but inconsistently or become residents for only a short period of time. The second, called the dispersal phase, is the period during which the slope of the species-time curve increases more rapidly than that of the sporadic activity phase. The new species which are responsible for this are usually only encountered a few times, are totally inconsistent

in their utilization, and individually probably only occasionally play a role in the metabolism of the community.

The length of transect should theoretically affect both the qualitative and quantitative results if animals move at random. This factor is of little importance because even the most primitive forms of animals have specific areas or paths of spatial utilization for short periods of time, thus destroying the randomness of movement. The transects were arbitrarily divided into 150 ft sections, but even these short sections were qualitatively representative of the complete tracks in similar vegetational structures. The additional sections of the transects simply enhanced the quantitative aspect of the study with relatively little additional work effort.

Quantitatively, the study of activity is far more complex. First and foremost the number of animals in each group will be the most important factor in producing activity. I have made no effort to determine the number of animals involved in each group for the simple reason that in areas which are not bounded by barriers, transients can make up a very important part of the total activity. There were many shifts in area of utilization and migrations, therefore, the number of individual animals which crossed even a section of transect could have been exceedingly large and meaningless. The major approach of this study thus far is not the number of animals that use an area over a period of time, but the amount of activity at discrete instances over a period of time. This is, in my opinion, by far the most important factor in animal studies. Coacting species must be within stimulatory range to affect a response. This range is limited by time and space.

Direct quantitative comparisons of activity from one year to the next were not possible due to probable size differences of residual spring populations, but the trends of the activity between the 2 seasons were fairly comparable. The consistent characteristic of changes in rates of activity over the season reflected phenological events which included spatial shifts in the populations.

The climate impinged upon phenological events by advancing, retarding or constricting periodical levels of phenological activity. Advances or retardation can occur in any situation where animals depend on a specific crop to prepare for overwintering. This would be particularly true in the case of *spermavores* such as red squirrels, chipmunks and probably in all mammalian populations where the end of the reproductive season affects a period of high food storage activity. In the latter case climate controls or at least modified activity. During the active season each weather system produces subfluctuations of activity within the phenological activity level.

Within each phenological activity level the variations in daily activity correspond to specific climatological events. A rhythm of community activity is established whereby: (1) all activity is lowest when high pressure stable air is present, (2) as the environ-

ment dries and diurnal temperatures increase under sunlight diurnal poikilotherm activity increases, (3) when the cloud cover increases and nocturnal temperatures remain high the nocturnal animals become active, (4) finally, rain causes hyperactivity in many of the small nocturnal forms and of course this is most apparent among the amphibians if temperatures are above their threshold.

The peaks of daily activity change in time. Diurnal species usually have bimodal activity curves, while nocturnal forms have unimodal curves. When climatic conditions for nocturnal animal activity are at their optimum, good segregation in the peaks of activity occur. When conditions are less conducive to high activity, such as on cold clear nights, all the animals are active in the first few hours after dusk. From a coaction point of view this constriction of activity into a short period of time is not too critical because of the low density of activity.

Termination of activity among the more primitive animals seems to be directly related to temperature. Amphibian activity is strictly nocturnal and temperature bound. When temperatures are not above 50° F at dusk *Bufo* activity is negligible. This temperature is less critical for *Rana* and *Urodela*, but the *Eurycea* only move during precipitation. Reptiles, the shrews, and *Microtus* are arrhythmic and as nocturnal temperatures cool, they shift from nocturnal to crepuscular and then to diurnal peaks of activity. The snakes obviously rest in situations which are susceptible to rapid heating, because they respond to very short periods of warmth.

Phenological events produce marked levels of activity or, in the more primitive forms, periods during which activity may be high if the climatic conditions are right. Spatial shifts in area of utilization are more closely related to the phenological events of the vegetation. Therefore, directly or indirectly, all animal activity is controlled by climate.

The activity of some of the higher animals is affected by weather systems, but most primitive forms respond to minute differences in specific weather elements. From a behavioristic viewpoint, the activity of the more advanced forms is more stable from one day to the next, but it is liable to undulate (rise and fall over a period of a few days), particularly in the reproductive season because of social grouping, mating activity, gestation, lactation, etc. The activity of advanced forms depends more on behavioral patterns whereas the activity of the more primitive forms is governed by physical factors. This constitutes a physico-ethological activity gradient.

To my knowledge this is the first comparative study of continuous community activity in an uncontrolled environment. Even though only a fragment of the possible forms of presentation are set forth at this time, the most essential parameters of activity at the community level have been presented.

Possibly the greatest contribution of this work is the technique itself. It has proven without doubt to be the most practical, simple, economic and least

biased way to get copious data on animal activity. Data on such phenomena as the time of phenological events, the effects of climate on activity, time of activity etc., are all procured simultaneously and can be analyzed in the light of identical parameters for other species occurring in the same community. Knowledge of the instantaneous density of community activity, along with its variability in any habitat would seem to be basic knowledge on which principles should be built. This technique offers the opportunity to get this type of knowledge.

At this point it seems paradoxical that probably the greatest deterrent to rapid progress in animal ecology in the past (the fact that animals move) is in fact the greatest asset in this approach to animal ecology at the community level.

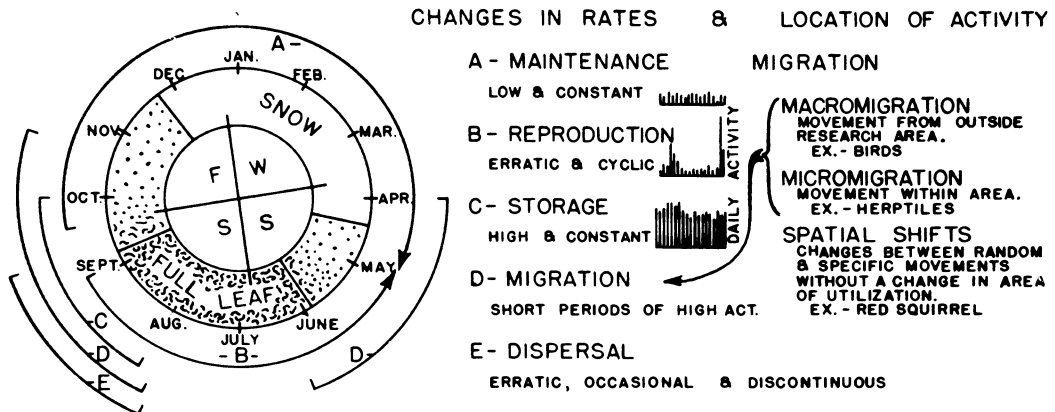
### SUMMARY

1. The time and location of activity of the components of 3 animal communities were determined by a sand transect technique. The technique consists of noting the direction and location of animal tracks made on 3 ft wide strips of fine sand several hundred feet long. The data were recorded every 2 hours night and day.
2. Three sand transects (all within 0.5 miles) were established by 1963; one 783 ft long in a field, a second of 450 ft in the woods and finally an ecotone transect which ran 450 ft through an open field and 300 ft into the woods.
3. In 1964 the ecotone transect was covered with a sheet of polyethylene 6 ft wide suspended 6 ft high. This permitted continuous tracking over a period of 165 days. Concurrent with activity measurements, climatological data were recorded.
4. The study produced approximately 182,000 transect crossings and 20,000 climatological data which included temperatures, barometric pressure, wind speed and direction, cloud cover, relative humidity and precipitation. Each transect crossing has a temporal and spatial dimension both of which can be influenced by biological and physical factors.
5. The community consisted of (a) invertebrates grouped as; arthropods ( $\frac{1}{8}$  inches long and larger), annelids, mollusks and nematodes with nematomorpha and (b) 58 species of vertebrates. Species, difficult to distinguish, were grouped together and this produced 38 major categories of vertebrates.
6. An analysis of spatial utilization in time, based on the 1963 data, revealed the following: (a) Significant shifts in area of utilization among and within transects, and situations where there was consistent preference for a restricted area. (b) The causes for periodic utilization of specific areas ranged from physical factors for the more primitive forms, through migrations between reproduction and feeding or overwintering and summer activity sites, to phenological events such as changes in food and cover value. (c) An analysis of the total woodland and field activity showed a greater tendency toward complete spatial utilization of the woods than the fields by the respec-

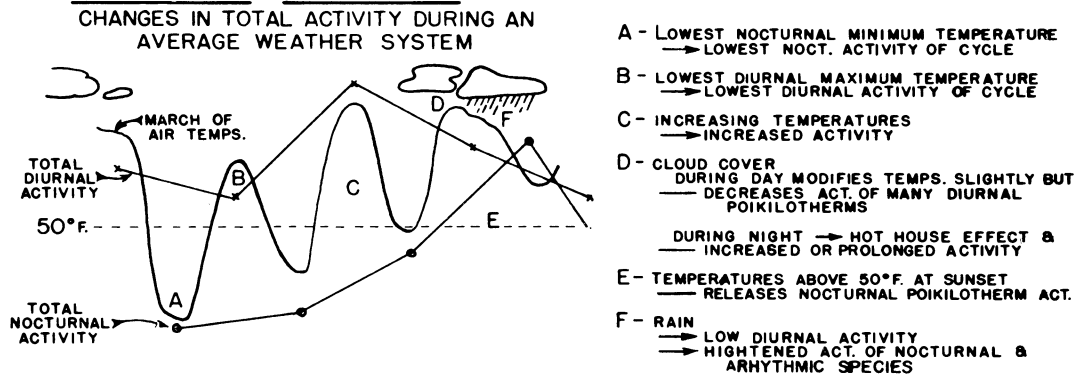
# A SYNOPTIC OUTLINE OF THE HIERARCHY OF CLIMATIC FACTORS WHICH AFFECT ACTIVITY

## 1 - THE YEAR - ANNUAL DIFFERENCES IN SIZES OF POPULATIONS

## 2 - THE SEASONS - PHENOLOGICAL ACTIVITY



## 3 - WEATHER SYSTEMS - METEOROLOGICAL ACTIVITY



N.B. SEASONAL ADAPTATIONS TO MEET AVERAGE METEOROLOGICAL CONDITIONS NEGATE ACT. VS. TEMP. RELATIONS

## 4 - TIME OF CLIMATIC EVENT - CLIMATIC ACTIVITY

- |  |  |
|--|--|
| <p>A - CLOUD COVER</p> <p>I · BEFORE NOON<br/>RETARDS POIKILOTHERM ACT.</p> <p>II · DURING THERMAL MAXIMUM<br/>SUPPRESSES POIKILOTHERM ACT.</p> <p>III · AFTER THERMAL MAXIMUM<br/>PROLONGS HIGH AFTERNOON ACT.</p> <p>IV · AT DUSK<br/>INCREASES NOCTURNAL ACT.</p> | <p>B - RAIN</p> <p>I · DURING THE DAY<br/>SUPPRESSES ACT. OF INSECTS<br/>INCREASES ACT. OF MICROTUS<br/>NO EFFECT ON NOCTURNAL FORMS</p> <p>II · AT DUSK OR SHORTLY AFTER<br/>HIGH ACT. IN MOST NOCT. ACTIVE FORMS</p> <p>III · AT OR TOWARD DAWN<br/>HIGH ACT IN MICROTUS, SOME AMPHIBIANS<br/>ZAPODIDAE DO NOT RESPOND</p> |
|--|--|

FIG. 23. A synoptic outline of the hierarchy of climatic factors which affect activity. Each major level predicates the range of the potential activity at the next lower level. Example—maintenance activity (A, Nov.-April) is low when compared to storage activity (C, Aug.-Oct.) therefore even under optimum climatic conditions of the 3rd and 4th level, the highest daily activity during maintenance will not be comparable to the daily activity during storage. The more primitive forms are usually affected by factors at the 4th level whereas more evolved forms are more independent of climate and presumably more affected by biotic factors. All species in this temperate area seem affected both by the year and the seasons (level 1 & 2).

tive constituents. (d) The activity of the animals at the forest edge was more constant over the 4 periods than in the deeper woods or the field. (e) Activity 150 ft inside the forest edge was usually higher and that of the second 150 ft lower than the mean of the activity along comparable sections in the deep woods. (f) The deviations from static random utilization of the habitat in (a) and (b) above were related to phenological events of short duration while (c), (d) and (e) were general spatial utilization considerations not strictly related to phenology.

7. An analysis of the 1964 data acquired under continuous tracking conditions permitted an evaluation of factors which might affect activity rates throughout most of the active season. The 1964 findings, coupled and integrated with those of the preceding year are summarized in the synoptic outline Fig. 23.

This outline shows locomotory activity in an uncontrolled environment is controlled essentially by biotic and physical factors at 4 levels, each of which controls the activity in the next lower level.

A. Annual Level—A biological phenomenon at the population level included in the hierarchy outline because of its importance in the schema which follow.

B. Phenological Level—Each phenological period (e.g., a) maintenance, b) reproduction, etc.) is characterized by a specific trend and/or level of activity. These phenological changes in activity rates are the most ubiquitous in that examples are found in practically every species and group studied. The activity trends in time at this level are the most predictable of all 4 levels.

C. Meteorological Level—Through each weather system an oscillation of activity occurs. Both nocturnal and diurnal activity are lowest throughout the first day following the passage of a weather system. The highest activity for diurnal animals occurs on the last clear day of the cycle, whereas the highest nocturnal activity occurs on the warmest cloudy night, usually the last night of a cycle. If rain occurs during the night the activity of many species will increase. This response is higher and more consistent than that produced by climatic events and a greater number of species are affected.

D. Climatic Level—The rates of circadian activity, particularly the more primitive forms, are often controlled by climatic events. Within an active period, any deviation from characteristic climatological events could cause a change in the rate of activity. Characteristic climatological events are defined here as the mean march of temperatures for the specific date along with clear skies. Higher forms of mammals and birds are virtually unaffected by factors at this level, at least during the greater part of the summer.

The hierarchy shows that detailed analysis of activity needs be done using carefully selected examples, (a) within a single year's data, (b) taken during one phenological event, (c) on equivalent types of days in the weather systems, (d) taking into account that one climatic factor might either override or reinforce another in their effect on the rate of activity, and

that the time and length of an event can also effect the rate of activity.

8. When community activity is high there is a greater dispersion of the hours of peak activity of the different species than when activity is low.

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