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STEPHEN ALFRED FORBES

WILLIAM TRELEASE

HENRY BALDWIN WARD

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A COMPARISON OF THE
ANIMAL COMMUNITIES OF CONIFEROUS
AND DECIDUOUS FORESTS

WITH 16 PLATES AND 25 TABLES

BY
IRVING HILL BLAKE

Contributions from the
Zoological Laboratory of the University of Illinois
under the direction of Henry B. Ward
No. 292

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY IN ZOOLOGY IN THE
GRADUATE SCHOOL OF THE UNIVERSITY OF ILLINOIS

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INTRODUCTION

The amount of detailed study given in the past to the community ecology (synecology) of land animals has been much less than that devoted to the ecology of particular species (autecology), a much older branch of the subject. One of the earlier studies in community ecology, from a modern aspect, was that of Davenport (1903), who studied the animal communities of a salt beach. The animal communities of deciduous forest, throughout developmental stages to the climax, have been described by Shelford (1912, 1913), with particular emphasis on succession, and its climax animal community by Adams (1915). Adams (1906, 1909) has given accounts of the animal ecology of northern coniferous forest, and he and his associates (1920) have published the results of an ecological reconnaissance into coniferous forest of the alpine type. These papers were qualitative rather than quantitative studies.

Perhaps in part as a result of the valuable findings obtained in quantitative studies by various plant ecologists and by marine zoölogists, of whom Petersen (1911) may be cited as an example, more recent papers in synecology of terrestrial animals have shown a tendency towards the quantitative method of attack. This method has been employed by McAtee (1907), Beebe (1916), Wolcott (1918), Sanders and Shelford (1922), and Weese (1924).

The present paper deals with the results of several studies of land animal communities and their habitats, made at different times under different environmental conditions. It is hoped to bring out some of the facts of the physical and biotic environments of the communities discussed, the composition of the communities as such, and their relation to certain ecological problems of succession, stratification and hibernation. The viewpoint, and with it the point of emphasis in investigation, has been different for different portions of the work. In the study of the animal communities of the alpine coniferous forest and its predecessors, for example, the weight of attention fell on the process of succession of animal forms, and its relation to plant succession and response to physiographic and climatic conditions. When working in the coniferous forest of the low country, on the other hand, the interest of the investigation seemed to lie particularly in the problems of stratification, and the quantitative and qualitative distribution of the animal societies, as correlated with the results of instrumental measurements of such factors as temperature,

humidity, evaporation and light. The study of the deciduous forest community was essentially a winter study, and while carried on in the same way and with the same ends as the last, its emphasis fell naturally on hibernation, and the responses of the animal societies of the lower strata to the climatic fluctuations.

The following account of the results of these investigations may be subdivided into three parts: (a) a study of the animal ecology of alpine spruce-fir forest, including the various fell-field and tundra stages of which it is the climax, (Figs. 1, 2, and 3) (b) a summer study made in pine-hemlock forest at low elevation, with special emphasis on stratification, (Fig. 4) and (c) a winter study of the hibernating forest-floor population of elm-maple forest. (Fig. 5).

The question of the ecological nomenclature employed calls for particular discussion. It has been repeatedly insisted by various ecologists that biotic communities are in themselves units, and that at last analysis they should be so treated, both plants and animals being considered in their intrinsic and mutual relationships, as well as in relation to physiographic and climatic factors (Clements, 1920). A nomenclature covering plant communities in their various geographic, local, stratal and seasonal subdivisions has been long in use and often revised. A similar nomenclature for use in animal ecology was employed by Shelford (1925). The work of Weese (1924) employs an adaptation of the phyto-ecological nomenclature of Clements to the animal communities of deciduous forest. More recently the attempt has been made by Shelford and Towler (1925) to develop a nomenclature for biotic communities, based on both the plants and animals, and expressing in itself the taxonomic characteristics, permanence or the reverse, seasonal and stratal aspects, et cetera. In the present paper the writer has attempted to follow this classification of animal communities. It should be understood that the names of minor communities based on animals which were numerous in the author's collections and appeared to be characteristic of the stratal and seasonal communities discussed, are put forward in the most tentative way. Several seasons of quantitative collecting should be done in the various strata of a single habitat, before the various sub-communities can be finally named after definite species, with any assurance that the species used are the characteristic predominants of the sub-communities named.

In this discussion the term predominant will be used for species abundant in the habitat (and hence giving a part of its characteristic aspect) and for species affecting the habitat from any angle. The term is a general one. A dominant species is one whose effect on the general habitat is decisive, controlling its character and hence entire biota.

True dominance appears to be a rare phenomenon among terrestrial animals, and is noted only in the few instances where, as in the case of

the short-grass plains of the western United States, herbaceous vegetation was probably kept in a sub-climax condition by great herds of grazing animals.

In the case of denuded areas, the activities of tiger-beetles, digger wasps and spiders, feeding on insects blown in by wind, washed by waves or carried by the predominant predators, open the soil and add organic matter. A similar activity on the part of alpine invertebrates, especially spiders, was noted during this study. The animals in question inhabited the areas of rocks and bare soil produced by weathering and erosion. The animals do not control the habitat as do forest trees for example, but exercise an influence on both the habitat and the biota and are known as influents.

Of the animals collected in sufficient numbers to be considered an important part of the various communities, most exert a minor influence and are known as subinfluents. They may be defined as species which, because of restricted numbers, restricted stratal or seasonal occurrence or for other reasons, have a less effect on the habitat, or the biota balance of the community. Types of subinfluents noted were phytophagous insects, predaceous insects and spiders, and forest-litter animals such as spring-tails and millipedes, whose massed effects on changing the composition of decaying plant debris are of considerable importance to the habitat.

Of less importance to the habitat as a whole is a species that is a dominule; such a species is said to be dominant in a microhabitat of restricted size, within the general habitat. Examples noted were groups of phytophagous insects on their scattered host-plants, and groups of scavengers working on decaying organic matter, such as the body of a dead animal. Such dominules tend by their activities to destroy the microhabitat which they dominate (Shelford).

Climax communities (Clements, 1916) which under existing climatic conditions will undergo no further change, have been referred to as associations. Subclimax communities, in process of succession towards the climax, have been called associates. Seasonal communities, characteristic of different periods of the year, are spoken of as seasonal, and stratal communities, occupying different levels of the same habitat, as stratal societies or societies, depending on their permanence.

THE ANIMAL ECOLOGY OF THE UPPER SLOPES OF MOUNT KTAADN

SCOPE OF WORK

The work on which this study is based was done during a reconnaissance made in the summer of 1923. A base was established at an elevation of 2,400 feet on Basin Pond, and another higher up at Chimney Pond, at an elevation of 2,900 feet. An outlying camp was maintained from time to time on the so-called Saddle, at an elevation of 4,275 feet. From these points the various stations were visited and studied, collecting being done at typical places. With the exception of a single maximum and minimum thermometer, instruments for the study of the environment were not available. In compiling the lists of animals for the various stations, certain species have been added from the literature and from information gained in correspondence, particularly in the case of vertebrates; the sources of this information have been given in all cases. Much more data could be gleaned from the published taxonomic lists, if the local habitats were given; as this is frequently not done, many species listed as occurring on Mt. Ktaadn are not included, since it was impossible to place them in the scheme of classification by habitats which was a part of the plan of study. Exceptions to this have been made in the cases of species where the combination of elevation and restricted food habits of the animal make it possible, in the absence of other data, to assign it with some confidence to a given habitat. Where the habitat was known, or could be with reasonable certainty inferred, it seemed advisable, considering the general inaccessibility of the area and the small amount of zoological work that has been done there, to include what published records were available in the present lists. On the other hand, of the many species collected and determined, only such are considered here as approach, either *numerically* or otherwise, the status of predominants.*

In considering the local environments of the various animal communities, it has seemed wise to include rather full accounts of the plants found, taken in part from lists made in the field and in part from published work of various botanists. This is done in general to give as detailed an idea as possible of the animal habitats, and particularly to facilitate further studies of food relations of various phytophagous species to their environment.

*Dominants of Clements (1920) and Weese (1924).

In general it may be said that the principal aim in this part of the investigation was to trace the process of animal succession from bare rock to forest, gaining what light was possible on its factors and causes.

THE ENVIRONMENT

The special ecological significance of Ktaadn is due primarily to its height. This is great enough—in a low and generally flat country—to have made its upper slopes a refuge for alpine species when, at the retreat of the last ice sheet, they were marooned by returning warm conditions (Adams, 1905). On the plant side it is quite obvious, even from a casual glance at the vegetation, that these arctic, or at least alpine species are being invaded by more mesophytic forms that are gradually spreading upward, in the face of severe handicaps of montane soil and climate. The persistence of their advance hints at eventual extinction of the less adaptable and less abundantly growing natives of the Arctic fell-fields. What is true of the plants will be seen to be equally true, even if less immediately obvious, of the animals of these upper regions of the mountain.

The general topography of Mount Ktaadn and its relation to the surrounding country have been so often and so well described (Hamlin, 1881; Tarr, 1900), that the writer will attempt no more than such a sketch as will render comprehensible the location and physiography of the areas studied. The location of the mountain is the north central part of Maine, between the eastern and western branches of the Penobscot river. It is stated by Harvey (1903a) to be $1^{\circ}, 37', 15''$, or about 112 miles, north of Mount Washington, the highest point in New England, and is itself the second highest point. The general conformation is that of a long, table-topped mountain, rising rather abruptly from the surrounding country, and much less subdued, especially on the eastern face, than is the case with many other mountains of the northeastern United States. There are a number of special features other than height that should be considered from the standpoint of a biotic environment.

First of these to be mentioned is area. Ktaadn is remarkable for the large extent of its upper regions, the entire mountain being about nine miles long and of varying width, the whole covering a very considerable area of alpine biota. The central plateau covers more than five hundred acres (Hamlin, 1881) and smaller areas of greater elevation on the south and larger areas in the vicinity of the northern peaks, increase to very respectable proportions the total alpine areas. Such opportunities for the study of mountain life over a considerable extent of territory are rare among eastern mountains, and for this reason Ktaadn presents to the ecologist some advantages over mountains that are its superiors in height. The equal exposure of the mountain to weather conditions on all sides, a fact caused by the isolation mentioned below, is another factor of some

importance in considering the habitat relations. Thus the effect of prevailing winds and other climatic factors on the mountain life show themselves very plainly, uninfluenced by protection from neighboring heights. Another special feature, which will be seen to be important in the consideration of the environment of various communities, is that of drainage. The precipitation, as will be seen when the climatic factors are taken up in detail, is decidedly heavy as compared with that of coniferous forest at lower levels. But the rapid run-off on the steep slopes and the seepage of water from the scanty soil down among the underlying boulders on the level areas, combine with the high evaporating power of the air to rapidly remove the effects of the abundant rainfall.

Certain features of the local topography are also of importance in determining the distribution of the various biotic associates.

Portions of the walls of the glacial cirques, especially prominent on the eastern side of the mountain, are so steep as to support no life, being washed by water and scoured by the detritus of erosion of higher regions. If, however, there is any opportunity for soil and water retention, even here plant immigrants make good their stand, and at least a visiting animal population occurs. On the long dirt and rock slides conditions are more precarious, for frequent erosion gives plants little opportunity to establish themselves save at the borders of these slides, where conditions are somewhat more stable. Here is a characteristic biota, which seems to be in some respects a combination of types found in the various succession stages on the plateau above. Plant succession on the plateau, which may be considered as typical of the process over most of the mountain, involves (Harvey, 1903a) successive associates of crustaceous lichens, reindeer-Iceland mosses, alpine tundra and krummholz, all leading up to the climax *Picea-Abies* forest of the entire region. This conception served as a general guide to the writer in selecting stations for study, although, as will be seen later, it seemed necessary in considering the animals to combine some of these stations and subdivide others. For the present we may accept the stages as given by Harvey and consider their local distribution.

It is customary to consider the distribution of mountain biota as showing at least rough zonation with reference to altitude. This condition occurs on mountains sufficiently high to afford a true climatic timberline. Katahdin, however, appears not to be high enough to possess such altitudinal zonation, and the local distribution of the various plants and animals is determined by other factors than those of altitude. For this reason we look in vain for any set altitudinal order of the various stages of succession, even under identical conditions of slope exposure. Just below the summit occur small mats of the climax trees, though dwarfed and prostrate from edaphic conditions and exposure to strong and continuous winds. On

the other hand, there are wide treeless areas at altitudes far below those of considerable growths of stunted but thickly-growing spruce and fir. In a similar way the earlier stages of plant succession, involving various steps from rock through alpine tundras to krummholz, appear wholly determined by physiographic and edaphic conditions, indubitably earlier stages occurring many hundreds of feet below older ones. This explanation is made in order that it may be understood why the various plant and animal associates are scattered in groups of various sizes very irregularly, and not necessarily correlated with altitude. Thus it will be seen that stations consisting of extensive areas of primitively bare rock may exist, as the one chosen for study did exist, considerably below the altitude where occurred a well established mat of alpine grasses and sedges, representing the second stage of tundra succession.

The *general topography* of the mountain has already been discussed, particularly in its relations to biotic communities. Ktaadn is characterized among eastern mountains by its isolation, rising from the heavily wooded lower lands, with no serious rivals in its vicinity. Its gradual lower slopes rise, in most places to nearly three thousand feet, before terminating somewhat abruptly at the steep ascent to the tableland and upper slopes. This upper region, which constitutes the mountain proper, has been described (Harvey, 1903-a) as a "long, narrow, fish-hook shaped, serrated crest, bristling with peaks and divided by the low central mountain, the 'saddle', into the North and South Mountains from which jut out spurs in all directions, enclosing several well-defined basins." The highest, or West Peak, is in the southern group, with an elevation of 5,273 feet.

The mountain is composed of granite, the lower portions being gray in color and hard, the upper red, and readily weathering to form at first a coarse, and later a finer, granitic soil. The character of the soil in the local areas studied will be taken up in more detail later.

There have been no climatic studies made on Ktaadn, and little has been done in this regard on any of the New England mountains. The United States Weather Bureau maintained a station on Mount Washington (about 160 miles south and west of Mount Ktaadn) at an elevation of 6,293 feet, during the summer months of 1859, through the years 1871-1886 inclusive, and intermittently thereafter, mostly during the summer months, until 1892. Most of the data taken has been published, and some unpublished data have been kindly communicated by the Bureau. The University of Vermont maintained an observation station on Mount Mansfield (4,075 feet) during the summer of 1919, during which temperature, humidity, evaporation, wind velocity and sunshine were recorded. A short study was made on Mount Marcy (5,344) by Adams and his associates (1920), embracing temperatures, evaporation and solar radiation; this included only a period of five days.

The writer had at Ktaadn a maximum and minimum thermometer, whose reading had been corrected by a standard instrument. This was exposed in the shade of spruce-fir forest at Basin Pond (2,400 feet) from June 12 to July 29, with one break between July 23 and July 27. The station was that selected as the lower of two representing climax conditions (Station E). The results of these readings, a maximum and minimum for each twenty-four hour period, are shown as a graph (Fig. 8). It will be seen that the daily variations are considerable, and more marked, on the whole, for the maxima than for the minima. Even in the case of a shaded thermometer, the daily ranges are seen to be:

Maximum	17.5°C
Minimum	2.5°C
Mean	9.0°C

The temperature ranges between different strata, and between open and shaded areas, while not measured, must have been marked.

From July 30 until August 18, with occasional interruptions due to absences on side trips, the same instrument was read twice daily in similar habitat at Chimney Pond, 500 feet higher (Station E-2). This point lies in the great South Basin, at the foot of the steep ascent to the highest peak, and has generally been considered as a region of climatic stress. It did not seem remarkable, therefore, that the daily ranges should be somewhat greater:

Maximum	19.0°C
Minimum	3.1°C
Mean	11.0°C

Since these readings were taken during the latter part of the study, when the temperatures were gradually falling, as is indicated by the graph (Fig. 7), the comparison of the actual temperatures, as contrasted with the ranges, with those taken earlier at the lower station, cannot be of value. The entire data indicate a low summer mean temperature, varied by considerable extremes in both directions.

On Mount Washington, the mean monthly temperatures as observed by the United States Weather Bureau for the years 1873 to 1886 inclusive, are as follows, expressed in °C:

January	-17.8	July	8.9
February	-16.2	August	7.6
March	-14.5	September	3.4
April°	-6.8	October	-1.8
May	-.3	November	-9.7
June	6.5	December	-15.4

It will be seen from these figures that the temperature conditions expressed are relatively severe. The mean maximum temperature over the same period of years was 9.2°C the mean minimum temperature -20.8°C. The monthly mean minima are always below the freezing point. A portion of this data has been plotted as a hythergraph (Fig. 9), which will be discussed later. At present it may be pointed out that the mean monthly temperatures are distinctly lower, and the climate corresponding more severe, than that of Orono, lying considerably farther north, but with an elevation of only 129 feet.

There are no instrumental studies of precipitation for Mount Ktaadn. The records from Mount Washington, however, are significant, and are in decided agreement with what has been observed and reported—but never actually measured—for Mount Ktaadn. Both mountains lie sufficiently near the sea to be, in general, subject to a maritime climate as distinguished from a continental one, modified by such factors as their altitude may serve to produce. The effect of this on precipitation is greatly augmented, as the upper slopes are sufficiently high to “intercept moisture-laden clouds and precipitation is almost daily and frequently excessive” (Harvey, 1903-a). On about half the days of the writer's visit, there was more or less rain, either on the upper slopes or over the entire mountain. This was frequently of many days duration, and sometimes almost torrential in character. The mountain has always had a popular reputation for heavy precipitation. Judging from the recorded conditions on Mount Washington, as well as from the observations of various persons on Mount Ktaadn, the weight of precipitation must fall as rain during the warmer season. But the reports of lumbermen who worked from Basin Pond (2,400 feet elevation) for several winters, indicate the presence of a heavy winter snowfall. In general it may be said that abundant precipitation occurs, and the xerophytic aspects of some of the plant communities are due to other factors, such as rapid run-off and high evaporating power of air. The hythergraph (Fig. 9) gives the condition on Mount Washington. It will be seen that there is a large precipitation, well distributed, and falling more in the warmer portion of the year.

The only study of evaporation on northeastern mountains, so far published is the short study of Adams (1920) on Mount Marcy, already referred to. Here there was a correlation between increased altitude and increased evaporating power of air, apparently modified for certain stations by the character of the plant cover and the amount of available moisture in the substratum. But even without measurements, it is evident that evaporation on the upper slopes is very great. The wind velocity, referred to below, coupled with the presence of only a thin soil and scanty plant cover, especially in the upper stations, makes for a high degree of water loss. In spite of the abundant rainfall, little or no standing water is found

in depressions of the rocks, except as these are of considerable size. The ground and alpine mat are soon dried on the surface after even the heaviest rain; the great evaporating power of the air thus offsets some of the effects of the large precipitation.

The scanty data on air movement, aside from general observations not made with instruments, come from Mount Washington, where the average velocity over a period of twelve years was 105 miles per hour. The velocities of wind on Mount Ktaadn are apparently of the same order, although there have been no measurements taken with instruments. It is a matter of common observation that very strong winds are the rule, and the vegetation shows the same modifications of growth-form (Harvey, 1903-a) that have been described for the plants of the higher mountain. This high rate of wind velocity has been noted in connection with evaporation, and it no doubt increases the stress of the other climatic factors, such as temperature and precipitation extremes, in the effect on the biota.

Studies on light are wanting, the nearest approach being the solar radiation studies carried on on Mount Marcy by Adams, with the aid of black and white spherical atmometers. These showed a general increase of light as the upper stations were approached, correlated with the decreasing plant cover.

In an attempt to get some idea of the conditions of the soils of the upper slopes, with particular reference to plant and animal succession through the various habitats, a number of soil samples were collected from various stations and later submitted to chemical and physical analyses. The results are given in Table I. Two important soil factors, temperature and hydrogen-ion concentration, were not investigated for lack of proper equipment. The results are of some interest, as showing certain apparent differences between tundra and early forest soils, in montane conditions. It will be seen that of the dry matter (the proportion of water not being considered as significant because of the time that elapsed before the analyses could be made) the greatest percent of inorganic material occurs in the sample taken from early (grass) alpine tundra at station C (Fig. 1), while the difference in this regard between the late (heath) alpine tundra at station C-2 and the early forest (krummholz) stage at Station D (Fig. 2) do not seem significant. Correlated with this is the fact that the first of the three soils named possesses the lowest organic content (39.6 parts per hundred) while the difference between the amounts of organic matter in the heath tundra and krummholz (respectively 75.5 and 74.1 parts per hundred) is insignificant. It might appear from this that the qualitative changes from a purely mineral to a partially organic soil have taken place during the gradual transformation of grass to heath tundra, and that by the time the latter is reached the soil if deep enough is able to support the krummholz, as far as wind, moisture and other climatic conditions permit it to become established.

The nitrogen relations are less simple, and perhaps averages of further samples would alter them. They indicate a higher percentage of nitrogen for the late than for the early tundra, but a surprisingly low nitrogen percent for the krummholz soil. Adams (1920) found a somewhat higher nitrogen value for the krummholz as compared with the tundra soil, as would naturally be expected. The acidity figure, given by titration with $n/100$ $\text{Ba}(\text{OH})_2$, is highest for the krummholz soil; the relatively low acidity of the soil from heath tundra, as contrasted with that from grass tundra, is difficult to account for. It is likely that the investigation of the specific acidity of these soils by the methods of color indicators would yield more illuminating results.

The primary soil formed by erosion of rock is at first a purely mineral one. With the process of biotic succession, the remains of organisms, beginning with the remains of the pioneer plants and animals, add more and more organic material. This is indicated by the increase of organic matter and corresponding decrease in purely mineral material, noted in the comparison of soils from early and late tundra stages. It is an ecological truism that this process is accompanied by the process of plant succession. The details of the accompanying animal succession, as observed in the alpine communities under consideration, will be considered.

THE BIOTA

The peaks and upper surfaces of Ktaadn display large rock areas, tundra-like stretches, and compact islands of krummholz. It is over these areas that the process of succession was studied. Before, however, going into the details of the various stations, and the plants and the animals found there, it will be necessary to say something of the animals of this upper region as a whole, and especially of the vertebrates, which from their larger size, better powers of locomotion, and superior powers of adaptation, show a more general distribution over the upper slopes, and less restriction to the minor succession stages than the invertebrates. In fact, with a very few exceptions which will be spoken of in due course, it might be said that the vertebrates of Ktaadn present two, and only two, great communities, and that even between these two there is considerable overlapping of particular species, or rather, that one community, the climax, possesses a total vertebrate population inclusive of all or nearly all the species of the entire area, while the other, subclimax area is inhabited by a vertebrate population composed of certain species of the climax animals, while others do not appear in these early associates. It will be seen from a comparison of the tables (Tables II, III, IV, V and VI) that the number of vertebrate species appearing in the subclimax stages, but absent from the climax, is extremely small; indeed, perhaps a more extended investigation of the climax would show that there were none. These two commu-

nities are those of the heavily wooded belt of coniferous forest from which the steep-walled upper slopes abruptly rise and the alpine plateau itself.

It is not to be understood that any distinction can be drawn, separating the animals of one taxonomic group ecologically from those of other groups inhabiting the same area; we cannot speak of "vertebrate associations." On the contrary the community, as a biotic unit, must be considered as made up not only of all the animals but of all the plants of a habitat, and even these organisms present important relations with the physical environment, as well as with each other. But when it happens, as in the present case, that a group of animals ranges indifferently over a series of associates, to the individual stages of which certain other animals are more closely confined, it would seem to make for brevity and even for unity to discuss them as a unit in their relations to the entire diversified series of habitats over which they range. This is in agreement with the usage of plant ecologists (Clements, 1916), who consider that a formation, such as the coniferous forest (climax) which we are considering, is composed not only of the areas dominated by climax species but also of areas dominated by subclimax species; in this sense, the subclimax rock, tundra and krummholz stages are a part of the formation. It is interesting to see that the larger animals of the tundra are almost identical with those of the climax forest. It suggests that the larger animals, especially but not wholly vertebrates, use the subclimax area as a part of the formation, in accordance with the conception stated above. A similar condition has been suggested (Shelford, 1913) for the relations of some of the larger animals, especially mammals, to the various subclimax stages of deciduous forest.

So far as known, amphibians and reptiles do not occur on the upper slopes. The long distance from suitable breeding-places is probably the reason for the absence of the former, which, as will be seen, are fairly abundant in various places lower down.

Small birds appear not to frequent such unprotected places as the plateau of Ktaadn, despite the fact that there is abundant food in the form of numerous insects and fruits of the thick-growing ericads, especially blueberries and cranberries, but also *Cornus canadensis*, bearberry, and other fruits. Comparing the tables (Table IV, V) the marked absence of small passeriform birds will be very evident. Two forms, the junco and the white-throated sparrow, do occur, but they are exceptions among a much larger number of small birds that stay behind in the lower forest. Of the few birds listed, a large proportion are raptorial. The goodly population of small mammals of the upper regions, coupled with the fact that they are perhaps more easily seen and captured on the open tundra than in the thick lower forest, may account for this. Besides, these birds are powerful in flight and able to maintain themselves in the constant high winds as the smaller species are unable to do. They hunt over the lower

forest, however, as well. The grouse is probably a visitor, coming to feed on the abundant fruits of the heath plants.

Considering the mammals of the mountain (Tables II, III) we find that a larger number of species is listed from the tundra and krummholz than is listed solely from the climax forest. Of course, it should not be overlooked that the list is actually much smaller for the tundra, since all the forms found there, or almost all, are found also in the spruce-fir forest. But if we should strike out from Table III the species which are largely associated with the local, waterside communities, such as pond- and streamside animals, we see that the proportion of forest-dwelling mammals that range more or less freely out onto the tundra is even larger than that suggested by the lists as they stand.

Adams (1920), in speaking of Mount Marcy, says "No evidence of permanent residents among vertebrate life were found by us in the alpine area." He quotes Batchelder (1896 and correspondence) however, on the presence of several species of mice and shrews.

Of the mammals listed for the upper stations of Mount Ktaadn, three, the white-footed mouse, the red-backed mouse and the short-tailed shrew, live as summer residents, at least, on the open tundra among the piled rocks and alpine turf. The red squirrel is a frequent visitor in these areas, but his true alpine home is among the krummholz, as might be expected, and the same is no doubt true to a less extent for the porcupine, which appears to den indifferently, in summer at least, "in the fir scrub and rock heaps" (Dutcher, 1903). The varying hare appears more abundant, to judge from the "sign," in the krummholz, but it too appears to occupy the tundra to some extent, since Dutcher took it "on the tableland." He gives the masked shrew only as a krummholz animal, whereas from the report of Batchelder it probably could be found by extensive search on the tundra.

The case of the bog-lemming is of some interest. Dutcher, in 1902, found the whole mountain top showing abundant old microtine sign, but was able in extended trapping to take only two specimens, which were taken from the krummholz. In 1923, the writer found the evidences of a large colony of microtines on the grassy tundra of the tableland, just below the summit, consisting of characteristic holes, run-ways and grass-cuttings. Extensive trapping failed to take a single specimen here or in other localities, and the work appeared to be old and disused, but probably, from its appearance, had been occupied at least during the preceding summer. Two other points are of significance in this connection. Dutcher, in two months trapping with about ninety traps, covering all the typical areas of the mountain, took only nine specimens of the white-footed mouse, and states that they are not abundant. On the other hand, he does not mention the red-backed mouse as occurring on the upper slopes at all. The writer found, in 1923, that these last two animals were

very abundant at all levels, and especially at the upper stations. These facts are suggestive, if no more, in the light of work that has been done in this country and abroad on cyclic fluctuation in the numbers of mice and other animals in a given locality (Elton, 1924; Howell, 1923; Seton, 1920). These authors suggest a periodical fluctuation in numbers of many animals, to be explained, in part at least, by cyclic climatic changes, and for some species of mice a 10-11 years cycle has been proven (Elton). Nothing is known of the climatic conditions on Ktaadn or the other New England mountains during the years 1902-1923 inclusive; but the markedly different findings of Dutcher and the author, using the same methods of study on two species occupying the same area, suggest a similar rhythm of increase and decrease for these two species. It is known that several species in a given area may thus increase and decrease together, or within a year of each other. These things suggest also the value of observation being carried on in alpine areas through a series of years, if this could be done for a single locality.

The carnivores of the upper stations of Ktaadn are three in number, as reported. Nothing is known of their abundance there, although the guides report the foxes fairly common in winter, while the lynx has been reported as a winter visitor. The small brown weasel was taken by Dutcher in the krummholz, but since he says it is abundant at all altitudes, it must be found also in the upper tundra regions where it would find a rich prey among the teeming rodent population. The larger carnivores, especially in winter, probably feed extensively on the varying hare.

The most interesting animal of the Ktaadn tundra, now no longer found there, was the woodland caribou. Up to about twenty-five years ago, the winter feeding grounds of these animals were the tundra areas whose mosses and ericads, cleared of snow by the winds, furnished an abundant pasturage. About that time the herds were slaughtered or driven off, and the survivors no longer visit the mountain or indeed the state. Harvey says that the caribou herds came "from the north" and Dutcher that there had been "two migrations of caribou from Northern Maine," the last within six years of his visit. On the other hand, Mr. Dudley told the writer that the migration to and from the mountain was annual, the animals passing the summer in the bog-forest which covers so much of the adjoining area, and is interrupted by more open boggy areas. No doubt the first two statements apply to general migrations by which at varying intervals the numbers of these animals were increased in the whole region, while the last refers to local seasonal migrations. Ecologically the caribou is of interest as a typical tundra animal which, living in the forest, has as far as possible maintained its tundra habits, clinging to the scanty areas of low and high tundra that break the great expanse of ever-green woods.

Considering the tundra vertebrates as a group, both in their biotic and physical environmental conditions, we may say that with one important exception, the caribou, they are a group of coniferous forest animals which have made themselves at home in the earlier successional stages of that habitat. For certain of the lower forms this was impossible, either because of breeding habits restricted to water or for other reasons; thus we find no amphibians nor (s. f. a. k.) reptiles in the upper regions. For animals that can bear the more stressful climatic conditions of the upper areas, the higher stations furnish a region of abundant food supply, probably more so than is found in the forest itself, considered as a whole. For certain types of animals, especially those that can take refuge in rocks and stunted scrub, the tundra or krummholz or both furnish entirely adequate shelter and materials for abode. Thus we find a very large percentage of the woods mammals, especially the smaller species, habitually occupying the tundra and krummholz stages as well. A considerable number live entirely on the tundra; to this group belong the white-footed mouse, short-tailed shrew, red-backed mouse and probably masked shrew and weasel. Another group makes its abode in the krummholz and feeds on the tundra; here belong the red squirrel and varying hare, and perhaps the porcupine. Still a third group, while making its headquarters in the spruce-fir forest, are temporary residents of krummholz and tundra; these are the red fox and Canada lynx, and perhaps the woodchuck, concerning whose occurrence at the upper stations, however, little is known. The caribou and probably the bog-lemming are, on the other hand, true tundra animals.

If we now compare the number of forest birds found in the upper stations with the number of forest mammals found there, we see at once that the proportion is much smaller, and only a very few of the smaller species are found, of which the hardy junco may be named. As far as at present reported, about one-half of the forest species occurring also on the tundra are strong-winged raptorial forms, and if we omit the somewhat doubtful occurrence of the ruffed grouse in considerable numbers, more than half. The relative absence of small birds as compared with small mammals is particularly striking. The food supply, as has already been suggested and as will be seen more clearly when the invertebrates and plants are considered in detail, is probably more abundant on the tundra and equally abundant in the krummholz, as in the climax itself. The materials for abode, the importance of which was suggested by Shelford (1913), must be equally well supplied by the krummholz. There is no reason to consider enemies more abundant; indeed there is some evidence, based on various carnivores which do not reach the upper stations, that they are less so.

Shelford (1914) has shown that among stream animals the communities may be divided on the basis of extent and nature of response to varying strengths of current, which is the dominant physical factor in that habitat.

There seems to be considerable evidence that wind is one of the dominant physical factors in mountain climates in general, as will be recalled in connection with what was said concerning air movement under the climatic environment. There is a huge literature on the effect of this factor on the growth-form of alpine plants, where the results are very marked; this has been treated for Ktaadn by Harvey. Animals, on the other hand, adapt by functional response or mores (Shelford) rather than by structural changes. This seems suggestive that the restriction of small birds largely to the forest itself, while the small mammals are equally or more abundant on the upper slopes, may be a response to the physical factor of air movement, which thus acts as a restrictive factor in the local distribution of these animals. In this connection it may be said that there appears to be some evidence of the action of this factor on the distribution and response of certain Ktaadn insect types, as will be seen later.

Pardosa groenlandica (Rock) Associes

As a type area for study of pioneer animal conditions, a station, to be known in this discussion hereafter as Station A, was established on the northern slope of the mountain, at an elevation of 4,800 feet and studies made here were supplemented by other studies made in similar habitats. This area, which has been fully described from a geological standpoint by Smith and Sweet (1924) was several acres in extent, large enough to be typical of much biologically similar territory in the upper areas. The surface consists of small rocks, partly rounded by the processes of weathering and attrition, interspersed with some larger ones and with a few large boulders scattered here and there. The surfaces of the rocks, large and small, are largely covered with crustaceous lichens, and to these and to some foliaceous forms and some lithophytic mosses the vegetation is chiefly limited. These plants are characterized as pioneers by their independence of other forms of life, either plant or animal. A slight invasion of alpine tundra has occurred in the form of isolated islands, small in extent, among which the growth of deer-hair (*Scirpus caespitosus*) is most conspicuous. The characteristic plants are the crustaceous lichen *Buellia geographica*, which is the most abundant plant; the foliaceous lichen *Umbilicaria*; and the mosses *Andreaea petrophila*, *Rhacomitrium sudeticum* and *R. acidulare*. This is an area of considerable slope and rapid drainage has not permitted the retention of much water or of the granitic fragments of erosion which are the forerunners of soil. It is also an area of great exposure to the high winds and of great temperature variations within short distances (Smith and Sweet).

Important effects may be accorded to certain animals of the rock area, whose influence on the scant granitic soil produced by the erosion of the rocks, must be similar to those mentioned above as produced by tiger-

beetles and digger-wasps on lake beaches (Shelford, 1913). Judged by these standards the influent animals of the *Pardosa groenlandica* (Rock) Associes are: *Pardosa groenlandica* (Th.), *Lephtyphantes* sp., *Epeira carbonaria* L. Koch, and possibly *Caecilius* sp., the last, however, being a resident phytophagous form.

Certain other forms are predominant to the extent of being conspicuous from numbers, and hence giving a characteristic aspect to the associes. These have a less direct effect on the habitat, and some of the more conspicuous are undoubtedly wind-blown from adjacent habitats. Such forms are not important, and their influence on the habitat is distinctly lesser. They are therefore called subinfluents. Here may be listed *Circotettix verruculatus* (Kby.) and *Upis ceramoides* (L.), together with certain cicadellids and aphids.

This animal population is hardly more varied than the plants, but very interesting in its relationships. An examination of the lists of species (of which only characteristic predominants are given above) shows them to be made up of two distinct elements, local animals characteristic of the area, and winged visitors coming or blown from adjacent communities. These, in turn, are divided into two groups, phytophagous and carnivorous. The phytophagous animals which are at home in this community appear to be: first, the psocids, which, with their cocoons, were common on the undersides of rock, where they breed. They are lichen-feeders, and must find abundant food. The snapping locust is given by Morse (1921) as a form partial to such areas. Probably most or all of the other phytophagous forms are true inhabitants of adjacent tundra or krummholz areas. The spiders form an interesting group in this associes. The webs of *Lephtyphantes* are found in rock crevices, protected from the winds. Of *Epeira carbonaria* Emerton (1914) says that it makes "a round web between the stones which it closely matches in color, and among which it falls at the slightest jar." The large *Pardosa groenlandica* is a true inhabitant of this rock region and, like the last named species, is very sensitive to footfalls on the rocks, disappearing into crevices when disturbed.

It will be seen that the animal population which lives as permanent residents in this pioneer stage is represented by few species. The native phytophagous animals could hardly supply food for the several species of predaceous forms, but a continual stream of visitors (perhaps blown) from the neighboring more richly populated areas seems to supply their needs.

Deltocephalus (Sedge) Associes

Unforested area, apart from rock surfaces, occupies a large extent of the upper fifth of Ktaadn, and shows several aspects. Its alpine nature is indicated by the presence of *Dispensia lapponica*, *Rhododendron lapponicum*, *Salix wa-ursi* and *Arctostaphylos alpina*, all found frequently in exposed situations.

Early stages in tundra development appear in many places where soil, beginning to accumulate among boulders, is able to support fructifere lichens, such as *Cladonia*, mosses and liverworts such as *Bazzania trilobata*.

For the study of these conditions a station was established on the alpine tundra of the tableland below the summit, at an elevation of 5,060 feet (Fig. 1). Two pioneers among vascular plants, *Scirpus caespitosus* and *Arenaria groenlandica*, which appear at the earlier stages, have largely disappeared with the increasing acidity of the raw humus which develops from vegetation under low summer temperatures. Various sedges and grasses have formed a definite turf. Xerophytic mosses also are frequent, a few lycopods, and *Potentilla tridentata*. Less commonly occur *Prenanthes nanus*, *P. Bootii* and *Solidago macrophylla*. In this stage of tundra development a very large proportion of the plants are cryptogamic or anemophilous. To the latter the high winds are decidedly beneficial in transportation of pollen and seeds. Of the forms enumerated only *Arenaria*, *Potentilla* and—for pollination only—the less frequent *Prenanthes* and *Solidago* are dependent on animals.

For the purposes of this discussion, it will not be wise to attempt a detailed division of the plant associates of the early and late tundra series. Abundant lichens are: *Cetraria islandica*, *Cladonia rangiferina* and *C. alpestris*. *Polytrichum* is present in several species. *Lycopodium Selago* is conspicuous in rock crevices. Dominant tundra forms are *Juncus trifidus*, *Deschampsia flexuosa*, *Scirpus caespitosus*, and the flowering plants *Arenaria groenlandica*, *Potentilla tridentata*, and *Solidago cutleri*. Subdominant species include *Hierochloa alpina*, *Carex brunnescens* and *C. rigida Bigelowii*. *Diapensia lapponica* and mats of *Salix uva-ursi*, *S. herbacea* and *Arctostaphylos alpina* occupy considerable areas. In the later stages of tundra development *Vaccinium uliginosum* and *Vitis-Idaea minus* dominate, while *Kalmia polifolia*, *K. angustifolia* and *Ledum groenlandicum* constitute extensive stands in many places.

Turning now to the animal associates of the tundra, and to Station C in particular, the increase in number of species of animals over plants in this first step of succession is greatly marked, and considering that the plant list is probably much more nearly complete than the lists of animals, this fact is even more striking. A large number of groups are represented, and animals of all habits of life, phytophagous, predaceous, and parasitic. This associate, much more than was the case with the preceding one, is a self-sufficing unit, a literal microcosm (Forbes, 1887). It might almost be said that, whereas a scarce, little varied biota existed on the rock areas, the increase of plant variety by arithmetic ratio on the early tundra had been accompanied by an increase of animal variety in algebraic ratio. The selection of predominants is rather difficult, since probably no single species dominates the habitat as, for example,

some plants dominate their habitats. But the most numerous animals, which by their numbers probably produce the maximum animal effect on the habitat, are undoubtedly the cicadellids, which are present in large numbers and some variety. There is besides a considerable population of other phytophaga, among which certain aphids are noticeable, but neither for numbers nor variety do they approach the leaf-hoppers, of which a number of undetermined species have been noted.

Animal subinfluent, exerting a degree of influence on the sessile plant dominants by eating foliage, or affecting the numbers of phytophaga by preying on them are, in part: *Deltocephalus pulicaris* Fall., *Cymus luridus* Stal., *Aphis* sp., *Epeira displicata* Hentz., *Pardosa muscicola* Emerton.

Subinfluent, generally less numerous and exerting influence to a lesser degree are: *Macrosiphum pisi* Kalt., *Psylla* sp., *Elasmotethus cruciatus* (Say), *Rhopalosiphum* sp., *Phaeogenes hemiteloides* Ashm., *Acidota crenata* (Fab.).

Predominants, present in such numbers as to be conspicuous, but whose relations to the biota of this associates are not sufficiently well known to admit of more detailed ecological classification, are: *Coenosia nigrescens* Stein., *Mitopus morio* Fab., *Acropiasta* sp., *Micropterys montinus* (Packard), *Clepsiorthus assiduus* (Cress.). Of less importance appear *Megaselia rufipes* Meig., *Schoenomyia litorella* Fall., *Asaphes americana* Gir., *Salpingus virescens* Lec., *Epurea* sp., *Aenoplex betulaecola* Ashm.

It will be seen that a considerable number of predaceous forms feed on the plant-eaters. Among these the Pardosas are most abundant. Other spiders and nabids are also present, and a large number of parasitic Hymenoptera. The only strata are ground and herb, but characteristic ground-dwelling animals were less abundant than herb-living forms. Only two species of ground-beetles were taken, one in the larval stage, and two staphylinids. A careful search for animals dwelling in the ground was very scantily rewarded. During the summer apparently most of the animals of the shallow soil leave it for life on the surface.

Cymus discors (Sedge-Heath) Associates

Representing transition between the life of the early and late stages of tundra animal communities, an area, to be known hereafter in this discussion as Station C-2, was selected. This was near the summit and consisted of mixed patches of grassy tundra, intermixed with heath plants, the latter representing the later condition of tundra. This area, as well as others similar to it, was examined by the usual methods of collecting and study.

Subinfluent: *Cymus discors* Horv., *Lygus pabulinus* (L.), *Hyperaspis bigeminata* (Rand.), *Amblyteles promptus* (Cress.), *Melanoplus femur-rubrum*

(DeG.), *Macrosiphum* sp., *Meadorus lateralis* (Say), *Calophis* sp., *Euceraphis* sp., *Elater moerens* Lec., *Crepidodera helxines* Lec.

Subinfluent (less numerous than those listed above): *Melanoplus mexicanus atlantis* (Riley), *Botanobia frit* L. var., *Winthemia 4-pustulata* Fab., *Bothriothorax novaboracensis* Howard, *Spilocryptus cimbivorus* Cush.

Predominants (prominent in the associates aspect): *Coenosia flavicoxa* Stein., *Hypocera clavata* Lowe., *Scatella lugens* Lw., *Phora aterrima* Meig., *Melanochelia tetrachaeta* Mall., *Berycyntus* sp., *Thanasimus dubius* (Fab.), *Perilampus stygicus* Prov. These are listed in approximate order of abundance.

Judging from the collections, it appeared that the predominant (in the general sense) animals were in about the same variety as in the sedge tundra. The more varied plants support an extensive population of phytophaga, among which no single group seems to stand out with the prominence of the cicadellids in the last associates. The red-legged grass-hopper is a common form and is listed among the subinfluent species, since it is present in sufficient numbers to influence the habitat through its feeding on the foliage. Stink-bugs, leaf-bugs, four species of click-beetles, two of leaf-beetles and two of sawflies feed on the plants. There is some evidence, however, that the animal associates revolves about the various aphids, which are present in considerable numbers. There are several genera and probably several additional species, sufficiently numerous to be very prominent in collections taken by sweeping among the heath plants. The number and character of the predaceous forms taken is also in accord with the conception of aphid predominance among the animals. Six species of ladybugs, one of which, *Hyperaspis bigeminata* (Rand.), should be assigned the status of an animal predominant, the neuropteran *Leuctra* and a number of parasitic Hymenoptera, including braconids and ceraphronids, have been collected from this community; these are all known to prey on aphids either in the adult or larval stage or both. The ground-beetle *Amara* was taken running on the ground, and seems to be rather characteristic, the various Diptera less so. Midges, fungus-gnats, syrphids, hump-backed flies and anthomyiids are constant here, and the last two are possibly to be considered as numerical sub-influents.

Pardosa uncata (Heath) Associates

The heaths mark the climax in tundra vegetation. Plant distribution is very irregular. Previous note has been made of a few species characteristic of locations of great exposure and thin soil, such as *Diapensia*, Lapland rhodora and alpine bear-berry. Many more species are found in slightly more favorable conditions. *Vaccinium uliginosum* is the plant dominant

in large areas. *V. pennsylvanicum angustifolium*, *Kalmia polifolia*, and *K. angustifolium*, each have areas over which they are respectively dominant. *Vaccinium Vitis-Idaea minus*, *Empetrum nigrum*, and *Ledum groenlandicum* are very abundant. Here, of course, pollination is dependent on insect life, which will be seen to be sufficiently abundant. The fruits of the ericads, as in the preceding stage, furnish a very considerable food supply.

Subinfluents: *Pardosa uncata* Thorell, *Mecostethus lineatus* (Scudder)¹, *Athysanus arctostaphyli* Ball², *Athysanus elongatus* Osborn,² *Platymetopius acutus* (Say)², *Anatis 15-punctata* (Oliv.), *Coccinella transversoguttata* Fald.

Subinfluents (less numerous than the above): *Pheletes* sp., *Chloropisca glabra* Meig., *Formica sanguinea* var. Only a small collection of animals was taken from this station, of which the predominant species are listed, together with a considerable number of records taken from the literature on this or similar areas of the mountain. Predominant animals appear to be cicadellids of several species, with the spider *Pardosa uncata*. *Athysanus arctostaphyli* and *A. elongatus* are particularly characteristic as feeding on the dominant plants. In the ground was taken *Pheletes* larvae and under loose stones the ant *Formica sanguinea* var. Two species of coccinellids no doubt feed on small insects that infest the dominant plants. The fly *Chloropisca* belongs to a family largely characteristic of meadows and is perhaps an immigrant—or blown in—from the grassy tundra.

Linyphia nearctica (Krummholz) Associates

Where slight depressions in the expanse of the tundra have accumulated sufficient humus and offered initial protection from wind, fir and spruce have developed as definite islands. These two forms, *Picea mariana* and *Abies balsamea*, in separate stands, cover large areas on the saddle and the slopes above. So closely do the individual trees grow that it is difficult to force a passage through them (Fig. 2). The extreme stature is attained at the most western point of the "saddle" (Harvey, 1903a), where the trees approximate ten feet. Here then, as over the entire mountain and in the lowland of the immediate vicinity, the climax plant stage is *Picea-Abies* forest.

The shade of the close-growing trees is so thick that in many places there is practically no forest floor vegetation. Where mosses appear, a means of retaining moisture is furnished. In such a situation the death of a tree offers a wind-protected, well-watered opening. Such a spot becomes populated with plant species characteristic of openings in the

¹Morse (1921).

²Osborn (1915).

coniferous forest at lower levels. *Amelanchier oligocarpa* is fairly common. Although seasonal societies are not sharply differentiated as a rule, on account of the low temperatures that persist throughout the summer, *Linnaea borealis* var. *americana* is conspicuous only in June. The most abundant species growing on the forest floor are *Chiogenes hispidula*, *Oxalis acetosella*, *Cornus canadensis* and *Trientalis americana*. Associated with them are *Clintonia borealis*, *Maianthemum canadense*, *Coptis trifolia* and *Streptopus roseus*.

The low-growing trees, twisted close to the ground, which constitute krummholz, offer protection to small mammals such as squirrels and hares. They present mechanical obstructions against pursuers, whether cursorial mammals or raptorial birds. Their dense shade and the continuous evaporation from the moss about their roots afford equable atmospheric conditions in contrast with the rapid fluctuations of these and other climatic factors in more exposed parts of the mountain. If the fruits, leaves, bark and roots of the immediate stand do not furnish sufficient food, plenty can be obtained among the heaths of the adjacent tundra.

Subinfluent: *Podisma glacialis* (Scudder)¹, *Gnathosa brumalis* Th., *Theridion zelotypum* Emerton², *Epeira displicata* Hentz, *Notolophus antiqua* L. (juvenile), *Linyphia nearctica* Banks.²

Subinfluent (less numerous than the above): *Neuratelia scitula* Johannsen, *Cystoma pilipes* Lw., *Lycosa* sp., *Scatophaga furcata* Say. The last named could be perhaps best considered as a dominule or subdominule, frequenting the microhabitats supplied by decaying fecal or other organic matter. They are by no means confined to this associes.

The krummholz vertebrates have already been considered. The invertebrates have been less studied than those of some of the other associes; collections made include the forms given. Particularly characteristic are the spiders; *Gnathosa* was taken under stones and in the thick moss, in which it habitually occurs. Two species are listed by Emerton (1920) as particularly characteristic; it will be seen that these, together with a young *Epeira* which the writer found very abundant, are both spinners. *Theridion zelotypum*, according to Emerton, "spins large, coarse webs between the spruce branches, with nests in which the female and her brood of young live." *Linyphia nearctica* is also found on spruce. The irregular, delicate strands of the young *Epeiras* were found by the writer on a warm August day abundantly stretched between the tips and branches of the semi-prostrate, breast-high conifers. The krummholz thus is seen to furnish the first habitat in succession which supplies favorable conditions for any general and varied population of spinners, the few species of this habit found heretofore being confined to spaces between

¹Morse (1921).

²Emerton (1914).

rocks or among low heath plants and grasses. Among the krummholz, on the other hand, the branches of the alpine trees furnish a place for attachment of webs, while the thickness of the growth to some extent protects them from the force of the excessively strong winds.

On the forest floor, we find besides *Gnathosa brumalis*, two lycosids, one of which was fairly abundant.

Thus we see in the krummholz, as illustrated by the spiders, for the first time occurring a definite stratification of animals into societies, a thing not possible in the earlier biotic associates, with their shallow soils and low herb cover.

Another characteristic animal of this community is the White Mountain wingless locust (*Podismalacialis*).

Fungus-gnats (*Neuratelia scitula*) and dance-flies (*Cystoma pilipes*) are abundant under the dense shade of the scrub, where conditions for the former are particularly suitable. Two species of anthomyiids and two of sapromyzids were taken, and their larvae no doubt feed on the abundant decaying vegetable matter. The caterpillars of *Notolophus antiqua* were taken, one of the few Lepidoptera taken or observed in the upper stations, whose high rate of air movement is perhaps less suitable for insects of this character. Among the Hymenoptera are Ichneumonidae, Belytidae and Scelionidae; the second are known to parasitize dipterous larvae.

Rheumaptera hastata (Upper forest) Association

A small collection of animals was made in the upper regions of the climax forest, between Chimney Pond (2,900 feet) and the foot of the steep slide leading up to the plateau and upper stations. The plants are similar to those described below for Station E; this upper climax forest will be known as E-2. The invertebrates taken are listed.

Subinfluent (probably none affecting directly the true sessile dominants): *Rheumaptera hastata* L., *Argynnis atlantis* Edw., *Malacosoma disstria* Hon. (juvenile), *Hepialus mustelinus* Pack., *Acronycta* sp. (juvenile), *Psocus* sp., *Platynus sinuatus* (Dej.), *Galerucella cavicollis* (Lec.), *Coccinella* sp. (juvenile), *Simulium venustum* Say.

Here psocids were abundant, feeding on lichens. The ground beetle *Platynus sinuatus* was taken among stones and mosses on the ground, and the leaf-beetle *Galerucella cavicollis*. On the forest floor occurred the larva of one of the coccinellids. Three species of Lepidoptera were taken from this station, the spear-marked black (*Rheumaptera hastata*), swift (*Hepialus mustelinus*) and a dagger (*Acronycta*). The number of these and other Lepidoptera in the climax forest, as contrasted with the great scarcity of this order at the upper stations, suggests that, as in the case of the birds, air movement may be a factor in their local distribution.

This is almost certainly the case with species like the swifts, which even in the forest do not appear to fly usually at any great height. The spear-marked black was an abundant species throughout the lower forest, but was not observed or taken at any of the upper stations.

Sciurus hudsonicus (Spruce-Fir) Association

The studies were mostly made in the climax *Picea-Abies* forest of the South Basin at Basin Pond. The elevation was 2,400 feet, high enough to illustrate the biota of the mountain sides up to the level of the slides. The station, known as Station E, was situated on a moraine ridge a few rods back from the swampy shore of the pond; in some places *Thuja* ran to the edge of the water. In other spots a strip of *Chamaedaphne* intervened. The ridge itself consisted of a soil of decomposing Spagnum, from which projected glacial boulders and partly buried rocks. The characteristic plants were *Picea* and the abundant and profusely-blooming *Kalmia angustifolia*, *Viburnum cassinoides*, *Amelanchier oligocarpa* and *Nemopanthus mucronata*.

From the plant standpoint, this region is the most mesophytic under consideration in this study. While Basin Pond itself is swept by heavy winds, the surrounding forest offers to animal life ample protection from storms. Food is abundant in berries, seeds, bark and leaves of many kinds. Inaccessibility for human beings may be mentioned as another factor making for seclusion, of importance particularly to the larger animals. As has already been discussed in detail, practically all the vertebrate life in general, and the bird life in particular, center in this part of the mountain.

Subinfluent: *Serropalpus barbatus* (Schall.), *Agelena naevia* Walckenaer, *Amaurobius sylvestris* Emerton, *Epeira trivittata* Keyserling, *Zilla montana* Koch, *Syrphus torvus* O. S.

Subinfluent (less numerous than the above): *Mesopsocus unipunctatus* Müll., *Pogonocherus penicellatus* LeC., *Papilio turnus* L., *Eupethicia* sp., *Leptomeris inductata* Gn.? (juv.), *Olethreutes* sp., *Colias philodice* Godt., *Sarcophaga aldrichi* Parker. (Perhaps the last named should be classed as a dominule, whose true ecological position is that of a predominant in the microhabitat furnished by the decaying body of a dead animal).

Predominants (conspicuous in the habitat, but not further classified ecologically): *Fannia canicularis* L., *Chrysope sordida* O. S., *Camponotus* h. p. *ferrugineus* Fabr., *Aedes fitchii* Felt, *Culiseta impatiens* Wlk., *Platyura subterminalis* Say, *Prosimulium hirtipes* Fries., *Chrysope niger* Macq., *Tabanus astutus* O. S. var., *Xylota curvipes* Loew., *Tinea* sp.

The invertebrates listed are those more prominent in the collections and records. Faunistically they form a rather interesting combination

of alpine and sub-alpine forms with species widely distributed at lower levels. Ecologically the invertebrate predominants appear to be spiders of eight genera and eleven species. There are also two species of ground-dwelling phalangids and two of ground-dwelling mites, so that the arachnid population of the forest floor of this associates is very large and varied. Many live on the mossy ground under the thickly growing conifers and among the crevices of the numerous rocks. In such places are found the rough webs of *Amaurobius*. In scrub, or attached to dead limbs or stubs at that level, we find the orb-webs of *Epeira trivittata*, and *Agelena naevia* builds its funnel-shaped webs among low herbs in openings in the forest. Among the low trees are found the imperfect orbs of *Zilla montana*. The distinct stratification of the spiders, especially the relatively large numbers of ground dwelling-forms, is of interest. One of the dominant physical factors in this as in the other mountain habitats is the strong wind. It is certain that the spinners of erect orbs are at a disadvantage in such conditions, as compared with those which either run down their prey like the *Lycosas* or build low, little-exposed webs like *Amaurobius* and *Agelena*. It was observed that the webs of *Epeira* were soon torn to pieces by the wind.

The insect population is large, both in individuals and species and only certain species will be given particular discussion. In openings of the forest the Locustidae were abundant; the two-striped locust, the northern locust and the banded locust all being taken near the forest margins of artificial clearings; none of these are forest species. Particularly characteristic of such moist forest conditions are the two Cicadellidae, *Deltocephalus sylvestris* and *Graphocephala coccinea*, found feeding on many plants of the lower forest strata. In the ground-stratum was found the staphylinid *Antobium pothos* and the larva of a cephaloid. A number of other beetles were collected, of which the most characteristic appeared to be the cerambycid *Pogonocherus*. In this moist forest station Diptera were very abundant. Tipulidae were common, three genera and species being represented. Four families, whose relations to man are such as to bring their activities much to his attention were unfortunately prominent in the community: the Culicidae were represented by *Aedes fitchii* and *Culiseta impatiens*; the Tabanidae by two species of Chrysops and one of Tabanus; the Simuliidae by *Prosimulium hirtipes*; and the Muscidae by *Musca domestica*. The last named was a man-brought importation due to lumbering operations, but the others are typical and numerous in the natural habitat. Here were found two syrphids, *Syrphus torvus* and *Xylota curvipes*, while the Myceteophilid *Platyura subterminalis* was abundant in favorable spots locally.

The most interesting feature of the habitat was the relatively large number of Lepidoptera as compared with those found in the upper stations.

Eight species were collected, and probably a dozen in all were seen. Evidently the climax forest is the true montane home of this group in general and only hardy species or individuals can cope with the conditions of the open tundra, where they are never abundant.

In general, we may say that the spruce-fir climax shows, by its animal as well as its plant life, that it is in part a wave of upward-pushing biota from the more temperate forest below, invading the lower boundary of the sub-alpine forest. Here we find a large number of species, showing a mixture of the two populations. The climax habitat shows a list of characteristic species, not found in the subclimax stages. These species of the climax are arranged in stratal communities or societies, although this fact was not particularly studied for any group except the spiders; there is no reason, however, to suppose that this stratification does not extend to the whole animal population.

Aeschna (Pond-Bog) Associates

Some collecting was done and the conditions were studied in a semi-aquatic community furnished by a pond-bog near Pamola Pond, at an elevation of 2,700 feet. The pond itself is a small body of water, occupying what is evidently an old glacial depression and held in place by the moraine whose glacial structure, indeed, is very plain at one point where it has been cut through by a ditch in aid of lumbering operations. On the eastern and southern sides of this pond the moraine ridge has a stunted growth of spruce and fir, the climax forest of the Great Basin of Ktaadn. On the other sides, the pond is being invaded by a regular sphagnum bog complex, the sphagnum mat overhanging the deep water close to the shore in spots, and being followed by the typical marsh shrubs, among which *Chamaedaphne* is most common; the stunted *Picea-Abies* forest brings up the rear, and the whole seems to furnish a rather typical example of the filling of a glacial pond by vegetation. Northwest of the pond itself, and connected with it by a flooded bog, is a small, shallow bog-pond, where the process of filling has so far advanced as to give the impression of rather a swamp than a pond, and some of the spruce-fir forest nearby is evidently growing on what was once a part of the old pond. The general environment is shown in the illustration (Fig. 3).

From the standpoint of plant succession, the most significant feature of this small sphagnum bog is its possession of subalpine species, such as *Empetrum nigrum* and *Vaccinium uliginosum*, not found elsewhere until the high slopes above the steep ascent are reached.

The greater number of plants are those common to sphagnum bogs of this latitude. The steps in development from an open pond are plain. Sphagnum forms the basis for *Scheuchzeria palustris* and *Drosera* follows, and later *Sarracenia* with *Vaccinium oxycoccus* and *Smilacina trifolia*.

Carex is represented by *trisperma* and *pauciflora* *Kalmia* is abundant, especially *K. polifolia*, on the numerous islands of soil rising slightly above the water. Individual trees of *Picea mariana* and *Larix laricina*, stunted and unhealthy looking, represent the encroachment of arboreal forms, frequently on small islands separated as yet from the main shore by narrow aisles of standing water (two or three feet deep in late August). At one point *Thuja occidentalis* appears.

The absence of orchids, noted also for Lake Tear bog on Mount Marcy, is explained by Harvey as due to isolation.

The persistence of subarctic forms completely obliterated from other parts of the lower slopes indicated the tremendously slow development of the sphagnum bog. It is, however, being gradually filled in and surmounted by sufficient humus to support mesophytic forms. Near the advancing trees are beginning to appear such plants as *Osmunda cinnamomea*, *Cornus canadensis*, *Clintonia borealis*, and *Nemophanthus* and *Ame-lanchier oligocarpa*.

The air temperature, in the shade and just over the surface of the water varied from 17°C to 20°C, at 3:30 P M on afternoons in August. The temperature of the water, close to shore in the shade of vegetation was 12°C at a depth of 6 inches; at the same depth, but 8 feet out from shore, and therefore in the sun, the temperature ranged between 13°C to 16°C.

Subinfluent: *Aeschna* sp., *Gerris* sp., *Gyrinus affinis* Kby., *Gyrinus lugens* LeC., *Trepobates pictus* (H. S.), *Lestes uncatatus* Kby., *Epeira patagiata* Clerck, *Coccinella trifasciata* L., *Leptura chrysocoma* Kby., *Tetragnatha extensa* (L.), *Misumena vatia* (Clerck), *Philodromus* sp., *Lin-noporus rufoscutellatus* Latr. (?), *Hydrophorus pirata* Lw., *Hilara tristis* Lw.

Subinfluent (less numerous than the above): *Misumena asperata* Emerton, *Dolomedes sexpunctatus* Hentz, *Notonecta* sp. (juvenile), *Sinea diadema* (Fabr.), *Euscelsis humidus* (Osb.), *Agabus discolor* (Harr.), *Hydaticus* sp. (juvenile), *Mamestra* sp. (juvenile), *Platypalpus flavirostris* Lw., *Frontina* sp., *Hyalomyodes triangularis* Lw., *Vespula norwegi-coides* Sladen, *Zaglyptus incompletus* (Cress.)

Dominules (predominant in microhabitats within the associates): *Aphis spireaephila* Patch (numerous groups on scattered Spiraea), *Sminthurus spinatus* MacGillivray, *Sapromyza sheldoni* Coq. (on decaying organic matter).

Predominants (conspicuous in the associates, but not further classified ecologically): *Chironomus* sp., *Siphylurus alternatus* Say, *Tanytus* sp., *Limnophilus rhombicus* L., *Lispocephala erythrocerata* Desv., *Arctocorixa* sp. (juvenile), *Sciara* sp., *Ochthera mantis* DeG., *Diplotaxia versicolor* Lw.

The animal population of this area is listed above (invertebrates) in part only. The list does not indicate, for the animals, any number of

boreal species, though *Coccinella trifasciata* may be so considered (Blatchley, 1910). The habitat showed two strata, water and herb. From the water were taken nymphs of *Arctocorixa*, *Notonecta* *Siphylurus alternatus*, and several species of gerrids, of which one (undetermined) species appeared as one of the numerical predominants. The adults of *Limnopus rufoscutellatus* and *Trepobates pictus* were taken, the latter being more common; also larvae of a *Hydatiscus* and three gyrenids, *G. affinis*, *G. lugens*, and *G. latilimbus*, the first two named being predominants. Here also was taken the larva of the pond-lily chrysomelid, *Galerucella nymphaeae*, on the yellow lily, and a trichopterous larva *Limnophilus rhombicus*. In the damp moss and debris around the roots of the swamp-plants, was found the dytiscid *Agabus discolor*.

The stratum of vegetation over the water yielded, to sweeping and individual collecting, a large and characteristic population of swamp animals. The webs of *Tetragnatha extensa* were found on dead branches of dwarf spruce; they contained mostly the remains of chironomids. The crab-spiders *Misumena asperata* and *M. vatia* were found, the latter living and breeding on *Kalmia*. Young *Philodromus* and specimens of *Dolomedes sexpunctatus* were also taken from the moist herbage. Emerton gives *Epeira labyrinthica* as characteristic of this habitat.

From the vegetation was taken *Sminthurus spinatus*. *Spiraea* growing along the edge of the bog was heavily infested with *Aphis spiraeaphila*; *Lygus pabulinus* was swept from the plants, as well as the caterpillar of a noctuid (*Mamestra*). A large population of characteristic flies were taken in flight or resting on the swamp plants. They included *Chironomus* and *Tanytus*, the mycetophilid *Sciara*, the long-legged fly *Hydrophorus pirata*, the dance-flies *Hilara tristis* and *Platypalpus flavirostris*, *Sapromyza sheldoni*, an ephydrid, *Ochthera mantis*, the chloropid *Diplotaxia versicolor*, the anthomyiid *Lispocephala erythrocerata*, and two tachinids, *Frontina* and *Hyalomyodes triangularis*.

Prominent in flight over the water was the dragon-fly *Aeschna*, while the stalk-winged damsel-fly *Lestes uncatus* was abundant along the shores of both ponds.

Other species taken in this habitat, mostly by sweeping from vegetation, are *Eucelis humidus*, from the heath-plants; the spiny assassin-bug, *Sinea diadema*; an aphid, *Macrosiphum*: *Coccinella trifasciata*; an ichneumon-fly, *Zaglyptus incompletus*; two species of saw-fly larvae; and the wasp *Vespa norwegicoides*. Here was taken the old tussock-moth, *Notolophus antivua*. The beetle *Mezium americanum* was probably introduced by the establishment of the lumber camp at Basin Pond, not far away.

The pond-bog community shows in general an assemblage of animals common to such habitats at all levels and in all types of forma-

tions. It is a distinctly local habitat, composed of characteristic species with characteristic mores, and is to that extent ecologically distinct from the coniferous forest climax which surrounds it. It is no doubt undergoing gradual succession, as is indicated by the vegetation, to the climax forest; this process was not studied for the animals, the time only permitting a survey of the most characteristic bog conditions. Enough has been done to indicate that the community is distinctly a local one, with an animal population distinct in composition and mores from that of the surrounding climax, by which, no doubt, it will eventually be succeeded.

The Steep Slide Animal Community

A small collection of animals was made, and the conditions briefly noted, on a steep slide leading from the head of the South Basin up to the tundra of the saddle. This station was at an elevation of 3,450 feet. The slope, which was as steep as rocks and earth would lie, was covered in the lower part by washed-down granite detritus, farther up by rocks. Save for lichens, vegetation on the slide itself was practically absent. The sides, however, are being invaded by various plants, among which *Solidago*, *Epilobium* and *Alnus* may be noted, with the usual rear-guard of krummholz spruce. This station showed a rather curious mixture of animals from the extreme stages of succession in both directions. The dominant animal appeared to be *Pardosa groenlandica*, a bare rock species also dominant in Station A. On the other hand, this was the highest station for the amphibians, the common toad (*Bufo americanus*) being observed here. It is known to exist otherwise only in the climax forest, but was here no doubt associated with the upward extension of that forest on the steep slopes. The caterpillars of *Malacosoma disstria* were heavily infesting stunted birch, and the cicadellid *Oncopsis* was found feeding on alder. The former was found otherwise only at levels below this station; the spider *Lycosa albobastata* was found here, and also above on the alpine tundra, while the harvestman *Mitopus morio* and the ubiquitous humblebee *Bremus terricola* occur both above and below; the latter appeared here on the goldenrod. It might be expected that these steep slopes would be a tension line between the animals of the upper plateau tundra and those of the climax forest, but it is interesting to see how well this is indicated by the presence in the same station at this level of animals as ecologically diverse elsewhere on the mountain as *Pardosa groenlandica* and *Bufo americanus*. No doubt this partly explained by the fact that at this level the forest advances directly onto the bare area, without intervening tundra stretches that occur with the shallower soil and greater wind exposure of higher altitudes.

DISCUSSION AND SUMMARY

The climate of Mount Ktaadn, as far as we have actual or inferred knowledge of it, is a rather typical montane climate, showing low mean and minimal temperatures, heavy precipitation and high winds, the last associated with high evaporating power of air. These factors are operative in all areas studied, but show a general increase with altitude and exposure. It is an entirely different climate from that of the low country coniferous forest lying around the base of the mountain and likewise entirely different from the climate of the tundra regions lying near sea level farther north (Fig. 9). Its hythergraph does not show similarity to either of these, although they overlap somewhat during the warmer part of the year. It is much cooler at all seasons of the year than the former, but never reaches the extremely low winter temperatures of the latter. The precipitation is greater than that of either.

From the standpoint of both ecology and faunology, these facts seem significant. There are a number of species found at high altitudes on the northeastern mountains, which are considered as boreal or possessing northern affinities, that is to say, they are identical with, or more or less closely allied to, species living much farther north at lower elevations. We have generally considered that these species, of general distribution at low altitudes during the southern extension of the ice-sheet, found on the retiring of the glacial margin the same climatic conditions at high altitudes that occurred farther north near sea-level, and hence these arctic-alpine areas became refuges for groups of boreal species which were, as it were, left stranded on the mountain-tops. It is interesting to see that the conditions in these areas, as represented by the hythergraphs based on the Mount Washington data, appear those of a climate decidedly different from that of the Ungava regions. Since the species appear to be structurally constant in both places, there must have occurred physiological differentiation and such species are perhaps to be considered as physiological ones. Undoubtedly what is needed here is a study of the physiological life histories (Shelford, 1913) of the same species occurring on the high tundra of the New England mountains and the low tundra of the regions lying farther north. Such information is at present entirely lacking, but a similar phenomenon has been investigated for species of Cicindellidae living both in Illinois and Manitoba; in this case there was a distinct correlation between the life histories of these two widely separated groups of individuals of the same species, and the climatic conditions respectively operative.

Mingled with these truly alpine animals are a number of other forms of general distribution in the northern coniferous forest climax at lower levels, or of even wider distribution, and the population is a mixture of these two main types. This entire population, or series of animal

communities, is involved in a process of succession, by which, as the naked and eroding rock at all levels is gradually becoming covered by the climax forest of the region, the characteristic animals of the areas involved are also undergoing corresponding and progressive changes. The process is complex, involving as it does biotic, edaphic and climatic factors, respectively operative to different degrees in the different stages and under various local conditions. In general it may be said to consist of the following successive associates, leading gradually to the animals of the climax forest:

A biotic community capable of living on bare rock, in the practical absence of soil. The plants of such a community are chiefly lichens, and are independent of animals. The resident animals are forms capable of living on the sparse plant growth, or predaceous forms, including a number of highly characteristic spiders. This community is probably not self-supporting, from the animal side, but its predators depend in part for food on insects blown from adjoining regions. It is distinctly a one-stratum community, subterranean or rather sub-lithic, in part a response to the climatic factor of air movement. This has been referred to as the *Pardosa groenlandica* (Rock) Associates.

A biotic community consisting of the turf of alpine grasses and sedges that come to occupy the first thin soil formed by erosion and the decay of previous organisms, and its animal inhabitants. This shows a considerable increase in plant variety, and a more marked increase in animal variety, consisting of numerous phytophaga and their enemies. It appears to be a self-sufficing biotic community, a microcosm. It is the result of changes, principally physiographic but in part biotic, from the previous community, and is still to a large extent a one-stratum complex, the herbs and their inhabitants. If designated by the group of animals which are certainly most numerous in species and individuals, this stage would be called a cicadellid associates, the *Deltocephalus* (Sedge) Associates.

A biotic community composed of the alpine heath-plants which thrive with the accumulation of a better and a deeper soil, and the associated animal population. This community is also self-sufficient consisting of a varied population of phytophagous forms and various predaceous species. It has been evolved from that just described by a series of changes in which the biotic factors have probably been progressively more important, the physiographic ones less so. It is difficult to fix upon animal predominants sufficiently characteristic to be used in naming this associates, but the *Cymus discors* (Sedge-Heath) Associates has been suggested.

A biotic community consisting of krummholz coniferous forest and its animal denizens. This has been produced from the preceding stages by a complex of factors, which are, however, probably chiefly edaphic and biotic, rather than climatic. The animal population is to a considerable

extent that characteristic of climax coniferous forest, but some large vertebrates are lacking and there are highly characteristic invertebrates. This is a stratified animal community, but the herb society is scanty or missing and the tree stratum is hardly higher, in many places than the shrub society of other forests. From a characteristic animal, this is called the *Podisma glacialis* (Krummholz) Associates.

A biotic community consisting of the climax spruce-fir forest and its associated animals. This is a well-stratified and established formation, whose existence on the area it occupies will be very long under natural conditions. Its evolution, like that of the krummholz, has been edaphic and biotic, rather than climatic, but it is in itself a climatic climax. Under usual conditions, it would be (that is, when not subjected to attacks of such forms as the spruce bud-worm), difficult to name animal predominants; indeed, no animal usually found there dominates the habitat as the forest itself does. But if this association is to be named after one of its highly characteristic animals, it could be called the *Sciurus hudsonicus* (Spruce-Fir) Association.

CONCLUSIONS

The animals of alpine tundra communities show a definite succession, beginning with the communities inhabiting bare or lichen-covered rocks, and passing through subclimax stages until the climax association is reached in the animal community of northern coniferous forest.

This succession includes a gradual change in the animal life, especially as regards species; animals abundant in the earlier associates being absent in the later ones, and vice-versa, and the intermediate stages showing a more or less gradual falling off of earlier species and increase of later ones.

The various animal tundra communities are characterized by predominant or at least characteristic animals with different types of habits or mores, and these, in so far as they have been studied, show an adaptation response comparable with the structural responses of plants under similar conditions; this may be exemplified by the habits of the Pardosas, dominants of the rock animal associates, with those of the Epeiras, first prominent in the forest stages of succession.

The factors influencing the transformation of the earlier associates of tundra are probably largely biotic and edaphic, since the climatic differences of the various tundra areas cannot be decisive, although they have not yet been measured instrumentally. There is every reason to suppose that the animal associates are in the main determined by the plant associates, and that the reverse condition, has been important only indirectly. The indirect effects of the subinfluent consist at least in contributing their dead bodies to the enrichment of the soil.

On the other hand, the physical differences between the tundra environments as a group and the climax and subclimax forest stages appear to be considerable, especially as regards air movement, and may possibly have exerted a decisive influence on certain animals, confining them to the later (forest) associations.

The factors influencing succession over the various tundra areas have been only to a limited degree operative in the case of certain animals, especially but not exclusively vertebrates, and more especially the smaller mammals; such animals show less restriction to the boundaries set by various invertebrate and plant associates, or none at all.

ANIMAL ECOLOGY OF MAINE PINE-HEMLOCK FOREST

SCOPE OF WORK

Of the papers cited in the introduction as dealing in a quantitative way with the ecology of land animal communities, the most elaborate and the one covering the longest period of time is that of Weese (1924). This author, using recording instruments to measure the factors of the physical environment and the method of "quantitative sampling" for the study of the animal population, carried his work throughout the year. His paper presents a very complete account of the annual climatic and biotic cycle of the elm-maple forest where the work was done, the stratal and seasonal societies and their dominants, and the correlations between environmental changes and animal response.

The present portion of this study gives the results of an attempt to apply the same method to the study of the animal ecology of northern coniferous forest. This was of necessity a short-time study, embracing the summer months of 1923, during the latter part of which the most extensive of the biotic studies were made. It is not therefore to any degree a study of seasonal societies, but it is hoped that it will give some idea of the stratal societies and the physical conditions existing in coniferous forest for comparison with those of the deciduous forest as described by Weese for the same period of the summer. A rather large part of the work is concerned with the physical conditions of the habitat. As these are little known it was deemed best to devote a considerable portion of the limited time available to their investigation and the accumulation of instrumental data on the subject.

As it seemed hardly likely that the succession of climatic changes, through so short a period and at this time of the year, would be very marked, particular emphasis was laid on the question of stratification of these conditions, and the instruments were exposed with this in view. The environment was investigated in terms of stratification of temperature, humidity, evaporating power of air, and light. Some of the instruments used not being of the recording type, recourse was had to the expedient of reading them several times a day at periods considered as critical in meteorology.

The biotic data was obtained by the method described by Weese as sampling. It will be discussed in detail later. For the present it may be said that the collecting consisted in taking samples of the animal population of the strata where the physical factors were being instrumentally meas-

ured; the methods of taking these animal population samples were at all times kept uniform. It was not, however, possible to take and study these samples as frequently during the early part of the summer, because of the limitations of time imposed by other duties. For this reason the biotic studies for the month of August are more complete than those preceding.

The birds were not considered in the present study, which from the very nature of the collecting, chiefly concerns invertebrates. The area studied was trapped from time to time, however, to get some idea of the mammals present and their relative abundance. The results of this will be included in a separate portion of the discussion. The forest is too near cultivated areas and too much subjected to human influences, to make the findings on the mammalian population of more than local interest.

ENVIRONMENT.

The area studied is a heavy growth of white pine (*Pinus strobus*), Norway pine (*P. resinosa*) and hemlock (*Tsuga canadensis*), comprising a part of the forest under the charge of the Forestry Department of the Agricultural College of the state university at Orono, Maine. The stand consists of mature trees of large size and, while not virgin, has never been completely cut off, although individual trees have been taken out here and there. A little birch and alder occur, also a few young maples and white ash. The area is southeast of the university campus, and adjoins farm land on some of its irregular boundaries, while on others it is bounded by swampy land covered with young second growth deciduous forest. The elevation is about 115 feet, and the relief is slight, but with a little slope to a swampy brook in the eastern portion.

The undergrowth is scanty; individuals or small stands of a single species constitute the discontinuous vegetation. The intervening ground is covered with a thick carpet of coniferous needles, twigs and other organic debris. The shrub stratum is especially poorly developed. The number of plant species present is increased by the influence of open fields on two sides, south and west. The swamp and young forest on the northeastern boundary contribute a few forms not characteristic of the area as a whole.

Relatively few species of shrubs and herbs were noted in the vicinity of the stations. The shrubs were *Corylus rostrata*, *Rubus alleghaniensis*, *Lonicera canadensis*, *Ribes lacustre* and *Spiraea latifolia*. The most prominent herbs were *Coptis trifolia*, *Maianthemum canadense*, *Lysimachia quadrifolia*, *Aster* spp., *Rubus triflorus*, *Clintonia borealis*, *Solidago* sp., *Cornus canadensis* and *Aralia nudicaulis*.

The lowest part of the woods lies somewhat north and east of the station. In early summer it comprises a swamp through which runs

a small stream. Here occur several forms not seen elsewhere. The most conspicuous are: *Fraxinus pennsylvanica* (a few young individuals), *Cornus stolonifera*, *Typha latifolia*, *Viola* sp., *Onoclea sensibilis*, *Ranunculus abortivus* and *Galium trifidum*.

Along the borders of the coniferous forest, especially towards the north, the following arborescent forms appear, all as young growth: *Amelanchier canadensis*, *Prunus pennsylvanica*, *Prunus virginiana*, *Prunus serotina*, *Populus grandidentata* and *Salix* sp.

It will be seen that many shrubs and herbs are species in general characteristic of northern coniferous forest. Some even appeared among the sub-dominants of alpine spruce-fir forest on Mount Ktaadn. The presence of several species, such as red clover, in this type of habitat can only be explained by the adjacent agricultural lands. To this extent is the forest atypical of untouched habitats of this type. It was, however, the only area available for study that even approximated natural conditions, and the interior region where the collecting was done, as contrasted with the borders, was less affected with these invaders and more nearly agreed with the original forest biota. The general appearance of the habitat is shown in Fig. 4. The interior of the forest, showing the deciduous undergrowth and giving some idea of the stratification of the plant societies, is shown.

The soil was examined by methods used in the examination of the Mount Ktaadn soils, which in turn were adaptations of the procedure of Adams (1920) in the examination of the Mount Marcy soils. Chemical and physical analyses were made, but the specific acidity was not taken. The sample was taken as follows: the pine needles and other forest floor trash were brushed away, and a hole was dug in the ground. A sample of the upper eight inches of soil was shaved off with a spade and placed in a can. The results of the analyses are given in tabular form (Table VII). It will be seen that this mainly a clay and silt soil, possessing much less sand than the least sandy of the mountain soils examined. Its nitrogen content is also higher than that of any of the soils examined for the mountain. Its acidity was much lower than any except the heath tundra. This soil was quite wet during the earlier part of the study, but in the latter part of the summer it became drier and friable, at least down to the depth (about 10 cm) which was examined for animal population. No doubt this was in part due to the rather scanty herbaceous cover over portions of the area examined.

The temperature was recorded by means of thermographs, and self-registering thermometers, the latter being read at critical periods, as will be seen later for the individual instruments. The self-registering maximum and minimum instruments were all checked by a standard instrument, and were in turn used for setting the thermographs. Throughout the

period of study temperature records were taken for soil, shrub and tree strata, and for a considerable period during the latter part of the study records were taken for the dead leaf stratum as well.

The instrument used for the measurement of soil temperature was a maximum and minimum thermometer, which had been corrected by comparison with a standard instrument. This was placed in the ground, just below the layer of dead pine needles and forest-floor debris. The exposure was made as follows: 1.5 m west of the lower instrument shelter (see below), in a plat shaded by young maples and balsam firs, a rectangular hole was dug, .4 m deep, .3 m long, and .2 m wide. This was lined, sides and bottom, with wire-screencloth on a frame, to keep out debris and to keep the sides from falling in. The whole was covered with a heavy grating of wooden bars, overlapping generously on all sides, which was laid on the ground to cover the opening. This grating was in turn covered with galvanized wire screen, on which was placed a mat of dead needles, organic trash from the forest floor, top soil and plants growing thereon, just as it was scraped up from the adjacent forest floor.

The whole was designed to make a chamber, in which instruments could be exposed, surrounded by the soil and covered by the dead leaf layer. The thermometer was exposed in this, a small hole being cut in the wire screen between two of the slats of the grating, through which the instrument could be drawn up, read, set and returned. At other times this opening was kept covered with a piece of bark.

Readings were taken twice daily, at 7 A M and at 7 P M with few breaks in this procedure. During the greater part of the study no attempt was made to take a set maximum (maximum reading immediately after setting), since this exposed the instrument so long to the air temperature that it tended to respond thereto, before it could be lowered into the observation cavity. The instrument, was, therefore, quickly withdrawn, read, set, and as quickly returned, usually before the air temperature had time to affect the mercury, and always before it had time to affect the indicator (reading). The results of the readings appear in tabular form (Table VIII) and in graphic form (Figs. 10 and 11, curve labelled C).

Temperatures of the leaf stratum were not taken until July 19. At that time a soil thermometer was exposed by being thrust 8 centimeters into the leaf and debris layer of the forest floor, in a spot shaded with young firs and birches (none over .8 m in height) 2.5 m east of the lower instrument shelter. It was thought that this would give a more reliable temperature for the leaf layer *on* the ground, than the thermometer exposed in the soil observation chamber *under* this dead leaf layer. The instrument was read twice daily, at 7 A M and at 7 P M, and during the latter part of the study an additional reading was taken in the early afternoon whenever possible.

The data so obtained are tabulated (Table IX) and shown as curve D in the plate and figures referred to above.

The air temperature at the level of the shrub stratum was taken by instruments exposed in an instrument-shelter of the standard Weather Bureau type, with louvered sides and slatted bottom, thus protecting the instruments from the direct effects of rainfall or sunshine, but permitting a free circulation of air around their sensitive elements. Throughout the study a United States Weather Bureau type maximum and minimum thermometer and a thermograph were left in this shelter, which was about .6 m above the ground on the north side of a large white pine. The thermograph placed here was frequently checked with the maximum and minimum thermometer, with which it was exposed. Its records were kept throughout the summer, but as its recording principle was somewhat defective, and it showed a consistent lag of at least two degrees, which could not be overcome by anything that could be done in the way of lightening the drag of the lever and increasing the air exposure of the responding metal parts, the records taken with it have not been included in the present report. In their place have been substituted records taken with the maximum and minimum thermometer.

This instrument, which from its accuracy was used in checking the others used in the study, was read as far as possible twice daily, at 7 A M and at 7 P M. During the latter part of the study another reading, in the early afternoon, was taken daily. The results appear in Table X and as curve A on the plate of temperature data cited above.

A thermograph was exposed in an instrument shelter, of the same type of construction as the one just described, which was suspended 11 m above the ground on the north side of a large pine, in a moderately thick growth of white and Norway pines (Fig. 4). While not at the top of the forest crown, this shelter was among the upper branches and far above the tops of the deciduous trees growing among the first growth conifers. The shelter was suspended by a rope and pulley from a protecting pent-house cover, and could be lowered to change the sheets and check the contained instruments, as was done every Monday and from time to time during the week. This thermograph was a very reliable instrument indeed, gave no mechanical difficulty and checked well, showing little or no lag, with the U. S. Weather Bureau type thermometer, when both were exposed to like conditions. From it was gained the data given in Table XI, and shown as curve B on Figures 10 and 11.

The record sheets on recording instruments were changed Monday morning. The method used in the translation of the recorded curve to figures of maxima, minima and means was a modification of that suggested by Weese. He estimated the mean temperature for each two-hour period on the ruled charts, and used the average of these means as the weekly

mean temperature. It was found by computing charts in this way and by the method of averaging the actual temperatures recorded at the end of each two hour interval that the results were practically identical over the period of a week, and inasmuch as this latter was somewhat of a time saver the method was adopted. Dr. M. S. Johnson, who suggested this method and has employed it himself, states that in all cases the results gained from computing charts by these two methods show insignificant differences, and this irrespective of whether the weekly fluctuations are great or small and the curves in consequence abrupt or smooth. For shorter periods no doubt the actual two-hours means would have to be computed. A base mean was computed in accordance with that used by Weese, that is the average for the week of the mean temperatures existing during the comparatively stable period of the day between 8 P M and 6 A M; this of course was not practicable for the simple instruments used, and was employed only in the case of the thermographs. Besides this the soil and leaf strata hardly show sufficiently marked fluctuations to make the attempt to determine a base or night mean of value, even had recording instruments been available.

For all stations absolute maxima and minima, mean maxima and minima, mean temperatures and extreme and mean ranges for each week of the study were computed; for the upper tree station was figured in addition the weekly base or night means and the deviations (mean) above them. The data is presented in Tables VIII, IX, X and XI, and in Figs. 10 and 11.

Since it has been seen that the soil temperatures show a marked lag behind the air temperatures, in their response to the general meteorological conditions, it will be best to take them up last. The air temperatures show two high points during the study, occurring during the weeks of July 14 and August 11, and were showing another marked upward tendency at the time the study was closed. The lower, earlier portions of the curves indicate the general rise of the spring temperatures up to the time of the July maximum; this is of course broken by minor fluctuations. The study was closed too early to show any traces of the autumnal fall. The actual fluctuations of the temperature as observed are probably not of any great significance; they do, however, show a considerable range of variability in the air temperatures of this habitat as a whole. If we consider now the stratal differences in temperature, we see that, while for a rather considerable period the temperature in the upper tree stratum is above that of the layer of air near the ground, especially during the middle and latter part of the study, still this is by no means always the case, nor as consistently the case as Weese found for similarly placed instruments in Illinois elm-maple forest. This may be explained by the position of the upper instrument which, while high

enough to be independent of ground and undergrowth influences, was not, because of the great height of the trees and the fact that their branches were thickest at the top, in the forest crown but below it, and hence covered by a heavy canopy of branches from the direct effects of the sun.

Of more interest in the present problem are the temperature relations of the layer of air just over the surface of the ground and those of the ground itself and the stratum of dead leaves that covers it. It is an axiom that soil temperatures in general and forest soil temperatures in particular, are more stable than the overlying atmospheric temperatures, and the causes are obvious (Adams, 1915). One of the factors in this phenomenon, the equalizing effect of the layer of forest-floor debris, is of interest in connection with the study made of temperatures found in this latter stratum. It will be seen that the temperature of this latter closely accompanies the soil temperature, but is, on the whole, more responsive to the general atmospheric temperature conditions, as might be expected, rising before the soil temperature in periods of rising temperatures and falling first during periods of falling temperatures. In general, our figures indicate a stratification of temperatures, with the steepest gradient between the leaf and shrub levels, whereas the two upper and the lower strata examined show temperatures accompanying each other more closely. All, however, show a fairly uniform agreement, maxima and minima developing together in the different strata with unimportant exceptions, and the temperature showing a general rise from the lowest to the highest strata.

If we now consider the temperature ranges in the different strata, we see a more complete stratification than is shown for weekly mean temperatures alone. The forest upper strata show a high degree of variation for a single week, and thence the index of variation decreases downward until we reach the soil, where the variations are smallest and the temperature relatively uniform. There is a well-marked difference in the extent of temperature variation between the tree and shrub strata, and some, but less conclusive evidence of stratification between the leaf and soil strata. But the great break, as in the actual mean temperature curves, lies between the leaf and shrub conditions. Here, as in deciduous forest "in summer the temperature increases from the soil upward to the forest crown; the temperature is most variable in the forest crown and least so in the soil" (Weese).

Humidity of the atmosphere was measured at the herb-shrub level and 11 m above the ground. The instrument used to measure the relative humidity of the lower strata was a hair-hygrometer which, after adjustment by a standard instrument, was exposed in the lower instrument shelter with the thermograph and maximum and minimum thermometer used for measuring the temperature of the lower air strata;

this shelter was in turn partly shaded by young maple and balsam fir. This hygrometer was used as the standard instrument, by which the hygrograph in the upper (11 m above ground) instrument shelter was set and checked. It was read twice daily, with a few exceptions, at 7 A.M. and at 7 P.M. During the latter part of the summer an additional reading was taken on most days early in the afternoon.

The only hygrograph (recording hair hygrometer) available for the study was exposed in the upper instrument shelter along with the thermograph used for recording temperature at that level (11 m above the ground, Fig. 4). It was a sensitive instrument, and checked well with the hair hygrometer used to set it, when both were exposed to the same conditions.

The tables (Table XII and XIII) and Figures 12 and 13 give the data obtained from these instruments, which was computed in a manner similar to that used for the computation of temperatures. Here, however, the base mean (Weese) is high instead of low, as the humidity almost always reached 100% sometime between the hours of 8 P M and 6 A M. Absolute maxima and minima, mean maxima and minima, mean relative humidity and total and mean ranges are tabulated for both stations; in addition the base mean for each week and the mean range below it are given for the upper station, where alone a recording instrument was available.

The curve of relative humidity of the herb-shrub stratum shows several high and low points which are not correlated with temperature differences, as far as can be seen. Neither are the extreme differences shown (18% of relative humidity) sufficient to be of any marked significance, since the fluctuations of a single day may reach a figure of 69% at the same station. The curve of mean relative humidity for the tree stratum is consistently lower, with a single exception, than that at herb-shrub level. This is the usual condition, because at the lower station the moisture-laden atmosphere in contact with the more or less damp forest-floor, is less rapidly removed by air currents and its place taken by the drier air coming from over adjacent cleared land. The average difference between these two stations for the period studied was 7.5% relative humidity, as compared with the figure 3.5% given by Weese for deciduous forest. The discrepancy is no doubt due to the fact that the present study was made entirely in the summer, when such differences are at their greatest. While the study of deciduous forest conditions by Weese embraced a complete annual cycle, his humidity data for the tree stratum were not taken during the early part of the summer.

The curves of mean ranges for the two stations (Fig. 13), show a condition of large variation, both relative and actual. Particularly is this true of the tree stratum. This agrees perfectly with the finding given

for deciduous forest that between the herb and shrub strata on the one hand and the tree stratum on the other there is "almost invariably greater mean relative humidity in the former situation and a greater mean daily range in the latter" (Weese). The most casual glance at the curves shows that this might have been as well said for the conditions of relative humidity stratification found by the writer. The mean daily range curves are entirely distinct throughout.

It will be seen that the upper strata of the forest air are regions of lower relative humidity and more marked fluctuations in this factor whereas the lower strata, adjacent to the ground, are regions of somewhat higher relative humidity and immensely greater stability. The significance of these factors and their effect on the animals will be discussed in due course.

Since the evaporating power of air has generally come to be considered as the most reliable general index of all the other physical factors which affect organisms of terrestrial habitats, an attempt was made to measure this factor in the coniferous forest area studied, especially in its relation of stratification. The instruments used were Livingston porous-cup atmometers of the spherical type, which were exposed at nine stations at various localities and strata of the forest habitat. Of these, the records of one instrument, a black atmometer exposed with a white one for measurement of light effects, have not been included, since there was no other similar instrument with which to compare it.

The instruments employed were new and standardized cups direct from the makers. They were restandardized at the close of the study, but were not standardized during the study, of which the actual duration was about nine weeks. For comparison with each other, the readings taken each week were changed by a coefficient to those of a standard instrument.

For field use the atmometer cups were mounted on quart bottles by the simplified non-absorbing mounting described by Livingston and Thone (1920). The weekly filling was done Monday, by means of a burette, the bottles being filled to a file-mark on the neck of the reservoir bottle. As indicated by the results, the quart bottles were larger than needed for weekly studies in this climate and habitat; for field-work in north-eastern (or probably northern) coniferous forest, a pint bottle would be sufficiently large, and would practically halve the amount of distilled water that must be carried.

The exposure of atmometers was as follows:

No. 1, Black spherical atmometer exposed one meter above ground, and 2 meters from the lower instrument shelter, under the leafy branches of a young maple.

No. 2, White spherical atmometer exposed 1 meter above ground with No. 1.

No. 3, White spherical atmometer exposed near surface of ground (0.3 meter above surface) near Nos. 1 and 2 and, save for height, under identical conditions.

No. 4, White spherical atmometer 2.5 meters above ground, in cylindrical basket of galvanized wire hanging from lower limb of small hemlock 4 meters northeast of the lower instrument shelter.

No. 5, White spherical atmometer exposed with the maximum and minimum thermometer in the observation chamber in the soil already described; the sphere was just beneath the grating, covered with the usual layer of pine needles and other forest-floor debris.

No. 6, White spherical atmometer exposed for two weeks at the beginning of the study on the ground among high grasses in a swampy glade on the eastern edge of the forest. There was no forest cover, in the ordinary sense of the word, although the glade was surrounded by a dense growth of high bushes, so that there was little wind, although the sun shone there brightly during most of the day.

No. 7, White spherical atmometer exposed 6.5 meters above the ground in cylindrical basket of galvanized wire suspended from the upper instrument shelter on north side of large pine tree (Fig. 4, about the middle of the picture).

No. 8, White spherical atmometer exposed 11 meters above the ground, in bracket attached to side of upper instrument shelter (Fig. 4).

No. 9, White spherical atmometer (same instrument as No. 6) exposed from July 7 in a position among grass and herbage on the western edge of the forest, where the latter meets a wide area of grassland. Here it remained until August 4, when it was destroyed by children.

The results of the entire series of observations are given in tabular form (Table XIV) and shown graphically. Figure 14 shows the curves of evaporation by stations, through the period of the study and Figure 15 the mean amount of weekly evaporation from each instrument for the entire period.

The curve of evaporation from the atmometers directly exposed to the air showed a general increase for the first three weeks of observation, thus reaching a high level which it maintained, with slight up and down fluctuations, for the next month. At the end of that period, evaporation in all forest stations decreased sharply, the most marked change taking place in the upper stations and thence decreasing gradually towards the ground stratum. Following two weeks of this decrease, the second week more gradual, the trend of evaporation again turned upward, and rather sharply, for the final week of observation. The earlier changes appear to be some degree independent of the amount of rainfall during the weeks when they occurred; thus the evaporation of the first three weeks mounted steadily, in the face of a decreasing precipitation, perhaps assisted by

the moderate rise of temperature during the same period. Also the high rate of evaporation maintained during the next four weeks accompanied a generally decreasing rainfall, the highest point reached on the week of August 4 following a period of two weeks when the precipitation was very light indeed. Following this, however, the evaporation fell off rapidly, as has been seen, and did not rise again until considerable precipitation had occurred. From these things we might infer that the conditions of coniferous forest are such as to cause a moisture retention, a reservoir, as it were, of the abundant precipitation of the winter and spring months; from this supply of moisture, evaporation increases, in part due to increasing summer temperatures, until the latter part of the summer, when evaporation falls off unless the moisture of the forest habitat is restored by further precipitation. In this connection it may be said that the condition of the soil and pine needles layer of the forest lower strata, as observed for moisture during the period of the study, exactly bore out this conception.

Of the various physical factors thus far considered, the evaporating power of the air shows the most complete evidence of stratification (Figs. 14, 15). It will be seen that none of the station evaporation curves overlap at any portion of their extent. It appears that the evaporating power of the air, as found in this habitat, shows two large breaks with steep gradients in stratification, one between the ground and leaf strata on the one hand and the herb stratum on the other; and one between upper shrub or high bush stratum and the tree station, low and high, proper. This will be most apparent if Figure 15 is examined without regard to columns 6 and 9, which represent evaporation at stations outside the forest proper, but it is also indicated in Figure 14. In other words, going from the floor of the forest upwards, we have first, under the leaf layer on the forest floor, a condition of very low evaporation; thence we pass, by the steepest gradient in the series, to the group of stations represented by Nos. 3, 2 and 4, which form a group of herb, shrub and high bush strata, between which the gradients are of the same order; above this is another steep gradient, separating stations No. 4 and No. 7; both these last constitute a group of tree strata proper, and between the two the gradient is again "easy." The cause of the first and sharpest cleavage will be evident at a glance; the cause of the second is suggested by looking at Fig. 4. It represents the crowns of the lower-growing deciduous underwood of the much higher coniferous forest.

If we take as a standard atmometer No. 2, 1 m above the surface of the ground, we see that there is a constantly lower evaporation here than in the tree 1.5 m above, and that the differences between the two levels are moderate in amount, and both actually and relatively higher with periods of high evaporation. The relative evaporation from these

two levels does not show the relations with precipitation for the period found by Weese for corresponding stations in elm-maple forest; so far so far as can be seen, the points of greatest difference between the evaporation at the two levels fall on weeks showing widely varying degrees of precipitation.

The evaporation from instrument No. 7, 6.5 m above the ground shows, as we have seen, a sharp and constant difference from that of No. 4 just discussed. This instrument was well above the tops of the deciduous underwood, and therefore might be expected to show evaporation of a different order of magnitude from that shown by all the instruments below their level. Not only is this found to be true, but its curve never even approaches that of the next lower stratum (No. 4) except at the time of lowest evaporation, and then not closely.

The maximum evaporation was that for instrument No. 8, exposed 11 m above ground. This followed throughout, however, the type of curve followed by the other instruments exposed directly to the air. It is of the same order of magnitude, as far as its weekly means of evaporation are concerned, as the 6.5 m instrument just below it (No. 7). The reason for this has already been discussed. It should be remembered in this connection, however, that the 11 m instrument was by no means at the forest top; an instrument placed there would have added at least a minor and perhaps a major evaporation stratum to those already discussed.

Turning now to the instruments which were exposed below the 1 m level, we see that atmometer No. 3, 0.3 m above the ground, showed a constant and definite curve lower than that of the 1 m instrument (No. 2), and following it within expected ranges throughout the study; this instrument shows one break in the record, occurring for the week of August 4. While this curve is constantly lower than the curve of the instrument next above it, it will be seen that the differences are moderate in amount, and that the evaporation differences are of the same order. The constancy of the differences, however, is of interest.

The most extreme results in the direction of small evaporation were obtained in the case of the instrument which was exposed in the observation chamber under the artificial mat of pine needles and debris. This instrument may be supposed to have given some idea of the amount of evaporation occurring from the top soil through the dead leaf stratum. It will be seen that the value is very low throughout the study, never exceeding a single cc and sometimes falling to almost nothing, although a measurable evaporation was always present. Still more interesting is the extent to which the extremely low curve agreed, in its weekly fluctuations, with the curves of the instruments exposed directly to the air in the strata above ground. It is interesting that the atmometer should be found

sufficiently sensitive to respond to differences communicated to it through a three-inch layer of forest-floor debris. The average weekly difference between the evaporation here and in the first (0.3 m) level above the ground is practically 8 cc for the habitat studied, the greatest found between the evaporating powers of any two adjacent strata.

The curves for evaporation at the forest-edge stations have not been given. The weekly mean of evaporation for the period over which they were studied is illustrated graphically in Fig. 15 where the columns representing these two stations are placed in the general series of forest stations, in the order to which their magnitude entitles them. If we examine column 6, the record for a swampy open glade outside the forest on the east, we see that it possesses the lowest evaporation value of that found for any station except the sub-leaf one. Here, in an open but swampy glade, surrounded by high grass, and cut off by surrounding bushes and by the forest itself from wind, and especially from the prevailing fair and drying westerlies, evaporation is even lower than anywhere above ground in the forest.

On the other hand, column 9, representing the mean weekly evaporation for an instrument exposed among grass and herbage on the western forest margin, and just at the edge of wide tracts of grassland, showed an evaporation higher than that observed anywhere in the forest below the upper strata. The influence of wind is no doubt preeminent here. The differences between these two forest margin stations indicate that conditions at this tension zone may be very different under different local conditions—more so, in fact, than stratal differences within the forest itself.

Considering further Fig. 15 it will be seen that the actual order of increase in evaporation, beginning at the lowest, as seen in the entire series of observations is: sub-leaf stratum, swampy forest-margin, herb stratum, shrub stratum, high bush stratum, dry forest margin, low tree stratum, high tree stratum. The actual figures of mean daily evaporation, as expressed in this order, are:

Station	5	*6	3	2	4	*9	7	8
Height in m.	-.08	0.3	0.3	1.0	2.5	0.3	6.5	11.0
Mean wk. evap. co.	0.2	6.2	8.2	11.2	14.0	17.4	19.7	21.0

Speaking of deciduous forest, Weese (1924) says: "The gradient in the evaporating power of air in the forest is very striking,—stations, less than a meter apart, vertically, showing definite and constant differ-

*Forest margins.

ences. This is particularly true at the lower levels. At the higher levels the gradient still persists but is subject to irregularities due to the greater exposure and lack of uniform conditions." All this equally true for coniferous forest, and even more regular and constant. The absence of seasonal changes in vegetation of the upper strata would tend to obviate some of the interlocking of the upper strata curves found by him as coming about the time of the leaf-fall. The relative seasonal differences of the evaporating power of air in coniferous forest might be as marked for spring, fall and summer, as those found by him in deciduous forest, especially in forests where there is an abundant herb, shrub and low tree strata of deciduous plants.

Here, rather than at the forest crown of coniferous forests, should we expect to find at critical seasons the stratal irregularities in evaporation most marked; probably even here conditions would always be stable as compared with those in deciduous forest, where the entire forest cover is shed in the fall, since the cover of the conifers would have a stabilizing effect. This has not been studied.

The only apparatus available for measuring the light in the present study was a Wynne exposure meter, the ordinary photographic apparatus of the sensitized-paper type; this was employed to get some idea of the relative light intensity under different conditions in the forest environment. This of course measures the actinic rays only (Shelford, 1912); it has been pronounced fairly satisfactory for that purpose (Bates and Zon, 1922), and was the only type of illuminometer available. Regular readings were not begun until the early part of August, and some of the first ones taken showed so wide a range of variation, under what appeared to be very similar conditions of light, cover, etc., that they were discarded. However, it finally seemed best to take what readings were possible, in the hope that by averaging a number of these, some idea of the relative light intensity at the different stratal levels might be obtained.

The readings were mostly taken in the early afternoon, and within as short a time as possible of one another; perhaps the average interval between readings may have been three minutes. The same sensitized sheet was used for all readings taken on a given day, to obviate any inaccuracy arising from the comparative freshness of the paper or the reverse. The darker of the two standard tints was the one used in matching, because, while this took longer to match in the darker localities, it was the only one which could be used with any accuracy in the stronger light, where the lighter tint was so soon matched that it was impossible to obtain even approximate accuracy. A stop-watch was used, and the readings as given are in seconds.

A record was made of the general weather conditions at the time of each reading, as far as they could be described by the observer. In

the longer readings the amount of light changed perceptibly during the time taken to match the colors; this is indicated on the records under remarks on weather conditions.

The readings were taken from the same stations throughout the study, which may be described as follows:

On the Ground: The place was five meters east of the lower instrument shelter, in a spot covered with the typical amount of shade from young saplings (beaked hazel, ash and alder) and, of course the conifers. The forest crown begins about 5 m from the ground in this place, and becomes thicker higher up, but always is of a rather open character. The data from this station are given in Table XV.

Above the Ground, 1.5 m. The actual locality was the same as for the ground reading, save for the elevation. The instrument was shaded by a growth of young maple. The data are given in Table XVI.

In Open Glade: 25 m north of the tree bearing the upper instrument shelter. This place was covered by a forest-crown shade almost, if not quite, as dense as that for the two previous stations, but was characterized by the almost total absence, over an area about 30 m square, of the growth of shrubs and young deciduous trees, especially maples, which was characteristic of them. (Fig. 4, right foreground). The data are presented in Table XVII.

In Open Grassland: 20 m from the western edge of the forest. This reading was taken in an attempt to get some idea of light intensity in the absence of forest cover, and hence the illumination of the forest crown, where it was impossible, for obvious reasons, to take actual measurements. The data taken at this station are shown in Table XVIII.

Considering this data, it appears that there is a very definite stratification of light in the coniferous forest habitat and that the light available in the lowest strata in a very small fraction of what is available higher up. In fact the imperfections of the method, especially of measuring the strongest light, probably make this fraction appear much larger than it actually is. It is interesting that the steepest light gradient should exist between the ground and the next stratum measured above it, a condition of things comparable to the position found for the steepest gradients of temperature, humidity and evaporating power of air. The relation between the light intensities in the glade and in the open tend in a general way to support the statement of Weese for deciduous forest, that the light which enters into large openings in the forest is little lessened in its intensity. Considering the reading made in the shaded but rather open glade, it is evident that the light there is a considerable fraction of that found in the grassland outside, whereas the light on the shaded forest or even above it under the shade of shrubs and small trees, is a very small fraction. The method employed was too rough to make these actual

figures of significance, either by themselves or for comparison with those taken with more elaborate instruments in other habitats, but the data indicate the fact, direction and to some degree the extent, of light stratification in the forest environment.

THE BIOTA

In studying the animals of the coniferous forest tract, and especially their stratification into societies, the methods of Weese (1924) were largely employed. The collections were taken most frequently during the latter part of the study; therefore the biotic data for the month of August is the most complete. Collections were made according to the quasi-quantitative method of sampling from the various strata, in the immediate vicinity of the stations where the instruments were exposed. Four strata were studied systematically, the soil, dead-leaf, herb and shrub; the tree stratum being neglected in the present study. On each date when collecting was done, these four strata were "sampled." The dates given are those on the last day of the week when the samples were taken, thus corresponding with the instrumental observations, which are dated on the day they closed. In a few instances during the latter part of the season additional collections were taken in the middle of the week. The animals from the different strata were collected as follows: Weese's original paper should be consulted for further details, as the writer closely followed his practice, in order that the data from the two habitats might be to some extent comparable.

Soil collections were taken from the upper 10 cm of soil, from which the leaf cover had been previously removed. The soil was explored over an area 2 ft square, being carefully dug over with a trowel to the depth of 10 cm. Whatever animals were found in this plot were placed in vials.

Leaf collections were made from the layer of dead leaves (largely pine needles) and other organic matter which covers the soil. This layer was swept up from the previously measured 2 ft quadrat, placed quickly in a cage-box made of very fine mesh wire-screening, and carried to the laboratory, where it was treated with ether and examined for its animal population.

Herb collections were made by ten sweeps of an insect-net with a 30 cm mouth over and among the plants of this stratum.

Shrub collections were taken in the same way at the higher level; paper bags were used for carrying the last two samples to the laboratory.

The quantitative results of these collections appear in Table XIX and in the form of a graph (Fig. 16). The latter gives by curves the total and stratal populations.

The curve of total population (A) is seen to be a very irregular one. Starting with a medium position for July 7 it falls steadily through July 14

to July 21, and then takes a sharp upward trend for the week following. By August 11, when the next collection was taken, the population had again fallen, and it continued to fall, reaching by the middle of the following week the lowest point observed during the study. By the end of the week it had again mounted abruptly, but suffered another fall during the middle of the week of August 25. But by the end of that week it had mounted to the highest point reached at all, whence it declined somewhat to the last collection which was still, however, above the average. The peaks of this curve all fall in periods of relatively low temperature, but this is probably not significant, although Sanders and Shelford (1922) found high temperatures accompanied increased animal population in a pine-dune animal associates, while Weese finds high temperatures in elm-maple forest conducive to low animal populations. It is unlikely that the animals of cool, moist coniferous forest would be restricted in numbers by temperatures no lower than the lowest of those recorded. Entirely similar types, inhabiting the still cooler alpine spruce-fir forests of Mount Ktaadn appear to be independent of much greater temperature extremes than this, in all matters save that of a daily rhythm of activity. The marked high points on the curve appear to be largely due to the presence of certain particular species whose numbers attained a maximum, rather than to any general increase in the numbers of any considerable number of the species making up the population. Thus one of the highest points is produced by the large numbers of *Chironomidae* taken on July 28.

If we consider now the size of the various stratal populations, we see at once that the shrub stratum contains the largest and also the most fluctuating animal population. This condition is the reverse of what has been described for deciduous forest by Weese, where the population of the herb stratum is uniformly larger than that of the shrub stratum. An examination of the curves given in Fig. 16 shows that for the area and season studied the numbers of shrub animals were rarely below, and often much above, the numbers of herb animals. The shrub stratum in fact to a large degree controlled the general population curve, especially in its extremes. This is probably in part due to the scanty herb cover in the coniferous forest habitat. The first of the two marked maxima shown by the shrub curve was, as has been said, caused by *Chironomids*; the second, that of August 25, was due to several species of *Hemiptera* and *Homoptera*.

The herb stratum was second in size and rather uniform, though presenting some fluctuations in numbers during the latter part of the season. These maxima were caused by several species of insects and young spiders, which will be taken up in more detail under the study of individual species in their relation to the stratal societies.

The population of the dead-leaf ground stratum was considerably lower, on the average, than that of the herb stratum, and might have been expected to have been lower still in comparison. No doubt this was influenced by the relatively low numerical value of the herb stratum in this habitat, as compared with the same society in deciduous forest. The soil stratum was of low value throughout, but very uniform. Its population is largely a resident one, as far as the dominant animals are concerned.

The entire animal population as collected is given numerically in Table XIX.

With a few exceptions only the predominant animals of the various strata will be discussed, present in such numbers, as compared to the other species, as to play an important part in the community. Certain animals were very scarce or wanting; only a single mollusk was taken during the entire season, *Phylomycus carolinensis* (Bosc), on August 22; the coniferous forest habitat is poor in this group (Walker, 1906).

The birds of the area were not studied. An attempt was made to get at the size and composition of the mammalian population by extensive trapping during the latter part of the season. The results of this were somewhat surprising. Only two species of mammals were trapped and one of these, the shrew *Sorex personatus*, was rare. The other, the short-tailed shrew *Blarina brevicauda talpoides*, was very abundant. In all the trapping done not a single specimen of the white-footed mouse, jumping-mouse or short-tailed meadow mouse was taken, although the first might have been confidently expected throughout the habitat, and the last in the grassy regions abutting on the swampy eastern area. It was not possible, because of lack of time, to investigate other territory in order to find out whether the scarcity of usually common animals was general in the vicinity. The area studied was not far from the college poultry-plant, and there were outlying chicken-pens within a few hundred yards. For this reason, there was always a number of smaller carnivores hanging around this forest tract, especially skunks and half-wild cats. It is possible that this fact may have had something to do with the absence of mice through the area studied; whether or not carnivorous animals show any preference to mice, as contrasted with the pugnacious and rank-fleshed shrews, is not known. The latter are certainly sometimes eaten. The red squirrel was the only other mammal noted.

If the general population curve (Fig. 16) is inspected, and still more if the curves representing the seasonal abundance of dominant species are examined (Figs. 17-20), it will be seen that the greater part of the study fell between the period of the high vernal rise in population and the later aestival rise, including only a little of the last part of the former but largely covering the latter. Further, if we omit from consideration forms

not strictly belonging to the forest habitat as such but incidental on the presence of nearby aquatic habitats, especially the chironomids, we see that this relation becomes even more apparent. The study did not last sufficiently long to show the entire march of the summer societies, but it indicates some of the phases of the series. Since the only well-developed seasonal society occurring in the study was the aestival, the dominants of that alone will be discussed in detail. These fall into well-defined stratal societies. Listed in order of abundance they are:

CLASTOPTERA (SHRUB) SOCIETY

Subinfluent: *Clastoptera obtusa* (Say), *Tetragnatha* sp. (juvenile), *Graphocephala coccinea* (Forst.), *Macrosiphum coryli* Davis, *Philodromus* sp., *Diaphnidia pellucida* Uhl.

LEIOBUNUM (HERB) SOCIETY

Predominants: *Chironomus dispar* Meig., *Chironomus modestus* Say, *Leioibunum politum* Weed, *Chironomus decorus* Johann., *Tanytus melanops* Meig.

Subinfluent: *Dicyphus famelicus* (Uhl.), *Nabis* sp. (juvenile).

TOMOCERUS (LEAF) SOCIETY

Subinfluent: *Tomocerus flavescens* Tullberg var. *separatus* Folsom, *Linyphia* sp. (juvenile).

HELODRILUS (SOIL) SOCIETY

Subinfluent: *Helodrilus caliginosus trapezoides* (Dugés).

It will be seen that the predominants are mostly arthropods. Mollusks were, as has been seen, almost wanting. Among the insects, only a few species of Lepidoptera and Hymenoptera had been determined when the study was completed; these orders may have contained predominant species. The same is true for certain dipterous larvae and for various myriapods, some of which were quite numerous in the lowest strata. It is interesting to note that no Coleoptera appeared among the dominants, and that this order was in general poorly represented; this a group which Weese found to be decidedly predominant in elm-maple forest. Here their place seemed taken by ecologically equivalent phytophagous Hemiptera.

Figs. 17-20 give the observed seasonal and stratal (for some species) distribution of the more important predominants. The curves of distribution through the season are in some instances separated to show the stratal occurrence of the species in different stratal societies, such curves being separated and placed one over the other. The time is the same for all the figures and agrees with the scheme used for the presentation

of temperature and humidity data (Figs. 10-13). The increments used in plotting the heights of the curves may be different for different species, and the polygons have been smoothed.

Clastoptera (Shrub) Society

Clastoptera obtusa (Say) Fig. 19, Aa and b.

According to Osborn (1916) the alder spittle-insect, under Maine conditions, hatches in late spring or early summer (July) and is common in the adult condition until early August, appearing afterwards, however, until September. It did not appear in the collections until August, when it suddenly appeared and thence its total population mounted until the close of the study. Its stratal distribution showed a marked downward movement for the middle of the weeks of August 18 and August 25, the numbers of animals decreasing in the shrub and increasing in the herb strata. It will be noted that this is accompanied by a period of falling temperatures. This was also a period of falling evaporation. With rising temperatures and rising evaporation the herb population fell to nil, and the largest number of this species recorded for the study appeared in the shrub stratum about the first of September. This insect is said by Osborn to pass the winter in the egg stage; whether or not the sudden appearance of the adults in numbers so late in the season was an inward forest migration, similar to that observed by Weese for many beetles, cannot be definitely stated. The facts suggest it, but since this animal does not hibernate in the adult stage they are less conclusive in this instance.

Tetragnatha sp. (juvenile) Fig. 18, c.

These spiders were all young, which were abundant in the shrub stratum, during the latter part of the summer, preying on the smaller insects. They were not taken until the later part of the study and thence were present in slightly varying numbers throughout the remainder of the season, being sometimes taken in the herb stratum. Their maximum as adults comes earlier in the summer, before the greater part of the collecting was done, and they winter as young in the forest floor (Emerton).

Graphocephala coccinea (Forst.) Fig. 19, Ba and b.

This widely distributed leaf-hopper occurred in collections taken throughout the study. From the records of its occurrence in Maine, summarized by Osborn (1915), it appears to be generally characteristic of the late summer animal society, no records being cited earlier than August. It is characteristic of the moist forest habitat and occurs generally there on the herbs (especially ferns) and shrubs, etc.; it has been taken from the spruce-fir forest of Mount Ktaadn, no doubt from deciduous herbs and underwood. In the present study the animal was distinctly more a shrub species, although a constant smaller herb population existed

until the end of the collections, when the species disappeared from this stratum. There was a gradual increase in the total numbers, the species maximum being reached about the middle of August. As in the case of the alder spittle insect (*Clastoptera obtusa* Say) there appeared to be a response to the falling temperatures about August 18, the numbers of individuals falling off in the shrub and increasing in the herb strata, thus indicating a downward movement of the animals with the descending temperature.

Macrosiphum coryli Davis. Fig. 20, A.

This aphid is one of the few dominants which show the peak of abundance as occurring in the early part of the period of study. From thence it fell off gradually, but was present in varying but smaller numbers throughout the remainder of the time. It was principally a shrub-society animal, but sometimes occurred at the herb level, and a single specimen was taken from the leaf layer—no doubt fortuitously. Adults and young were taken on various dates during the entire period when collecting was done.

Philodromus sp. (juvenile).

The young of this crab-spider (probably representing several species) were found at the same levels frequented by the adults earlier in the season, in low shrubs within two or three feet of the ground. They were occasionally taken from the herb stratum lower down, where they did not occur as predominants. Like the other young spiders they reached their maximum of abundance during the month of August.

Diaphnidia pellucida Uhl. Fig. 20, D.

This mirid, like most of the other dominant insects, had an aestival maximum, occurring in the early part of August, at which time it appeared suddenly in the collections. Thence it decreased rapidly in numbers, none being taken after August 25. It was sometimes taken from the lower (herb) strata, but was principally a shrub animal.

Leiobunum (Herb) Society)

Chironomus dispar Meig.

This species was the predominant animal in numbers, but a species locally present, due to the damp habitat and aquatic and semiaquatic conditions found on the eastern border of the area studied. From the numbers, however, and the fact that it is often found in such coniferous forest stations, it seemed best to consider it among the list of predominants, with the above explanation. Considering the population as a whole, the peak of the midges appeared in the first collections, and after that there was a marked fall in numbers, followed by a second rise the latter part of the month of July; from this the curve fell again abruptly, to rise somewhat in the early part of August, but not attaining another high point

during the period of the study. This group, then, did not take part in the late August population increase, but shows, like *Macrosiphum*, the last of a vernal maximum, and an additional mid-summer maximum besides. It is largely to this fact that we get the high point on July 28 in the general population curve, the contributing factor being a large number of Chironomids of several species taken on that date.

If now the particular species *Chironomus dispar* Meig. is considered, it appears that this species, while taking part in the vernal maximum of July 7, did not attain its second maximum until August 4, or a week after the general high point for the family. Between these two dates lies a period of lower numbers, caused by the sudden decrease from the July 7 maximum and the gradual increase to the early August maximum; after the last date the population of this species again falls, but some individuals were present up to the end of the period of study. The decrease, sharp in both cases, does not appear to be connected with temperature or evaporation.

Chironomus modestus Say

This midge, as far as our collections indicate, did not take part in the general maximum of population observed for the family on July 7, but its midsummer maximum coincided with and increased the family maximum of July 28. Thence its decrease was even more rapid than that of *Chironomus dispar*, and its numbers were relatively less throughout the remaining period of study.

Leiobunum politum Weed. Fig. 18, a.

This harvestman, which was mainly a herb species, though rarely taken from the strata above and below, appeared in the collections towards the latter part of July, reaching its seasonal maximum the week of the twenty-eighth and after a slight decrease reaching another but lower summit the week of August 18. Thence the fall in numbers was rapid until the very end of the study, when a slight increase came, accompanying rising temperatures and evaporation.

Dicyphus famelicus (Uhl.) Fig. 20, Ca and b.

This mirid was one contributing to the general aestival maximum. It appeared the latter part of July, and thence increased steadily in numbers until the week of August 25, when its maximum was reached; its numbers had declined abruptly a week later, when the last collection was taken. It was distinctly a herb stratal dominant, but at the summit of its abundance it appeared also in smaller numbers in the shrub stratum (C-a.). It feeds on *Rubus* (Britton, 1923), of which the herbaceous form *triflorus* was found here.

Nabis sp. (juvenile). Fig. 20, B

Nymphs of this genus were present in small numbers throughout the period of collecting, but reached a maximum about August 25, after

which they took part in the general decline of the following week. They were most abundant on the herb stratum, but were taken from the shrubs from time to time.

Chironomus decorus Johann.

This midge is included in its seasonal occurrence with the general population of Chironomidae. The general remarks about the family as a whole apply to it, as far as its seasonal and stratal distribution are concerned.

Tanyptus melanops Meig.

The same is true in general, for this species, as was stated for *Chironomus decorus* and for the family as a whole.

Tomocerus (Leaf) Society

Tomocerus flavescens Tullberg var. *separatus* Folsom. Fig. 17, b, c and d.

This spring-tail, the only species found in much collecting in the habitat, is a permanent resident and a numerical predominant of the dead-leaf stratum during the summer months. It is, however, sometimes found in small numbers in the ground (d), more rarely on the herb stratum (b). From its numbers it undoubtedly must work considerable change on the layer of decaying plant matter which makes up its real habitat. The fact that it was not taken in the first few collections was probably due to the fortuitous selection of an area where these animals were not found, such, for instance, as a very dry area. The maximum occurred on July 28; the following decline throughout the greater part of the collecting period is perhaps correlated with the gradual drying out of the leaf stratum, accompanied (d) by a partial migration into the soil, although the data is too scanty to more than suggest this. A very small rise in numbers came towards the very end of the study.

Linyphia sp. (juvenile). Fig. 18, b.

The population of young linyphiids showed in general the same course as the curve of the young epeirids, save that it developed more gradually despite its earlier start. The species first appeared early in July as straggling individuals, and gradually increased to a maximum the twenty-fifth of August, coinciding with the second maximum of the young *Tetragnathas*. There was a decrease and the evidence of a following increase towards the very end of the study. These were all young animals which would hibernate in the leaf litter. The maximum for the adults comes earlier, and the animals themselves are found in various situations higher up.

Helodrilus (Soil) Society

This was in general rather scantily populated for the period of study, and only a single predominant, a permanent resident, will be considered.

Helodrilus caliginosus trapezoides (Dugès) Fig. 17, A.

The presence of this lumbricid is in itself an indication that the station studied is not wholly typical of coniferous forest, but has had its animal population modified by neighboring agricultural lands. The writer has never taken it in the primitive coniferous forest around Mount Ktaadn, and in general such forests are poor in Lumbricidae. It was thought of interest to trace the numerical fluctuations of this resident soil animal, in order to see to what degree they could be correlated with various physical changes. The curve includes both adults and juveniles, but more of the latter, since the method of collecting favored the escape of the adults.

The first high point of the curve was that of the first date of collection, July 7. There had been previous rain, and the soil was wet, while the general condition of the forest floor was damp. Evaporation from the upper leaf strata continued rapidly and remained high for a period of weeks, during which the leaf and upper soil strata dried out appreciably; during this time the earthworm population of the upper soil, as judged by this single species, fell off as the animals retired deeper and out of reach of the collecting methods used. There was a slight increase July 21, correlated with the heavy rain of the period. The second and third apices correspond with the rainy weeks towards the end of the period of study, the difference between the two being probably unimportant, and due to the small local population of the quadrat selected for the second of these collections.

DISCUSSION

The coniferous forest habitat studied is a biotic environment of marked stratal differences in physical factors. These factors, in general, present a graded series from forest soil to forest crown, but the various strata fall into groups similar in conditions. These groups are: first, top soil and dead leaf strata; second herb, shrub, and high bush strata; third, low tree and high tree strata. The grouping is shown most clearly for evaporation. Since this is in itself a fairly reliable index of other physical factors and since the evidence from data on temperature and humidity tends, as far as it goes, in the same direction, we may assume that grouping with steep gradients between is the general condition. The strata, divided on a basis of the physical conditions, fall into "groups subordinate to groups." This is a suggestion of what has been pointed out, based on animal societies, for tropical forests by Brehm (1896).

The cover of tall conifers is a dominant influence through the entire association. Even more important in any single member of the series are the stratal societies peculiar to each layer. These determine more immediately the physical and biotic conditions under which animals live. This point will be considered further in speaking of animal response.

If we consider these strata in order from below upwards, we find that the upper soil stratum presents an environment of comparatively low but very uniform temperatures, minimum evaporation and minimum light. The animals inhabiting this stratum as more or less permanent residents are those whose reactions—and to some extent structure—are such as to find optimum conditions here: earthworms, the sparse mollusk population, ground and fungus beetles, and the larvae of a considerable number of other beetles and flies.

In the next layer above, the leaf layer, conditions are somewhat less equable. Our only instrumental data are for temperature, which is higher and more extreme than in the soil. Light is somewhat greater, undoubtedly, and moisture less. The differences in animal population between the two are very considerable, both for quality and quantity, nor are the animals common to both as numerous as we should expect. The few individuals listed as found both in the ground and in the strata above the leaf must be considered either wholly exceptional, as in the case of *Tomocerus flavescens*, or caused by the presence of animals, such as the spiders, whose adult and juvenile stages are passed in different strata. The real population of the leaf stratum seems out of all proportion to the physical differences between it and the upper soil. Conspicuous is the predominance of many young spiders during August, while the maximum of corresponding adult forms comes earlier and at upper strata.

All the data available on the physical factors agree that between this leaf stratum and the herb stratum next above it occur the steepest gradients in the series for temperature, evaporation and probably light. Both temperature and evaporation show not only a great rise but also a very marked increase in extent of fluctuation. An animal moving from one of these strata to the other certainly undergoes a very considerable change in its physical environment. The number of species making this change is comparatively small. Further, such are again largely species of spiders, whose adults habitually occupy the upper strata, and whose young were taken at all stages of their downward migration toward winter quarters in the forest floor. A very few species may be noted which seem to change strata rather indifferently at the adult stage; an example is *Camponotus herculeanus*. The population of the herb stratum proper is large, and more varied than that of any other single stratum analyzed. Predominant groups of animals present were mirids, cicadellids, and various families of Diptera.

The physical differences between the herb and shrub, while constant and by no means to be disregarded, appear to be of much less magnitude than those existing between the last two strata considered. They are, however, in the same direction, involving increase of evaporation and light, and a corresponding increase of the fluctuations of these, and

probably other factors not measured. In other words, differences between physical conditions at herb and shrub levels are less decisive than those previously discussed. This is indicated not only by the instrumental data, but even more by the animal population data. A large number of animals are common to both strata. Among them are several of the predominants. The animals found in the present study only at shrub level constitute a varied list; the predominants are several species of Diptera, although no single species appears particularly prominent; the same status may be accorded also to the cicadellids and the aphids, considered as groups.

The inhabitants of the forest above shrub level were not studied. We know from instrumental data that above this stratum, and especially beyond the tops of the low deciduous trees, the summer months show higher temperature, less moisture and greater fluctuation in both factors. If the inherent difficulties of a biotic study of this region could be overcome, the investigation would be very valuable, as it would give us the forms living in the evergreen foliage instead of the population of the deciduous substratum.

The animal population, as far as studied, shows a distinct division into stratal societies. This distribution seems to be determined by a combination of two factors; (1) physical differences between the strata; (2) biotic differences. For example, the alder-spittle insect was dominant in the shrub stratum, where belonged its food plant, a biotic factor; but a change in a physical factor, temperature, caused a downward, stratum to stratum migration. Other instances might be cited. It is probable that the physical factors become of greater importance at critical seasons, such as the later fall. Weese (1924) gives evidence that the lowering temperature and temperature fluctuations serve as a stimulus causing forest-border beetles to migrate first into the interior of the forest, and then downward to the lower strata for hibernation. A downward migration of the young of many herb- and shrub-dwelling spiders is a well-known phenomenon of the later summer (Emerton). On the other hand, a very large number of phytophaga indicate by their vertical distribution that the stratum in which they are found is determined by the presence of the host-plant.

A study of the population shows that many of the species are forest-margin or deciduous underwood forms, rather than animals necessarily belonging to the coniferous forest habitat. Certain other species illustrate the invasion of grassland forms, not found in such forests when remote from agriculture.

The seasonal societies, because of the short and non-critical period when the collections were possible, are less marked than the stratal societies. For the greater number of species, however, and especially for the

predominants, the evidence indicates an early summer (Aestival) maximum, the peak of which had passed at the time the collections were begun, or a late summer (Serotinal) maximum, developing during the latter period of study.

SUMMARY AND CONCLUSIONS

The coniferous forest habitat studied shows a very regular stratification of the physical factors of environment; this is most conclusively proven for evaporation, but is in general true for all physical factors.

The evaporating power of air increases with elevation above the forest floor. Based on this factor, the habitat could be divided into three main strata, and each of these into two or more sub-strata.

Temperature increases and humidity decreases in the upper strata, while both show greater range. These results, however, are less conclusive than those bearing on evaporation, and show less stratal difference.

Light intensity increases markedly upward from the forest floor. Its gain in successive layers of deciduous undergrowth is almost comparable to the rise in evaporation.

Biotic response to these conditions is expressed by the composition and distribution of the animal stratal societies. This response, however, is complicated in the various strata by the presence of influences which are themselves biotic. The ultimate response of the animal, at least during summer, is evoked by the combination of physical and biotic factors.

Physical factors are responsible for stratification in proportion to their intensity. During summer conditions in temperate climates, biotic factors tend to attain greater importance. During critical periods of climatic and physical stress, the situation is reversed. Thus under montane conditions, as seen in the Ktaadn studies, physical factors may be dominant at all seasons.

A seasonal series of societies as well as a stratal one, was shown by the animals of the area studied. Numerically the animal population, as a whole, displayed two high points—one in late spring, and another in late summer. These two maxima were not due to the appearance of a second apex for species reaching a high point in the vernal society. Among insects generally, they were caused by the appearance of different species; among spiders generally, by two distinct phases in the life history.

THE ANIMAL ECOLOGY OF DECIDUOUS FOREST IN WINTER

SCOPE OF WORK

This portion of the study was undertaken in an attempt to secure data on the animal population of deciduous forest in winter, with special reference to its stratal distribution. It was carried on in the same locality and by the same methods, as the study of Weese (1924), made in part during the winter of 1921-1922. It should give us an idea of the differences existing between the animal communities of a locality during the same season in different years, when examined by the methods of sampling. Since this study was made in winter, the predominants varied greatly from those based on a complete annual cycle, and the animals present in the largest numbers were the permanent inhabitants of the forest-floor strata; second in importance are the hibernating animals whose stratum of summer activity is higher in the forest, or outside the forest altogether. It should be understood that the data presented is distinctly that of a winter study. It does not give seasonal societies, although it indicates the passing of the last of the autumnal society into the hibernal one; its principal emphasis falls on the response of the animals of the winter society to changes in climatic conditions.

The study was continued to include the prevernal society; the results of this portion of the work will be presented at a later time. Certain groups of animals have not been included in the present report because of the impossibility of getting determinations on them in time; these include the Cicadellidae and some larvae.

The generally neglected dynamics of the hibernal society is dealt with in detail because of the following facts: 1, Winter survivors are the basis of increments to the population during the warmer months which follow; 2, winter conditions have important relations to—a, survival and b, rate of development in spring. The neglect of the study of this phase of insect activity in particular, is responsible for much confusion in economic entomology, and the same may be true for other groups of animals.

In addition to the quantitative study of the invertebrates an attempt was made to take a census of the winter birds and some general observations were made of the mammal population; no reptiles or amphibians were observed during the study.

ENVIRONMENT

This has been thoroughly described by Weese (1924) and its plant communities by McDougall (1922); these papers should be consulted. The local area embraced in the instrumental study and from which the collecting was done was practically identical with that of the first author. Collecting was commenced before the leaf-fall from shrub and herb strata; most of the ground was carpeted with a rather thin layer of organic debris. By November 6 many of the leaves had fallen from these strata, and a thick layer carpeted the ground. Not until December 22 was the leaf stratum frozen and the soil stratum partly so. On December 29 both were well frozen and covered with a 2 cm of snow, which had increased in thickness to 15 cm by January 5, and to 17 cm by the week following. By January 26 the snow had decreased in thickness to about 12.5 cm, and it remained thus for the next week. A sudden thaw on February 9 left the leaf and soil strata bare and very wet. This condition lasted through the next three weeks, but on March 2, the day of the last collection, leaf and soil strata were again frozen and covered with 5 cm of snow. The general appearance of the habitat during the greater part of the period of study is shown in Fig. 5.

The winter period is of course the time when all animals of terrestrial communities in temperate regions show inactivity as a response, at least in part, to the stressful climatic conditions. Under montane conditions this inactivity is probably absolute, as far as the invertebrates are concerned, and lasts during the long period when the ground is covered with snow and the shallow soil is frozen to the underlying rock. Under the less severe conditions found in northern coniferous forest, the snowfall is none the less heavy and long and the autumn freezing deep; the result is probably a practically quiescent condition of the animal population of the ground strata, perhaps as marked as that of montane tundra and forest. In the more temperate conditions where deciduous forest is the vegetation climax, the winters are less severe and the animal population of the forest floor shows a week to week fluctuation with the changing climatic conditions (Weese). In order to measure these climatic changes, for comparison with the accompanying biotic fluctuations mentioned above, a number of recording instruments were employed, their exposure being similar to that of Weese's instruments.

Temperatures were recorded at three levels. A thermograph was placed in a standard instrument shelter about 0.6 m above the ground in practically the same spot where Weese's 0.6 m instrument was exposed. This also sheltered the clock and recording apparatus of a distance thermograph, whose sensitive bulb was buried under 5 cm of dead leaves and 10 cm of top-soil. Another thermograph was exposed at a height of 11 m in a maple tree nearby. A standard Weather Bureau type maximum

and minimum thermometer was also placed in the instrument shelter; by this all the other instruments were set and checked. The changing of charts and treatment of the data gained therefrom was precisely like that employed in the coniferous forest study, save that the soil thermograph charts were graduated in degrees Centigrade, and therefore did not need the conversion which was employed on the other two. The tree instrument was started the week ending November 17, and its record contains one break, that occurring during the week of January 12. The other two instruments were started the week following. All three records, for the purposes of this report close with the week ending March 9. The results of the study appear in Figs. 21 and 22.

If we consider the air temperature 0.6 m above the ground we see that, starting on November 24, there was a sharp decline the following week, followed by a considerable rise. The next two weeks showed very slight depression but the week of December 29 brought the sharpest change and lowest temperature of the study, the mean temperature falling to -14.2°C . From this date until February 9 the general trend is upward sometimes by sharp changes; then occurs another depression, followed on February 23 by a rise to the highest point attained by this instrument since the beginning of the study; thence the temperatures fell off gradually until the end.

The record of the instrument in the tree accompanies irregularly that of the lower station, crossing from side to side, but, with a few exceptions, lower with falling temperatures and higher with rising ones. In other words, the temperature at the higher level makes more response to climatic changes, is more extreme. A reversal of temperatures takes place the week of December 8 with falling thermometer, and a second the week of March 2. Reversals on rising temperatures occurred during the weeks of January 5 and March 9.

The records of soil temperatures were not begun until after the fall overturn, or reversal of temperatures between earth and atmosphere; at this time it was already higher than the temperature of the air. With the exception of a slight rise for the week of December 15, the trend was steadily downward until January 12, the earlier fall being sharper than the later ones. The maximum depression of air temperatures for December 29 affected the soil not at all. The trend from January 12 until the end of the study was upward, gradually at first but later more markedly. The final week of the record shows another slight depression, following marked depressions of atmospheric temperature for the week preceding. With the exceptions of the two warm weeks of February 9 and 23, the soil temperature was above the air temperature throughout the period of the study. It was little affected by atmospheric temperature extremes in either direction.

If we now consider the temperature ranges at the different strata, we see that they show more plainly what was indicated in a general way the actual temperatures, that is, that the extent of range increases from the ground upward. From the soil to the atmosphere this is of course very marked; the curve of temperature range for soil never even approaches that of the air strata. The relations between the temperature ranges in the two air strata are less clear, and the curves show more crossing; but the upper stratum, 11 m above the ground, showed on the whole a greater range than the lower, 0.6 m above the ground, and this was decidedly marked for the weeks of highest temperatures. (Fig. 22).

If we compare this data with that taken by Weese in the same stations in 1921-1922, we see a similar type of curve for the same period of the year, consisting of a depression to a minimum point, followed by a general upward movement. The early winter fall of temperatures was somewhat less regular, and the low point was not reached until the early part of February. The minimum was not so low, and the subsequent rise was not so sharp as in 1924-1925. The winter of 1921-1922 was certainly the warmer and somewhat the more uniform of the two.

The relative humidity of the air during winter is probably of much less importance than the temperature, since the latter was so low as to cause freezing of the ground strata during most of the period of study. Even when the ground remained unfrozen the air temperatures were so low that most of the animal population remained, as will be seen, in the ground. Since, however, any factor must be known before it can be ignored, the relative humidity was taken throughout the period of study. The hygograph used in its measurement was placed in the instrument shelter 0.6 m above the surface of the ground. The sheets were changed, and the computations made as in the coniferous forest study. The data obtained is given in graphic form in Fig. 23. It will be seen that the curve of mean relative humidity does not show any very striking points for the period of study. Its lowest points fall in the dry portion of the late autumn, while the region of its highest general average falls during the periods of rain and thaw in February. The curve of daily variation is high and irregular during the early part of the study but falls rapidly during the winter, and shows less variation from week to week. With rising temperatures the range of atmospheric humidity also increased, but its weekly variations did not, at the end of the time covered by this report, again attain those of the late fall. It seems unlikely that humidity differences of the order shown, when accompanied by such low temperatures as existed, could be of much importance in determining the winter distribution and fluctuation of the animal population in the leaf and soil strata of the ground.

From this it will appear that the changes in the population of hibernating animals in the forest-floor are more probably influenced by the changing temperatures than by any other physical factor. The nature of the population, its stratal and weekly distribution and its predominant species will be considered next.

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The population sampling was done in the same way as in the coniferous forest study, save that during the period when the ground was frozen the upper 10 cm of soil of a quadrat, which alone were examined, were removed entire and examined for the animal population after thawing, instead of being gone over in the field. There is nothing in the data to indicate that the use of two methods in examining this stratum has caused any discrepancies in its record. The results of the quantitative part of the study, as a whole and by strata, are shown as graphs and in tabular form (Table XX). Fig. 24 shows the entire population curve, the separate curves of shrub and herb populations. Fig. 25 gives separately the curves of the leaf and soil animal populations. The weekly collection and analysis of stratal "samples" of animal population was begun several weeks earlier than the instrumental observations.

Beginning with the week of October 9 we have a series of weekly fluctuations, some of very considerable magnitude, lasting until the early part of December. The general mean of these shows, however, a somewhat downward trend, despite the rather high points reached on alternate weeks during late November and early December. The first high point reached was that of October 13. Thence there was a sharp drop to October 27. From this time on until instrumental readings were begun the fluctuations seemed to be determined largely by the air temperature, but to some extent were correlated for the lower strata with amount of moisture in the leaves and soil. For example, the collection of October 6 was taken on a cool day; October 13 was warm and sunny; November 10 showed an air temperature of 13°C. when the field work was done, while the following week, when the smallest collection to date was obtained, the temperature had fallen to 1°C, and there were flurries of snow. Beginning with November 24, the population curve falls with falling temperature during the next week, and rises with rising temperature the week following. The sharp drop in animal population during the weeks of December 8-22 was apparently caused in part by gradually falling temperatures in the soil and in part by the dry condition of the leaf and soil strata; the great drop in air temperature did not come until a week later. Beginning with December 22, the total population trend is upward, though many fluctuations, until almost the end of the study. The population apices roughly coincide with temperature apices, especially where these

last were unusually high. At the very close of the period of study the population fell sharply to the very minimum observed; this accompanied a temperature fall, moderate in amount but very sudden, from one of the highest points observed during the whole study.

The population as a whole appeared to fluctuate in numbers with climatic changes, especially temperature. Air temperatures seemed to be of more importance during the early part of the study, when more of the population was in the shrub and herb strata. Later changes of atmospheric temperature were less directly active on the animals, now almost exclusively confined to the forest floor. Exceptions appeared where sudden and extreme fluctuations of temperature, such as that of February 9, were sufficient to affect directly the temperatures of the forest-floor strata; this seemed more likely to occur on rising temperatures. It might be recalled that the sensitive element of the soil thermometer was buried at the lower limit of the lowest stratum sampled. The leaf stratum was more nearly exposed to the air, and more responsive, we must suppose, to changes in air temperature. There is biotic evidence, as will be seen, that this is so.

The shrub society as might be expected, was of importance only in the earlier part of the study. It contributed especially to the population apex of October 13, less to the lower apex of November 10. Thence the data for this stratum are based on a few hardy individuals and species which ventured out of hibernation during an unusually warm period.

The herb society curve roughly accompanied that of the shrub; differences between the two are probably fortuitous and due to the chance selections of comparatively well or poorly populated areas for sweeping on the various dates. After October 27 this stratum makes no important contribution to the whole population, and its occurrence at all in the record is determined by the same conditions given for the shrub animals.

A glance at the leaf society (Fig. 25) shows at once that after November 10 the population of this layer became the determining factor in the whole number of animals in a sample. Its curve follows closely and falls little short of coinciding with, the general population curve. Its predominants are the predominants of the winter population, and with very few exceptions were the only animals found in any numbers during the study. This is natural when we consider that of the two strata which are of importance in a winter study, this is the one most directly affected by climatic changes, especially in the matter of receiving warmth with rising temperatures. The curve for this society shows two groups of peaks preceded, separated and followed by low points. The earlier low portion of the curve, during the month of October, is probably due to the dry condition of this layer and the retreat of its population deeper into the soil. Indeed, the high value of the soil collections on some of these dates,

the highest found for the soil stratum throughout the study, is strongly suggestive of such a downward migration. With the fall rains and before the coming of extremely low temperatures, the curve for this stratum mounted higher and with minor fluctuations due probably to temperature, remained high until December 8. It then took part in and largely determined the great descent of population during the two following weeks, which has been already discussed. In fact, from this point on its story would be that of the population as a whole, of which it made by far the greater part.

The soil population was the most uniform of the animal societies. Its early high points have already been discussed. Its high points during the winter, none of which are so marked as to be entirely above suspicion as caused by the selection of unusually good quadrats for collecting, do nevertheless show apices which generally coincide with the apices for the leaf stratum. The most important exception to this is the collection of February 9, where the lowest soil population of the study occurred coincidentally with the highest leaf population. This was one of the most marked temperature fluctuations observed, and perhaps called into activity in the leaf stratum a larger proportion than usual of the animals usually remaining in the soil. There is nothing to indicate that the upper 10 cm of soil examined serves during colder weather as a retreat for animals otherwise found in the leaf stratum on the surface. If this were the case, the soil curve would rise as the leaf curve falls. There is no evidence of this. Obviously the animal population of the leaf stratum, on the approach of freezing temperatures, migrates downward to a point below the 10 cm level and probably below the frost line, which was not deep at any time.

At the same time it should be noted that the animals found hibernating in the forest-floor showed, practically without exception, a complete absence, as far as could be observed, of harmful effects of low temperatures. Throughout the greater period of the study the leaf layer was frozen, and the upper portion of the soil more or less so, and frequently frozen as hard as ice. Animals of all sorts, mollusks, myriapods, arachnids and insects, when thawed out of the leaves or the solid masses of frozen soil moved about actively and seemingly with vitality unimpaired. There was nothing in their appearance or behavior to indicate any marked winter mortality. Under these conditions of cold and freezing neither decomposition nor destruction by scavengers could take place, and it seems safe to infer that the scarcity of intact dead animals, coupled with the uniform activity of the live animals when thawed out of the frozen matrix, indicates that the death-rate among hibernating invertebrates frozen in the forest-floor is not as high as has been supposed. Of course many animals habitually pass the winter below the frost-line; such ani-

mals would be presumably destroyed or at least debilitated by exposure to freezing temperatures. The above remarks apply, however, to the animals normally found hibernating in the forest above the freezing level, and the observations on which they were based were made in what was an unusually severe winter for the locality.

To summarize the winter activities of the animal societies we might give a general account of what happened during the present study. At the time when collecting was commenced, the total population had fallen much below the autumn maximum caused by the influx of forest-border species coming in to hibernate in the shelter of the forest (Weese). There remained still, however, some evidence of this in the case of individual species. The animals left on the shrubs and herbs were few, and rapidly became fewer, crawling for shelter into the leaves and soil. The resident population of the soil and leaves, moisture-requiring and dark-choosing (Shelford, 1913) invertebrates, were few in number to the depths collected, but appeared more numerous than usual in the soil and correspondingly less so in the leaves. With the increase of available moisture in these lower strata, and before the ground was much affected by the chilling of the air, the population of invertebrates, largely residents in the leaf layer, rose, and with minor fluctuations remained high for a period of weeks. It then rather abruptly decreased with the chilling and possible with the drying of the leaf layer. The minimum point of population preceded the minimum point of air temperature by a week. From this time on the population, now consisting almost wholly of the leaf stratum animals, rose gradually, though fluctuating from week to week, until February 9, when a warm rain cleared away the snow and thawed the frozen soil and leaves. The population mounted at the same time to the largest total observed in the study. A lower temperature followed the next week, and the number of animals fell to less than half, presumably mostly retreating into the earth deeper than the samples were taken, though there is evidence that a few remained in the surface soil. A second high point the following week accompanied another rise in temperature; this was still caused by numbers of animals appearing in the leaf stratum. With the sharp fall of temperatures the week following the leaf and total populations dropped almost to *nil*, most of the animals reëntering the deeper layers of the soil, but a few remaining in the upper 10 cm. Throughout the period the soil population had undergone the least fluctuations. The warmest days had brought up a few animals to the herb and shrub strata; these disappeared with the falling temperatures.

The animals named as predominants below must be considered as entitled to that term only with reservations; that is, they are *numerical* predominants, the most numerous animals found in the area at the time

the study was made. Second, they are *seasonal* predominants in part; some of the species listed would not be found in the deciduous forest floor save at the season of hibernation. The most numerous species, however, are permanent residents of the lower strata of this habitat. With these reservations in mind and with the repetition of the statement that most animal predominants do not "control the habitat" as some plant predominants do, we may consider the species listed as good and valid seasonal and stratal animal predominants. Some of them are more than this.

The following species are listed by their stratal occurrence and the invertebrates are given in their respective societies in order of their relative abundance; the seasonal and in some cases the stratal distribution is plotted for most of the species in the plates.

Subinfluent:

Tomoceris (Leaf) Society: Enchytraeidae (undetermined), *Tomoceris flavescens* Tullberg var. *americanus* Schott, *Onychiurus subtenuis* Folsom, *Carychium exiguum* (Say), *Malihodes* sp. (larva), *Telephanus velox* Hald., *Lygus pratensis oblineatus* (Say), *Isotoma* sp., *Vitrea indentata* (Say), *Anyphaena rubra* Emer. (juvenile), *Cleiodogona caesioannulata* (Wood) (juvenile), *Leptothorax curvispinosus* Mayr., *Zonitoides minuscula* (Binney), *Gastrocopta tappaniana* (C. B. Adams), *Dictyna volupis* Keyserling, *Nitidula rufipes* (L.), Phalacridae (undetermined), *Zonitoides arborea* (Say), *Carychium exile* H. C. Lea, *Nabis ferus* (L.), *Leptocera* sp., *Linotaenia chionophila* (Wood), *Scytonotus granulatus* (Say), *Tipula* sp. (larva), *Phyllotreta sinuata* (Steph.), *Meracantha contracta* (Beauv.) (larva), *Myodochus serripes* Oliv., *Cantharis* sp. (larva), *Fannia* sp. (juvenile); *Peromyscus leucopus novaboracensis* (Fischer), *Blarina brevicauda* (Say), *Sylvilagus floridanus mearnsii* (Allen).

Fontaria (Top-soil) Society: *Lasius flavus* Fabr. subsp. *nearcticus* Wheeler, *Fontaria virginiana* Dry., *Pokabius bilabiatus* (Wood), *Onychiurus armatus* Tullberg, *Onychiurus fimetarius* (L.), *Ptilodactyla serri-collis* (Say); *Scalopus aquaticus machrinus* (Rafinesque).

A few species are listed which appeared at the beginning of the collections in the

Linyphia (Herb) Society: *Linyphia phrygiana* C. Koch, Lathrididae (undetermined), *Tetragnatha* sp., *Epitrix brevis* Sz.

A single mammal was noted as characteristic of the winter.

Sciurus (Tree) Society: *Sciurus niger rufiventer* (Geoffroy). The above lists include only a small proportion of the species taken in the weekly collections; they do, of course, include all species taken in such numbers as to entitle them to status as predominants in the societies where they occur.

Predominants of the Tomocerus (Leaf) Society

Enchytraeidae (Fig. 30, Bc and d).

This family of worms, on which it was not possible to secure determinations, was decidedly a predominant group in the leaf society, where they appear to be characteristic animals (Welch, 1914). They are constant residents, but may withdraw into the soil if conditions become unfavorable. They were found in the leaf layer during the early collecting, but seemed to retreat into the earth when the ground became drier during the fall, becoming very scarce in the collections until the late rains. They then became numerous in the leaves and fairly so in the soil, their numbers contributing much to the high populations of November 24 and December 8. With falling temperatures they became few in the leaves, some apparently lingering in the top soil, and finally disappeared from the collections altogether. They appeared again during the warm and wet week of February 9 and make up a notable part of the high curve for that date, disappearing almost completely with the low temperature and general population decline of the following week. They again became abundant the week following, and disappeared entirely during the cold Monday when the last collection was taken. From the numbers of the animals that may be found in the dead leaf layer during warm and wet weather, it may be that we have here not only a numerical but also a real stratal dominant, the gross effects of whose activities on the gradually decaying layer of organic debris may be considerable.

Tomocerus flavescens Tullberg var. *americanus* Schott. Fig. 30, Ab, c and d.

The seasonal and stratal distribution of this spring-tail is very suggestive of that of the Enchytraeids. In fact, its close agreement with those animals in its reponse suggests an analogy to the "behavior agreement" found by Shelford for aquatic and terrestrial animals (1913, 1914). The animal seems to be somewhat more tolerant of unfavorable conditions, however, remaining in the leaves and top soil in considerable numbers during periods of freezing, from which it emerges into activity, at least, unimpaired. It was rarely taken on the herbs. It seems likely that in this species, as well as in the other numerous Collembola, we may have real stratal predominants. Their numbers, constant presence and food habits suggest that the part they play in the organic changes going on in the forest-floor may be by no means as small as their size and lack of "economic importance" in the usual sense might lead one to suppose.

Onychiurus subtenuis Folsom (Fig. 29, bottom curve).

This species appeared for the first time with the rising temperature of January 5. Thence it fluctuated in small numbers until February 9, when it took an important part in the maximum of that date. Along with other species, it fell off sharply the following week, but, unlike most

others, it disappeared completely the warm week following, when most other species took more or less part in the second population rise. It might appear that we have here a less hardy species than *Tomocerus flavencens* which, called out of deeper hibernation by the unusually warm weather, was chilled back during the following cold snap, from which it was unable to recover.

Carychium exiguum (Say) (Fig. 26, I).

This snail was present in the largest numbers of any mollusk, but neither it nor any of the remaining forms was in the same order of abundance as those just named. It was present in the leaf layer in moderate and fluctuating numbers from the time of the autumn rains and consequent moistening of this layer until the end of the study. Its single high point coincides with the second population apex of February; it increased only slightly at the time of the first and greatest February rise. Inasmuch as these were periods of both increased soil moisture and rising temperature it would be difficult to assign to either the rise, which was general for several species of mollusks; but the general habits and responses of the animals leads one to suspect the former.

Malthodes sp. (larva) (Fig. 28, E)

This cantharid larva was the most abundant beetle; it appeared early in the collections and with increasing frequency and in increasing numbers as the study progressed. Its first marked increase came with the slight but distinct population rise that followed the low week of December 22. Its second maximum, curiously enough, falls on the week of moderately low temperatures that intervened between the two high weeks in February.

Telephanus velox Hald. (Fig. 28, Db, c, and d.)

This species is of particular interest as studied in detail by Weese in 1921-1922. He found it on the herb stratum October 3, and in the leaf stratum throughout the winter, with a maximum on November 7. Save that the hibernation migration took place later, the findings for the beetle in 1924-1925 were remarkably similar. It was swept from the herbage October 13, and showed an extraordinary maximum in the leaf stratum on November 24. Thence it appears in varying numbers all winter, its only other marked increase coinciding with the first "high" in February. This species was also taken in the ground from time to time and its appearance there in some numbers preceded the February rise.

Lygus pratensis oblineatus (Say) (Fig. 27 Fa, b, c and d.)

The tarnished plant bug appeared in considerable but varying numbers throughout the study, but for the winter season is undoubtedly to be classed in the leaf society. It appeared in increasing numbers on the shrub and herb strata during the early part of the study, disappeared from these strata in the order named and became abundant in the leaf stratum,

where its numbers underwent considerable fluctuations from week to week. Its first and greatest increase there coincided with the general rise following the period of lowest populations. Thence its numbers fell off sharply and then with rising temperatures gradually increased until February 16, its high points not exactly coinciding with the highest temperature points. On the date when the highest temperatures occurred, however, a few individuals appeared in the herb and even ascended to the bare shrubs. A few individuals also appeared in the soil early in the season. The fall distribution of this insect among the strata indicated an inward migration from the forest border, followed by a downward migration into the leaves, similar to that described by Weese for several species of forest-border beetles in this same habitat.

Isotoma sp. (Fig. 29, Cc and d.)

This spring-tail appeared in small numbers in the soil about December 29, and a few were taken in the leaves February 2. The great rise took place on February 23, and took part in the general high curve for that warm period. Its numbers at once declined, and it was not taken again in the collections.

Vitrea indentata (Say) (Fig. 26 Hc and d.)

This snail was found throughout the winter in hibernation in the leaf layer; its fluctuations during the early part of the season are probably not significant. At the time of the coldest week, the animal disappeared from the leaf stratum but was taken in some numbers from the soil. The maximum for the winter fell on the "high" of February 23, and was probably determined chiefly by moisture.

Anyphaena rubra Emer. (juvenile) (Fig. 26, Ca, b, c.)

These young clubionids hibernate habitually in the leaf stratum, where they were taken in varying numbers throughout the winter. Their records of stratal occurrence show a downward migration from shrub and herb strata to the leaves, during the whole autumn period. A few specimens were taken from the herb level on warmer days during the winter.

Cleiodogona caesioannulata (Wood) (juvenile). (Fig. 31 Cc, d)

This diplopod is a characteristic species of the animal society inhabiting the humus and ground litter on the deciduous forest floor (Adams, 1915; Weese, 1924), where it exercises subinfluence in altering the compounds produced by plant decay (Adams, loc. cit., and reference to Cook (1911c). It appeared in the samples taken by Weese during July and again in early November. In the writer's collections, *Cleiodogona* appeared first in the soil stratum on November 17, in the leaf stratum the week following (when it was not taken in the soil), and it increased in numbers in the leaves through the week following, reaching the high point for the collections on December 8. The following week the species disappeared entirely from the leaf stratum but were still present in considerable numbers

in the soil. They then disappeared entirely from the collections until the warm week of February 9, and for the next two weeks they were taken in some numbers in the leaves. The cold week of March second yielded none of these animals in the leaf stratum, but a considerable number remained in the upper 10 cm of soil. They were not taken again during the study. This species, as far as its stratal distribution is concerned, seems to behave like some of the mollusks. It was absent from the upper strata during the dry weather of the fall both in 1921 (Weese) and 1924. It reached its maximum when the forest floor was moist from the late autumn rains, and disappeared during the coldest part of the winter. Early spring rains and warm weather brought up numbers of these animals into the forest floor litter, but with falling temperatures they passed into the soil and thence into deeper hibernation at levels where they were not reached by the methods of collecting.

Leptothorax curvispinosus Mayr.

This ant is an example of a resident stratal predominant; maxima represent colonies of hibernating individuals which chanced to be in the quadrats selected for study on the dates in question. They are included because they represent a fairly numerous and characteristic species and suggest the discontinuous distribution of animals with such mores over the forest floor.

Zonitoides minuscula (Binney) (Fig. 26, G)

This land snail was collected in fluctuating numbers from the leaf stratum during the entire winter, not appearing until after the fall rains. The first rise in numbers was that of December 8, and was a part of a general population high, accompanied by a considerable rise in mean temperature; the second high point coincided with that of *Vitrea indentata* and was no doubt due to the same factor.

Gastrocopta tappaniana (C. B. Adams) (Fig. 26, F)

This species showed a rather different type of distribution from that of the species just described. It showed a high point early in the season, probably correlated with the moisture incident on the autumn rainfall, and then disappeared entirely from the collections until the "highs" of February, when it was again sparingly taken.

Dictyna volupis Keyserling (Fig. 26, B-a-b, and c.)

These young Dictynids showed the same stratal and seasonal distribution as *Anyphaena rubra*, already described, save that they did not appear above the leaves on the warm days in the latter part of the winter; they sometimes do so, however (Weese, 1924).

Nitidula rufipes (L.) (Fig. 28, C).

This species was found hibernating in varying numbers in the leaf stratum throughout the winter; it responded to the conditions existing

on February 9 and 23 by appreciable increases in numbers, no doubt called forth from deeper hibernation.

Phalacridae (undetermined)

The numbers and seasonal and stratal distribution of these beetles indicated the same inward and downward migration described by Weese for *Phalacrus politus* in this habitat; they appeared first on the shrubs, later on the herbs and thereafter and throughout the winter in hibernation in the leaf stratum. In the absence of specific determinations, their occurrence has not been further studied.

Zonitoides arborea (Say) (Fig. 26, E)

This species was taken only towards the latter part of the study and its only marked increase in numbers fell on February 23, the period when most of the mollusks showed a high point.

Carychium exile H. C. Lea (Fig. 26, D)

The appearance of this snail in the collections agrees well with that of *Gastrocopta tappaniana* but with no other species of mollusk found in any numbers. Its maximum fell in the late autumn, and was probably determined by moisture, but it did not appear again in the collections. It was found exclusively in the leaves.

Nabis ferus (L.) (Fig. 27 E-a, b, c and d).

Save that it was present in smaller numbers, this common nabid showed the same distribution in the collections as the tarnished plant bug; it appeared in the fall on herbs and shrubs, passed into the leaf stratum, and there remained throughout the winter, a few specimens being also taken from the soil from time to time. Like the plant bug and many other animals it appeared in small numbers above the leaves during warm periods in the latter part of February.

Leptocera sp. (Fig. 31, F-a, b, c, d).

This borborid appeared first in the collections at shrub level on October 6, and other individuals of the same species were taken in the herb society for this date. By the next week it had disappeared from the shrubs, but was present in increased numbers among the plants of the herb stratum. Here it appeared for the last time on November 10. It was collected in numbers from the leaf stratum on November 24, but disappeared with the falling temperatures of the week following. The temperature rise of December 8 was accompanied by considerable numbers of these flies in the leaf society. The following week they had disappeared from the leaves but a few were found in the soil. They were not taken thereafter. The data suggest a downward migration similar to that observed for other species, accelerated by falling temperatures and arrested by rising ones, to the level of hibernation. Weese took *Leptocera evanescens* Tuck. from ground and herb strata at various times through the winter of 1921-1922.

Linotaenia chionophila (Wood) (Fig. 31, A-c, d).

This centipede was a common animal of the leaf society during the fall. It appeared first in the soil collections, perhaps because of the dryness of this stratum during the early part of the study. Thence on it was common in the leaf stratum until the temperature drop of December 1, when it disappeared from the collections for the next two weeks. On December 15, when the temperature of the soil had risen somewhat, a few appeared in the soil stratum, and a few more were collected in the leaves during the warm week of February 9. Weese found this species on the forest floor from time to time during the winter.

Scytonotus granulatus (Say) (Fig. 31, E-c, d).

This millipede was a characteristic animal of the leaf stratum, from which it was collected in varying numbers from time to time during the period of study. Its periods of abundance appear to coincide with even or slightly rising ground temperatures. Specimens were collected from the soil stratum during the latter part of November, but except for this was a leaf-stratum form. Its habitat relations are no doubt similar to those of the other diplopods discussed.

Tipula sp. (larva) (Fig. 27, Dc, d)

Crane-fly larvae of the genus *Tipula* were fairly common in the leaves and soil during the fall and late winter. They reached their maximum numbers in the "high" of February 23; there is some evidence that they migrated a short distance into the upper soil during the following cold week and again returned to the surface leaves the next week, which was warm. With the return of extreme temperatures at the end of the study they disappeared, no doubt going to the deeper layers of the soil where they had passed the extreme part of the winter, and where they were not reached by the methods of collecting employed.

Phyllotreta sinuata (Steph.) (Fig. 27, C)

Leaf-beetles of the species named were taken in varying numbers and only in the leaf stratus during most of the study; they disappeared, however, for a short period during the coldest weeks.

Meracantha contracta (Beauv.) (larva) (Fig. 27, B)

The larvae of this tenebrionid appeared, chiefly in the leaves but a few in the soil, throughout most of the winter. They were more abundant in the early fall, when the ground strata were drier, disappeared about the time of the autumn rains, but were present throughout the coldest weather. They did not take part in the population rise during the month of February. This is a very characteristic influent of the leaf society, often appearing as a dominule in the microhabitats furnished by decaying down timber (Adams, 1915).

Myodochnus serripes Oliv.

The slender-necked bug appeared on the herbs in the fall, migrating into the leaves and thence into the soil. While most of the specimens were taken in the leaf layer, this was in the fall and there is reason to suppose that most of these animals hibernate deeper. The species was taken from among the dead leaves of this habitat by Adams during the season of hibernation (Adams); as he remarks, and as is true for certain other species found here by the writer and by Weese (1924), such examples "show how during the hibernating season many animals are to be expected here which at other seasons live in other habitats."

Cantharis sp. (larva) (Fig. 27, A)

The larvae of this cantharid beetle were taken almost entirely from the leaf stratum at intervals during the whole series of collections. They showed their maximum increase of population during the week of February 23, when so many species appeared in increased numbers.

Fannia sp. (juvenile) (Fig. 31, G).

The larvae of *Fannia* were very characteristic inhabitants of the layer of forest floor litter, the only stratum from which they were collected. They gradually decreased in numbers as the soil temperature fell, disappearing entirely from the collections during the coldest period. A few were taken during the middle of February; this was a period when the soil temperature was slowly and steadily rising.

Predominants of the *Fontaria* (Top-soil) Society

Lasius flavus Fabr. subsp. *nearcticus* Wheeler.

Two small communities of this ant were captured entire on October 13 and November 10, respectively. The same general remarks apply to them as to *Leptothorax curvispinosus*.

Fontaria virginiensis Dru. (Fig. 31, D-c, d).

This large myriapod is common in the humus and forest-floor litter of deciduous forest (Adams, 1915; Shelford, 1913). During the winter it appeared in the leaf litter only once in small numbers, and a few were taken from this stratum early in the collecting. With these exceptions, the species appeared only in the soil for the period of this study. The largest population appeared at the time of the general population increase during the warm weather of February, and accompanied a gradual rise in soil temperature. Two earlier but lower apices for this species, falling on December 1 and January 5, did not appear to be correlated with any particular changes in physical factors. They were perhaps due to the fortuitous selection of unusually well-populated quadrats. The species was not taken after the cold weather of March, until the close of the period of study on which the present report is based.

*Pokabius bilabiatu*s (Wood) (Fig. 31, B-c, d).

This centipede is reported by Weese for his ground stratum in July, October and late November. The writer found it in the soil stratum during the early part of the study, where it was a constant resident until it disappeared on December 8 with the lowering of the soil temperature. There is evidence of a stratum-to-stratum migration upwards from soil to leaf-litter during the week of November 10-17, followed by a return downward to the soil. The two warm, wet weeks of February 9 and 23 brought numbers of these centipedes up into the leaf-litter. With the colder week of February 16 and the decided temperature drop of March 2, the curves show that the animals dropped entirely out of the leaf society, and were present in smaller numbers in the soil. Doubtless most of them had withdrawn into the deeper soil where they had spent the colder weeks preceding.

Onychiurus armatus Tullberg. (Fig. 29, B)

Spring-tails of this species occurred in some numbers in the soil stratum during the latter part of January and the first of February; they were not taken at any other time.

Onychiurus fimetarius (L.) (Fig. 29, A).

The maximum abundance of this spring-tail fell on March 2, practically the only time it was taken. This was a very cold day, and the other species of Collembola, some present as numerical predominants during the preceding warm week, had disappeared.

Ptilodactyla serricollis (Say) (Fig. 28, B)

This beetle was collected from time to time through the entire period of study; it was sometimes taken from the leaf stratum as well, but was more common in the top-soil.

Predominants of the Linyphia (Herb) Society (Autumnal)

Linyphia phrygiana C. Koch. (Fig. 26, A)

Young of the hammock-spider were collected from the shrub and herb strata at various times during the fall and early winter, disappearing with increasing cold into retreats where they were not reached by the collecting methods employed. A scanty appearance of the species occurred during the warm week of February 9.

Lathrididae (undetermined)

Lathridid beetles of undetermined species were fairly common on the shrub and later on the herb stratum in the fall and early winter; the last were swept from the herbs on December 8. They were not taken thereafter nor in the lower strata.

Tetragnatha sp.

Young *Tetragnathas* were constantly taken from the herb stratum during the early part of the study; they disappeared on December 8,

reappearing in small numbers at herb level on February 23; they were not taken at any level during the intervening period.

Epitrix brevis Sz. (Fig. 28, A-a, b, c and d).

The results obtained for this chrysomelid support the conclusions of Weese on its autumnal migration and hibernation. Small numbers were present at shrub and herb levels on October 6, and large numbers on the herbs the week following. They then entirely disappeared from all strata until the warm week of December 8, when a few were taken in the leaf stratum. The species was not again taken above the soil stratum, and rarely there. Evidently hibernation is deep, as Weese suggests.

Vertebrates of the Winter Society

Vertebrate animals, except birds, are of few varieties and not particularly abundant in individuals in the area studied. The reason for this has been given by Weese; the forest was depleted of much life by a period of heavy grazing and consequent depletion of ground cover, and on the removal of this factor the isolation of the tract prevented the reestablishment of forms which had once become extinct or migrated. The forms which remain, however, are those characteristic of the habitat in an untouched condition.

No attempt was made to study the mammal population in detail; the following notes are from general observations made in various ways of the presence of common species, based on sight records, tracks in snow, partly-eaten food, etc. It will not be possible to do more than give a general idea of what mammals are present in this and similar habitats of the region, and the relative abundance of the more common species. The two most abundant mammals are unquestionably the white-footed mouse (*Peromyscus leucopus noveboracensis* (Fischer)) and the short-tailed shrew (*Blarina brevicauda* (Say)). The writer is indebted to Dr. M. S. Johnson for this information, gained in extensive trapping with both box and guillotine-traps for the former animals, that they are much the more abundant of the two. There is a great gap between the numbers of these animals and those of the next most numerous species, the fox-squirrel (*Sciurus niger rufiventer* (Geoffroy)) and the cottontail rabbit (*Sylvilagus floridanus mearnsii* (Allen)), of which the former is probably somewhat the more abundant. Less common appears to be the mole (*Scalopus aquaticus macrurus* (Rafinesque)), although its work was frequently encountered in digging out the soil collections. These represent the mammals that are definitely known to inhabit the tract under consideration. Other species, characteristic of the habitat (Wood, 1910) and some of them known to exist at present in similar wooded tracts within a few miles, are: the opossum (*Didelphys virginiana* Kerr), the chipmunk (*Tamias striatus lysteri* (Richardson)), flying squirrel (*Sciuropterus volans*

(Linnaeus), red fox (*Vulpes fulva* Demarest), raccoon (*Procyon lotor* (Linnaeus)), weasel (*Putorius noveboracensis* Emmons) and probably the long-tailed shrew (*Sorex personatus* I. Geoffroy-Saint-Hilaire).

Of these animals the only ones which would be likely to directly affect the rest of the animal community during winter are the short-tailed shrew and the mole. The activities of the latter at this season of the year are confined to levels below those where collecting was done. The shrews, however, probably feed to a very considerable extent on the hibernating population of invertebrates in the forest-floor.

During the period between January 5 and March 2 an attempt was made to take a bird census of the area under study. The area was visited for this purpose at least weekly and frequently oftener. An attempt was made to arrive at a quantitative result as well as a qualitative one; great conservatism was observed in making the estimates, which are therefore believed to be well on the side of safety. The results are given in Tables XXI-XXV, Table XXI gives the estimated numbers for species constantly present, their location in the forest and stratal occurrence. Table XXII gives the same information for frequent visitors, Table XXIII for occasional visitors, and Table XXIV for a few early migrants observed during the latter part of the study. Table XXV gives the list of species with numbers and dates when observed.

These data will be discussed only in relation to the effect of the winter birds on the hibernating invertebrates. Considering the species which are present in any numbers it appears that there are few if any of the actual residents which would be expected, from our knowledge of their food habits, to feed on the large population of insects and other invertebrates in the leaf stratum. The important birds are either seed-eaters or insect-eaters which, like the woodpeckers, get their food from the tree stratum. The flicker may occasionally feed on the forest floor, for it is sometimes seen there, but its doing so is apparently exceptional. It does not seem likely that the birds listed, either from their numbers or their food habits, can produce much effect on even the animals of the leaf stratum, and we know that many species hibernate out of reach entirely.

DISCUSSION AND SUMMARY

The present study began before the close of the autumn migration of animals from the forest border and from the herbs and shrubs of the forest itself into the leaf layer for hibernation. This migration had well progressed before the temperatures had become extremely low, but was no doubt incited by their gradual decline during the first part of the period of study. As far as this migration concerns forest border species, those migrate inward on their own strata and then downward to the forest

leaf-layer; this was determined by Weese for a number of beetles and the writer obtained evidence in the same direction for some other species. The downward migration may be delayed on the herb level, in the leaf level or in the upper soil, or the animals may disappear at once from the shrub level into deeper hibernation. As far as the forest-border insects are concerned, the movement towards winter quarters seems to be correlated with temperature changes, to be continued rapidly on falling temperatures and arrested more or less on rising ones.

Other animals, living earlier in the season in the upper strata of the forest itself, migrate downward at the same time. They behave in a very similar way as far as the effects of temperatures are concerned, entering the leaf stratum more promptly with falling temperatures. The evidence indicates that different species react differently to the factors inducing hibernation, and that the reactions for a given species are constant from week to week and from year to year. Certain forms migrate at once to the deeper strata and are not seen again until the time of emergence in the spring. Other species remain comparatively near the surface, in the top-soil or leaf strata or both, and seem to fluctuate in abundance in activity with the changing conditions. Ordinarily these animals are the ones which determine the fluctuations in numbers found in samples.

Extreme changes in either direction may cause marked differences not only in the size but also in the composition of the samples. Extreme cold in the soil layer reduces the population to some extent, but less than might be supposed; temperatures rising to the thawing point, especially if accompanied with abundant moisture, bring up a large population, composed in part of hibernating animals from various strata but mostly consisting of the moisture-requiring permanent residents of the forest-floor. On the other hand, cold or dryness in the forest-floor markedly reduces the numbers of the resident enchytraeids, mollusks and spring-tails. That certain species are much more sensitive than others is indicated by the very different seasonal distribution of various species of *Collembola* and mollusks throughout the period of study.

The changes in temperature, as shown by the curves, are much more gradual in the forest floor than in the air above it. Indeed, it is evident that the decline does not trap any great numbers of animals in the frozen upper layers, and does not seem to affect adversely most of the animals which do remain there during freezing. The invertebrate population of the upper ground strata, once the freezing point is approached, seems to consist of species which are able to tolerate complete freezing with little harm, but before this condition is reached many animals migrate downward. On the other hand, very warm periods call up from deeper

hibernation species never found during winter weather; on the return of the cold, these forms soon disappear, returning to the regions lower in the ground, probably below the frost-line.

The different reactions of various species to changing conditions of the physical environment is of great interest. We must assume that the winter is a period when biotic influences are at their lowest, and the maximum role is played by physical factors. To this extent the changing earth temperatures may be looked on as a series of natural experiments on the effect of changing the physical environment. The animal responses thus evoked appear distinct for various species of the same group. Thus certain species of Collembola, mollusks, etc., present at one period in distinctly predominant numbers, during other periods disappear wholly or in part and are replaced by other species from these same groups. These differences in predominants can hardly be considered societies, in the sense of the use of that term by plant ecologists. They are too brief, and their disappearance is probably caused merely by local withdrawal to deeper areas. They represent the response of some species to a particular complex of physical factors to which other species of the same group are negative or neutral. Such responses may be as definite specific characters as morphological ones.

It is an ecological axiom that animals react most accurately to physical changes of kinds affecting them under natural conditions. The invertebrate population of winter forest is a stratal population occupying, generally speaking, only the leaf and soil strata. We should expect to find its members responsive to changes within those strata, and to a large degree this proves true. Thus the curve of population only roughly coincides with the curve of air temperature, and this largely because the leaf stratum, in contact with the atmosphere, has its temperature more or less directly affected thereby. So far as could be observed there existed no correlation between animal population and atmospheric humidity; the changes in this factor are little indicative, in winter, of conditions in the soil and leaf strata. But soil and leaf moisture, though it was not measured and could not be separated in its effects from temperature, appears to be a factor of importance.

It has been said that biotic influences were at their lowest among the hibernating population of forest floor invertebrates. Most of the animals were in a quiescent or dormant condition when collected, although they soon revived when exposed to warmth. There was no evidence of activity among spiders, nabids or other predatory species, and on even the days when conditions were such that some animals were seen among the dead herbs and leafless shrubs, they were rather torpid. As has been seen, the effects of the activity of vertebrates on the forest floor animals are probably negligible.

CONCLUSIONS

Temperature is the climatic factor which seems to be of greatest importance to the winter forest population; this factor is well stratified, the higher strata showing greater extremes and lower mean temperatures. The stratum whose temperature is of importance to hibernating animals is the ground; here is the highest and most uniform of the three stratal temperatures studied. Atmospheric temperature is of importance only in so far as it affects the ground, and especially its leaf stratum.

There is no evidence that atmospheric humidity shows any direct correlation with the population of hibernating animals.

Moisture present in the forest floor appears to be a factor in the weekly variations in the numbers of animals in the samples. An increase of moisture in winter, however, is almost always accompanied by a rise in temperature, and the separate effects can only be inferred.

Biotic factors seem to play little or no part in the weekly fluctuation in numbers. Invertebrate predators are themselves quiescent at this time. The vertebrates feeding on the forest floor insects are not present in sufficient numbers in winter to have any marked effect.

The first response of animals to the falling temperatures is the descent of shrub animals to the herb level; this is characteristic both of inwardly migrating forest-border species, such as certain beetles, and of true forest shrub animals, such as many young spiders. From the herb stratum the animals pass downward into the leaves.

Some animals remain in the leaves for the entire winter; others until this layer becomes colder; others make only a brief stop; while the remainder pass directly into the soil beneath. Behavior in this regard appears to be a species characteristic. The members of the last group do not reappear, as a rule, during the winter.

The animal population fluctuates somewhat between the leaf and upper soil strata but less than would be expected. Conditions sufficiently severe to markedly reduce the number of individuals in the leaf usually drive the animals deeper into the earth than the upper 10 cm of soil. The reverse is also true; conditions which cause any noticeable increase in the leaf population do so by affecting the soil deeper than the top layer.

Many resident animals of the forest-floor show very marked response to changing physical factors—especially temperature and moisture—by migrating vertically. Such animals as spring-tails, Mollusks and enchytraeid worms are the numerical dominants of the forest-floor strata in winter, and probably at other times as well. From their huge numbers and constant presence some of these animals may be considered as pre-dominants of these stratal socies.

After the fall migration downward, the herb and shrub socies are insignificant in their contributions to the general population. The soil,

in its upper 10 cm., gives a rather uniform but low animal count. The leaf stratum varies enormously and determines, by its curve, the curve of the total population.

The animals in the leaves and upper 10 cm of earth are uniformly found in a condition of dormancy from cold. They are frequently frozen solidly into the earth and leaves for weeks at a time. There is no evidence from the present study that this exposure to low temperatures is injurious to them, as they become active when thawed out.

The large number of animals often recorded for a single week is partly due to the presence of one or more species which appeared exclusively at that time. This seems to indicate a capacity for response quite different among different species in the same group. It suggests, in addition to the recognized, morphological differentiation, physiological distinctions between species. The data at hand relative to the winter populations, etc., will be compared with that of Weese and others later.

GENERAL DISCUSSION AND SUMMARY

The process of biotic succession tends constantly to cover bare areas of the earth's surface with a climax biota of vegetation and its animal inhabitants; this climax is determined primarily by climate (Clements, 1920). Animal succession over such areas is correlated with—and to a large extent determined by—plant succession. Under favorable conditions the climax may develop swiftly, its dominants becoming well established in a comparatively few years (McDougall, 1918). Under greater stress of unfavorable climate and soil the subclimax stages may be of very long duration; the montane tundra studied in the first part of this survey is a preclimax stage of coniferous forest showing arrested development (Harvey, 1903).

The vegetation climax in all the areas under consideration is forest; for the first and second studies it was northern coniferous forest (northern mesophytic evergreen of forest of Shreve and Livingston, 1921) and for the second it was deciduous forest (McDougall, 1922). The general succession of biota following the last glacial retreat is pictured by the present day distribution of biotic types from the Arctic Ocean southward; that is to say, tundra, coniferous forest and deciduous forest, in the order named (Adams, 1905). We are therefore justified in considering that a study of these stages should give some idea of the process of animal succession accompanying the slow northward migration of climaxes at the close of glaciation. If we substitute for the subarctic low tundra the alpine high tundra of the northern Appalachians, we still have a comparable series, since a large proportion of the characteristic species is common to both.

Beginning with bare rock areas, which we may assume not to differ essentially as biotic habitats from similar areas left by the retiring ice-sheet, we find thereon a scanty covering of lithophytic plants, independent of animals. The animals present are principally small lichen-feeders and lycosid spiders belonging to species characteristic of this habitat in high and low tundra regions. Climatic conditions are extremely severe, temperatures ranging as much as 28°C. between sun and shade and wind velocities approximating 110 miles per hour. In the absence of any appreciable plant cover, these must exert a maximum effect on animal life. The dominant animals live in openings among and under the rocks, and their habits are adjusted to this type of life; the community thus consists of one stratum only. Succession from this stage waits on the formation of a soil, in which process both biotic and physical factors

are involved. There is evidence that the latter are of particular importance in these early stages, although the former cannot be ignored.

With the formation of finer rock fragments and the retention among them of a coarse granitic soil, to which the pioneer biota contribute a sparse organic component, we have the establishment of the early tundra, a shallow sod overlying rock and hence comparable to arctic low tundra, which overlies continually-frozen soil. On this sod and largely composing it are characteristic plants, among which grasses and sedges are most conspicuous. The whole furnished the home for an animal associates of different species and life histories from those inhabiting the rock area. The plants furnish a more abundant food supply and the dominant animals are species of Cicadellidae which are characteristic of such host-plants. Climatic stress is still as severe as on the rocks, but the soil and alpine grasses furnish a partial shelter during the frequent storms and low temperatures of the short summer, as well as a means of retaining moisture and heat. During the winter the thin cover of earth and dead herbage furnishes a place for hibernation; that it is efficient shelter is indicated by the numerous and varied population which appears in the late spring on the high tundra, as well as by studies made on animals hibernating in the frozen upper layer of earth in other habitats.

This associates has really two societies, soil and herb, but the animal population seems to leave the shallow soil almost *en masse* during the warm period of the year. Thence on, the process of succession is increasingly dependent on the biotic factors; the climatic factors, local or regional, are retarding in their effects. With the increase in depth and organic matter in the soil, the latter amounting to 34.5%, a succession to the last stage of tundra community is attained. The capacity for moisture and heat retention becomes greater as the soil and vegetation cover increase in thickness, and hibernation probably takes place under somewhat more favorable conditions. Further succession on the plant side is characterized by the heaths. The animal community is different from that of the early tundra, the differences, however, being chiefly caused by the appearance of phytophaga, especially cicadellids and aphids, associated with the plant dominants, while the grass-eating forms of the early tundra disappear. Although species have changed, there seems no reason to expect a marked change of mores, nor is there any evidence of such a change. The dominant animals are still such as are characterized by short summer activity and long hibernation periods. The heaths are so low as to be of no more than herb proportions, and stratification of the animals remains unchanged. At this stage of succession, in addition to the various associates of invertebrates, some of the vertebrates of the climax forest appear, either as visitors or as more or less permanent residents; especially is this true of small mammals.

With the establishment of the heaths, the tundra series comes to an end. On the increasingly deep soil, due to the deposition of organic material by successive generations of plants and animals, the forest is able to become established, bringing with it forest conditions and forest animals. Here, however, the local climatic factor of wind makes itself felt, and the first forest to gain a footing is the krummholz or elfin-wood. On the advent of its low-growing but dense thickets the habitat changes. Evaporation is reduced, the terrific velocity of air-movement felt in the open becomes much lessened, and temperatures are much more uniform. Perhaps as important as any of these, the new habitat furnishes an abundance of materials for abode. The conditions required for distinct stratification into animal societies become present for the first time, and stratification of the biota is important in all later stages. In the krummholz it is shown especially well by spiders.

The development of the krummholz into climax coniferous forest is not accompanied by any very marked changes in the whole biotic association, although stratification becomes more marked, and there is a large increase in the number of animal species. It is possible that this is due in part to the removal of the conditions of climatic stress which are connected with krummholz formation, but there is no direct evidence that this is so. Rather is it due to the more varied nature of the coniferous forest habitat at lower levels, and its interruption by local habitats, such as bog, meadow, streamside, slash and forest-margin communities. In other words, the animal communities of the climax forest, as compared with those of the krummholz, seem more closely correlated with the massed biotic conditions than any particular physical factors.

Coniferous forest presents a well-stratified habitat, where conditions are much more uniform, for any given period of the year, than those found in any of the preclimax stages. This uniformity is caused in part by the absence of the alpine conditions which have held tundra and krummholz in a subclimax state, and in part by the influence of the forest cover itself. Its most marked physical feature is the constancy and sharpness of the various strata; this is in turn correlated with, and principally caused by, the stratification of plant societies. It is accompanied by a stratification equally sharp, as far as it has been observed, for the animal societies.

Beginning in the forest floor we have in the soil a level of relatively constant temperature, whose summer mean is 14°C, with a mean range of only 2.3°C. Moisture is usually high and light scanty. We must assume that all these factors are present in higher percentage than in the shallow tundra soil. This stratum has a small but rather constant summer population; its winter population has not been studied, but it must be increased by immigrants for hibernation. The predominant

animals are those characterized by a considerable moisture requirement, tolerance of fairly low summer temperatures and a preference for darkness; the ground-dwelling larvae of *Elater* will serve as an example.

Next above this is the leaf stratum, largely composed of dead coniferous needles. Its physical conditions are somewhat different from those of the soil stratum. Temperature averages about 1°C higher than in the upper portion of the soil stratum, but moisture is still abundant; daily evaporation is only .08 cc from the lower part of the leaves. The characteristic animals have a greater capacity for adjustment to changing conditions than the soil animals possess, as evidenced by the fact that they may occur in leaf, soil or, more rarely, on the herbs. A predominant animal in this stratum is the spring-tail *Tomocerus flavescens*. Leaf and soil strata together form a ground society or super-society; physically this is indicated by the fact that the differences between them, while constant, are of moderate amount; biotically it is indicated by the fact that some animals habitually divide their time between these two strata, as temperature and moisture vary.

In the herb stratum there is another and more marked increase in temperature, with a mean temperature of 17.1°C and a mean range of 7°C. Evaporation also rises sharply, reaching 8.2 cc. at herb level. Differences of the same character exist between the herb and shrub and shrub and high bush strata, which have a mean daily evaporation of 11.2 cc and 14 cc respectively; there are smaller differences here, it will be observed, than that existing between leaf and herb strata. Forest temperatures in summer thus increase upwards in amount and range, and the same is true for evaporation and light. The animals of the high bush stratum have not been studied. The stratal occurrence of the animals of the next three strata below is what we should expect if it were due in part at least to physical factors. Thus, a rather large number of species habitually pass between herbs and shrubs and vice versa, while a much smaller number divide their time between the leaf and herb strata. This is of course under summer conditions, and refers to animals which during a given stage of their life cycle habitually divide their activities between the strata in question. This is apparently a temperature response in some cases, such as the downward migration of *Clastopera obtusa* and its return to the shrubs with rising temperatures. The tendency is seen to be for animals to make the traverse only between strata which are separated by moderate gradients.

Above the high bushes, the coniferous forest may possess a layer of low deciduous trees, and above them lies the forest crown itself. The animal population has not been studied. The instrumental observations indicate changes in the same physical factors and in the same direction, as those already mentioned. The sharp gradient falls between the high

bush and low tree strata, with a mean daily evaporation of 14 cc and 19.7 cc respectively.

The hythergraphs indicate that coniferous forest of the climax type, as distinguished from the subclimax stages of its northern or upper montane border, is in general a region of less climatic severity. The effects of climatic factors are modified by the forest cover of climax trees and sub-stratal plant societies. During the spring, summer and fall the animal population falls into stratal societies, which are in agreement with the stratification of physical factors and vegetation. The latter seems to be of obvious importance to the phytophaga, but since even they respond to physical factors by stratum-to-stratum migrations, and since stratification occurs among such animals as spiders, which possess no direct relations with the vegetation, it seems probable that the physical factors are extremely important and perhaps decisive. During the winter the invertebrate life and to some extent the vertebrate life of this forest becomes concentrated in the ground strata, and the community reverts for the time being to a one-stratum society, like the tundra community of its early successional history.

The climax of the entire series which we are discussing is deciduous forest, wherever climatic conditions permit this to replace the conifers. The area where such succession can take place is one of higher mean temperatures than the region of climax coniferous forest. Deciduous forest of elm and maple, as studied by Weese (1924) under summer conditions seems to possess a stratification of measurable physical factors which agrees in all important respects with that found for the coniferous forest, although mean temperatures are distinctly higher throughout the year, the difference being approximately 5°C.

The difference between shrub and herb temperature as contrasted for coniferous and deciduous forest is under 1.5°C, and evaporation from atmometers at the same height and exposure in the two habitats gives even closer comparisons:

	Mean daily evaporation in cc	
	Coniferous forest	Deciduous forest
On ground under vegetation	8.2	7.3
1 m above ground	11.2	11.2
2.5 m above ground	14.	12.4

It will be seen that differences are small or lacking. The whole suggests a general and stratal similarity of the physical factors in the two habitats. It must be remembered that the evaporating power of air is an index of many other physical factors, such as temperature, humidity and air movement.

The stratal societies of animals described by Weese for elm-maple forest appear in decided harmony ecologically with such societies observed

by the writer for coniferous forest. This may be illustrated by comparing lists of equivalent predominants from the summer shrub societies of the two habitats:

Coniferous forest	Deciduous forest
<i>Clastoptera obtusa</i>	<i>Empoasca viridescens</i>
<i>Tetragatha</i> sp.	<i>Tetragatha laboriosa</i>
<i>Graphocephala coccinea</i>	<i>Erythroneura obliqua</i>
<i>Philodromus</i> sp.	<i>Xysticus elegas</i>
<i>Diaphnidia pellucida</i>	<i>Epitrix brevis</i>

It will be seen that while there is no positive identity of species (the writer's Tetragnathas were too young for determination to species) there is a decided ecological similarity between the respective dominants, some of which belong to the same family. Even where the animals are widely separated taxonomically, as in the case of *Diaphnidia pellucida* and *Epitrix brevis*, their similar habits, life-histories and relations to the community, justify their consideration as ecologically similar. There are thus no greater differences between the animals of corresponding strata, or between the mores of the prominent species, than might be expected to occur between different associations of the same formation, although most of the species are different.

Certain widely ranging species occur in both habitats; examples are *Phylomycus carolinensis*, *Hahnia agilis*, *Linyphia phrygiana*, *Theridion frondeum*, *Gypona 8-lineata*, *Scaphoideus autontinens*, *Camponotus herculeanus pennsylvanicus*, *Formica fusca* and *Myrmica scabrinoidis schenoki*. Their presence in corresponding strata of both coniferous and deciduous forest indicates that to such animals the local conditions of the biotic association are of major importance; the general climatic conditions of less importance, or none at all within the ranges considered.

The various animal societies in both coniferous and deciduous forest are thus seen to be composed of animals with similar mores, of whatever species, or to phrase it differently, both habitats possess stratal societies composed of animals which are ecologically equivalent. These animals respond in a similar way to the measured stratification of physical factors and to their fluctuations, as well as to the observed stratification of plants. There is some evidence that the comparison between the two habitats is as close for seasonal societies as for stratal ones, but coniferous forest was not studied for this at critical periods. What evidence exists tends in this direction.

It hence appears that ecologically it is the forest cover, that is, the biotic association as a whole, that is of importance in determining these two animal communities. The nature of the cover, which is in turn dependent on the climate, is a secondary consideration. Stratification of

animal communities is thus seen to be fully developed in the preclimax forest, as soon as the forest cover becomes well established. So far as we have evidence, it agrees in all important particulars with the same phenomenon in climax deciduous forest. The cover of tall trees, with substrata of lower vegetation at different levels, appears to be the determining factor for the presence of a typical forest animal community. The nature of the trees, the character (within the limits discussed) of the climate, are of less value. Given such a biotic complex has been described, it becomes inhabited by a statified animal community during the warmer portion of the year.

With the advent of autumn in both forest habitats, there is a general change of the distribution of population. Urged by factors which are not fully known, but among which temperature is probably of prime importance, there begins a downward migration of the animals of the upper strata. This may be preceded or accompanied by an inward migration of forest-margin species (Weese). The entire phenomenon has already been discussed, and it will only be said here that it results in the reduction of the forest community, during the winter, to the status of leaf-soil society. What animal activities exist are confined to vertical migrations in the forest-floor, correlated with temperature and moisture fluctuations. In the coniferous forest habitat the cold is usually so sustained and the covering of snow so deep and enduring, that it is doubtful whether any important vertical movements take place. Under the milder conditions prevailing in the deciduous forest formation snow often does not lie through the entire winter, and warm rains may entirely thaw and wet the leaf and soil strata from time to time. Here vertical migrations may assume large proportions, such a warm and rainy period increasing the population of a two-foot quadrat by hundreds of percent. The amount and character of such response seems to be in some cases a species characteristic; thus among several species of collembola and mollusks, certain ones appear definitely for one period and set of conditions, other species at other times and under different conditions. This phenomenon has not, however, received any detailed study.

Many animals pass the winter in the leaf and top-soil strata, where they are solidly frozen in during considerable periods. The present study afforded no evidence of particular mortality among the animals so exposed.

Winter is thus a period when the forest loses its stratification of animals (birds, some mammals and some tree-inhabiting insects excepted). It is a period when the greatest climatic effect is shown in the restriction of the activities of the community and when, as has been shown, biotic interrelationships are of least importance. It might be said that there exists here an analogy between the forest floor in winter and the early

tundra; both are single-stratum communities where climatic effects are marked and restrictive and biotic effects of comparatively low value.

Further studies in the whole community cycle of forest and tundra communities, especially in their response to the annual rhythm, would no doubt throw much light on the problems of ecological distribution. It seems evident that the relations between such distribution and measurable physical factors are less simple than has been supposed, nor do studies of physical factors made in different habitats at the noncritical period of the year yield, in themselves, data which will explain why certain animal communities are found there. Studies of the entire biotic complex of a given habitat involving the collection of quantitative as well as qualitative data on animal populations, are needed and if possible such studies should be carried through one or more annual cycles in the same habitat and locality. It is suggested that alpine conditions, though they present special problems, might furnish a valuable field for such investigation; there the entire period of activity is condensed into a few months, during which all the seasonal societies could be studied, from the time of emergence to that of hibernation.

CONCLUSIONS

Alpine tundra animal communities in the northern Appalachians, as contrasted with those at higher altitudes, show succession of predominants and mores from associates inhabiting bare rock to those characteristic of northern coniferous forest.

The animal communities of coniferous and deciduous forests have a different taxonomic composition; only 4.5%, all non-predominants, are common to both. Stratal societies are ecologically similar in the two habitats; thus a shrub predominant of coniferous forest, such as the cicadellid *Graphocephala coccinea*, is represented in deciduous forest by species, such as *Erythroneura obliqua*, possessing a similar type of life history. The same is true for the other strata.

The climatic difference between the two habitats are sufficiently marked to affect the biota; the deciduous forest, at 44°N. lat., possesses a mean temperature higher by 4.1°C and a relative humidity lower by 5.5% than those found in the coniferous forest, at 45°N lat.

The physical differences between corresponding strata of coniferous and deciduous forest are insignificant; the evaporating power of air at the same height and exposure is approximately the same for both.

The stratal societies within these two communities are correlated with physical and biotic differences at different levels; their vertical distribution is independent, within the limits considered, of the climatic conditions determining the association as a whole.

Hibernating animals in deciduous forest show by vertical migrations a stratal response to changes in physical conditions; there is no evidence of excessive mortality during hibernation.

Negative evidence in regard to the physical conditions in the coniferous and deciduous forest habitats indicates the importance of investigating life cycles of both species and communities in their relation to annual rhythms, as the most promising method of attacking the problems of ecological distribution.

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Table I
Soil Data
Soil samples from Mt. Ktaadn.

Station	Water %	Dry matter, %	Organic and volatile substances in dry matter, %	Ash %	Organic and Volatile N %	cc. Ba(OH) ₂ per 10 gms.	Depth of sample	Clay and silt %	Sand %
Alpine Tundra (Grass)	28.22	71.78	28.37	43.41	0.49	1.5	8 in.	36.4	63.6
Alpine Tundra (Heath)	18.36	81.64	61.70	19.94	0.76	0.6	8 in.	22.3	77.7
Krummholz	21.14	78.86	58.48	20.38	0.38	1.8	1 ft.	41.0	59.0

100 parts dry matter contain

	Organic and Volatile	Ash	Nitrogen in organic matter	Depth of sample
Alpine Tundra (Grass)	39.6	60.4	1.70	8 in.
Alpine Tundra (Heath)	75.5	24.5	1.23	8 "
Krummholz	74.1	24.9	0.65	12 "

Quantity of water in relation to dry matter is probably not significant, for although the samples were kept in tightly corked bottles until analyses could be made, a considerable time elapsed before this could be done.

Table II
Biotic Data

Mammals Recorded from the Upper Stations of Mount Ktaadn

Common Name	Scientific Name	Author
Red Squirrel	<i>Sciurus hudsonicus loquax</i> Bangs*	B. H. D.
White-footed Mouse	<i>Peromyscus maniculatus abietorum</i> (Bangs)	
Porcupine	<i>Erethizon dorsatum dorsatum</i> (Linnaeus)	
(Bog-lemming)	<i>Synaptomys sphagnicola</i> Preble	B. H. D.
Short-tailed Shrew	<i>Blarina brevicauda talpoides</i> (Gapper)	
Red Fox	<i>Vulpes fulva</i> (Demarest)	R. D.

Canada Lynx	<i>Lynx canadensis canadensis</i> Kerr	P. S.
Red-backed Mouse	<i>Evotomys gapperi gapperi</i> (Vigors)	
Woodchuck	<i>Marmota monax monax</i> (Linnaeus)	R. D.
Varying Hare	<i>Lepus americanus virginianus</i> (Harlan)	B. H. D.
Caribou	<i>Rangifer caribou caribou</i> (Gmelin)	B. H. D.
Shrew	<i>Sorex personatus personatus</i> I. Geoffroy	B. H. D.
Weasel	<i>Mustela cicognanti</i> Bonaparte	B. H. D.

The species are listed roughly in order of their occurrence through the succession stages, the animals noted first being those found in the earlier associates. Many of them range through a number of successional stages indifferently. The species given in parentheses is the only one that is not found also on the lower slopes covered with Picea-Abies forest (Stations E-2, E).

The authorities given for some of the records are:

- B. H. D. = B. H. Dutcher, "Mammals of Mt. Ktaadn, Maine" 1903
 P. S. = Percival Sayward, "A Winter Ascent of Mt. Ktaadn," 1915
 R. D. = Mr. Roy Dudley, who was Dutcher's guide.

* The single specimen collected by the writer was referred by Mr. Gerrit S. Miller, Jr., to *Sciurus hudsonicus gymnicus* Bangs.

Table III
Biotic Data

Mammals Recorded Only From the Lower Station of Mount Ktaadn.

Common Name	Scientific Name	
Water Shrew	<i>Neosorex albibarbis</i> Cope	*
Marten	<i>Martes americana americana</i> (Turton)	*
Mink	<i>Mustela vison vison</i> Schreber	*
Meadow-mouse	<i>Microtus pennsylvanicus pennsylvanicus</i> (Ord.)	*
Jumping-mouse	<i>Zapus hudsonius hudsonius</i> (Zimmerman)	*
Jumping-mouse	<i>Napaeosapus insignis insignis</i> (Miller)	
White-tailed Deer	<i>Odocoileus virginianus borealis</i> (Miller)	
Black Bear	<i>Euarctos americanus americanus</i> (Pallas)	*
Fisher	<i>Martes pennanti pennanti</i> (Erxleben)	*
Moose	<i>Alces americana americana</i> (Clinton)	

The first part of the list contains species which have been recorded from the upper as well as the lower regions of the Picea-Abies taiga, especially from Chimney Pond (2,900 feet elevation) and thence up to the foot of the steep slopes; the latter part of the list contains species listed only for the lower slopes of the mountain. None of these animals have been reported from the upper plateau regions.

Mostly (records marked *) on the authority of Dutcher.

Table IV
Biotic Data

Birds Recorded from the Upper Stations of Mount Ktaadn

Common Name	Scientific Name	Authority
Ruffed Grouse	<i>Bonasa umbellus</i>	R. D.
Sharp-shinned Hawk	<i>Accipiter velox</i>	
Broad-winged Hawk	<i>Buteo platypterus</i> (?)	
Bald Eagle	<i>Haliaeetus leucocephalus</i> (?)	A. H. N.
(Crossbill)	<i>Loxia curvirostra minor</i> (?)	A. H. N.
White-throated Sparrow	<i>Zonotrichia albicollis</i>	
Slate-colored Junco	<i>Junco hyemalis</i>	
(American pipit)	<i>Anthus rubescens</i>	A. H. N.

The species in parentheses are the only ones that have not also been recorded for the lower slopes covered with *Picea-Abies* forest.

The authorities for records not taken by the writer's party are: Mr. Arthur H. Norton, of the Portland Society of Natural History (A. H. N.), and Roy Dudley (R. D.), who was Dutcher's guide in 1902.

Table V

Biotic Data

Birds Recorded Only From the Lower Stations of Mount Ktaadn

*	Common Name	Scientific Name	*
	Canada Grouse.....	<i>Canachites canadensis canace</i>	
	Red-shouldered Hawk.....	<i>Buteo lineatus lineatus</i>	
	Hairy Woodpecker.....	<i>Dryobates villosus</i>	
	Downy Woodpecker.....	<i>Dryobates pubescens</i>	
	Arctic Three-toed Woodpecker.....	<i>Picoides arcticus</i>	*
	American " ".....	<i>Picoides americanus</i>	
	Northern Flicker.....	<i>Colaptes auratus luteus</i>	*
	Olive-sided Flycatcher.....	<i>Nuttalornis borealis</i>	
	Bluejay.....	<i>Cyanocitta cristata</i>	
	Canada Jay.....	<i>Peresoreus canadensis</i>	
	American Crow.....	<i>Corvus brachyrhynchos</i>	
	Purple Finch.....	<i>Carpodacus purpureus</i>	*
	Cedar Waxwing.....	<i>Bombycilla cedrorum</i>	
	Black-and-white Warbler.....	<i>Mniotilta varia</i>	*
	Myrtle Warbler.....	<i>Dendroica coronata</i>	
	Magnolia Warbler.....	<i>Dendroica magnolia</i>	
	Black-poll Warbler.....	<i>Dendroica striata</i>	
	Winter Wren.....	<i>Nannus hiemalis</i>	
	Brown Creeper.....	<i>Certhia familiaris americana</i>	*
	White-breasted Nuthatch.....	<i>Sitta carolinensis</i>	*
	Red-breasted Nuthatch.....	<i>Sitta canadensis</i>	
	Black-capped Chickadee.....	<i>Penthestes atricapillus</i>	
	Hudsonian Chickadee.....	<i>Penthestes hudsonicus littoralis</i>	*
	Golden-crowned Kinglet.....	<i>Regulus satrapa</i>	
	Hermit Thrush.....	<i>Hylocichla guttata pallasi</i>	
	Golden-crowned Kinglet.....	<i>Regulus satrapa</i>	
	Hermit Thrush.....	<i>Hylocichla gutta pallasi</i>	

* = records furnished by Mr. Arthur H. Norton.

Table VI

Biotic Data

Amphibians and Reptiles from the Lower Stations of Mount Ktaadn

Common Name	Scientific Name	Remarks
Spotted Salamander.....	<i>Ambystoma maculatum</i> (Shaw).....	Tadpoles
Salamander.....	<i>Eurycea bislineata</i> (Green).....	Adults
Common toad.....	<i>Bufo americanus</i> Holbrook.....	Adults and tadpoles
Green-frog.....	<i>Rana clamitans</i> Latreille.....	"
Wood-frog.....	<i>Rana sylvatica</i> LeC.....	"
Common Garter Snake.....	<i>Thamnopsis sirtalis</i> (L.).....	"

Table VII

Soil Data

Soil Sample from Coniferous Forest at Orono

Depth of Sample	Water %	Dry Matter %	Organic and volatile substances	Ash %	Organic and vola- tile N, %	Cc. n/100 NaOH per 10 grams	Clay and Silt	Sand
			in dry mat- ter, %				%	
8 in	26.95	73.05	46.25	26.80	1.25	0.7	66.7	33.3
100 parts dry matter contain								
	Organic and volatile			Ash	Nitrogen in organic matter			
8 in	63.3			36.7	2.71			

Quantity of water in relation to dry matter is probably not significant, for although the samples were kept in a tightly covered can until analyses could be made, a considerable time elapsed before this could be done, and some water loss may have taken place.

Table VIII

Temperature Data

Temperature in ground under dead leaf stratum of coniferous forest.

Week Ending	Abs Max	Abs Min	Mean Max	Mean Min	Mean Temp	Total Range	Mean Range
June 30	15.6	9.4	13.6	11.3	12.4	6.2	2.3
July 7	15.7	10.6	14.0	11.6	13.0	5.1	2.4
July 14	18.3	12.5	16.0	14.7	15.2	5.8	1.3
July 21	15.8	11.4	14.4	11.8	13.5	4.4	2.6
July 28	16.7	11.7	15.6	13.4	13.3	5.0	2.2
*Aug 4	16.7	11.7	15.9	13.3	14.1	5.0	2.6
Aug 11	18.3	10.6	16.9	14.0	15.3	7.7	2.9
Aug 18	18.1	11.7	15.8	13.3	14.6	6.4	2.5
Aug 25	15.6	10.9	13.9	11.7	13.2	4.7	2.2
*Sept 1	17.0	13.9	16.0	14.2	15.2	3.1	2.0

* Figures based on data for less than seven days

Table IX

Temperature Data

Temperature in dead leaf stratum on ground in coniferous forest

Week Ending	Abs Max	Abs Min	Mean Max	Mean Min	Mean Temp	Total Range	Mean Range
*July 21	16.1	13.3	15.5	13.3	14.5	2.8	2.2
July 28	17.2	12.2	15.5	13.6	14.5	5.0	1.9
Aug 4	21.1	12.2	16.6	13.3	15.6	8.9	3.3
Aug 11	22.2	12.2	18.0	15.0	16.7	10.0	3.0
Aug 18	17.8	12.2	15.6	13.4	14.5	5.6	2.2
Aug 25	15.6	12.2	14.2	13.1	13.9	3.4	1.1
*Sept. 1	17.0	14.4	16.1	15.0	15.6	2.6	1.1

* Figures based on data for less than seven days.

Table X

Temperature Data

Temperature .6 meter above the surface of the ground in coniferous forest

Week Ending	Abs Max	Abs Min	Mean Max	Mean Min	Mean Temp	Total Range	Mean Range
June 16	23.3	0.6	10.6	7.7	8.8	22.7	2.9
June 23	28.4	4.5	21.7	14.9	17.9	23.9	6.8
June 30	29.4	8.9	24.8	13.3	16.2	20.5	11.5
July 7	28.9	7.2	22.9	13.4	17.8	21.7	9.5
July 14	30.0	13.3	24.9	18.3	21.2	16.7	6.6
July 21	27.2	7.8	20.4	14.6	17.1	19.4	5.8
July 28	27.2	7.8	22.8	14.5	19.6	19.4	8.3
*Aug 4	28.1	5.3	22.7	13.2	17.6	22.8	9.5
Aug 11	29.8	5.6	24.7	16.0	20.0	24.2	8.7
Aug 18	23.9	7.0	19.4	12.8	15.7	16.9	6.6
Aug 25	23.3	6.7	18.7	12.2	15.1	16.6	6.5
*Sept 1	26.1	15.0	21.1	16.8	18.6	11.1	4.3

* Figures based on data for less than seven days

Table XI

Temperature Data

Temperature 11 meters above the surface of the ground in coniferous forest

Week Ending	Abs Max	Abs Min	Mean Max	Mean Min	Mean Temp	Base Mean	Total Range	Mean Range	Mean Range above Base
June 16	22.2	6.1	19.1	10.3	13.6	11.7	16.1	8.8	6.6
June 23	25.0	6.7	22.8	10.0	15.4	12.5	18.3	12.8	9.2
June 30	27.8	10.0	22.1	12.5	16.8	14.4	17.8	9.6	6.5
July 7	27.3	9.4	24.1	13.3	17.0	13.9	17.9	10.8	10.1
July 14	27.8	13.9	25.4	16.1	20.5	18.2	13.9	9.3	7.2
July 21	26.7	10.0	21.7	13.4	17.2	15.3	16.7	8.3	6.5
July 28	27.8	10.0	25.5	13.9	18.5	16.3	17.8	11.6	9.6
Aug 4	28.3	7.8	24.8	12.0	18.1	15.5	20.5	12.8	9.3
Aug 11	30.6	12.2	27.9	16.8	21.1	17.9	18.4	11.1	8.7
Aug 18	22.8	7.2	21.7	11.6	15.2	13.9	15.6	10.1	7.8
Aug 25	22.8	8.3	20.6	12.2	15.9	13.4	14.5	8.4	7.1
*Sept 1	26.7	16.1	23.2	16.7	18.9	17.8	10.6	6.5	5.3

* Figures based on data for less than seven days

Table XII

Humidity Data

Relative humidity .6 meter above the surface of the ground in coniferous forest

Week ending	Abs Max	Abs Min	Mean Max	Mean Min	Mean R. H.	Total Range	Mean Range
June 16	100.0	31.0			77.4	69.0	
June 23	96.0	44.0	81.8	65.2	73.5	52.0	16.6
June 30	100.0	45.0	93.1	76.0	84.5	45.0	17.1
July 7	98.0	56.0	83.7	75.0	92.5	42.0	8.7
July 14	100.0	38.0	89.4	77.5	84.9	62.0	11.9
July 21	100.0	36.0	83.0	69.8	76.4	64.0	13.2

July 28	100.0	45.0	96.7	74.2	85.4	55.0	22.2
*Aug 4	98.0	40.0	90.5	68.0	79.2	58.0	22.5
Aug 11	100.0	48.0	85.8	62.8	74.4	52.0	23.0
Aug 18	100.0	44.0	99.0	71.1	85.0	56.0	27.9
Aug 25	100.0	49.0	94.2	74.4	84.3	51.0	19.8
*Sept 1	100.0	58.0			90.7	42.0	17.0

* Figures based on data for less than seven days

Table XIII
Humidity Data

Relative humidity 11 meters above the surface of the ground in coniferous forest

Week ending	Abs Max	Abs Min	Mean Max	Mean Min	Mean R. H.	Base Mean	Total Range	Mean Range	Mean Range below Base
June 16	82.0	31.0	74.1	44.6	62.5	65.6	51.0	29.5	20.4
*June 23	95.5	30.0	92.9	35.6	71.3	65.5	65.5	57.3	23.9
June 30	100.0	27.0	89.4	49.7	69.7	79.3	73.0	39.7	29.1
July 7	99.0	31.5	98.8	41.7	74.2	93.4	67.5	57.1	51.6
July 14	100.0	23.0	94.9	48.1	74.2	82.5	77.0	37.8	34.4
July 21	100.0	27.0	77.2	27.0	72.6	86.2	73.0	50.2	40.0
July 28	100.0	33.0	98.6	46.0	75.7	87.3	67.0	52.6	41.4
Aug 4	100.0	22.0	97.6	37.0	73.1	85.4	78.0	60.6	40.7
Aug 11	100.0	34.0	97.6	44.3	77.9	87.3	66.0	53.3	42.9
Aug 18	100.0	31.0	99.0	55.3	84.8	96.2	69.0	43.7	40.2
Aug 25	100.0	26.0	98.6	56.3	81.0	92.3	74.0	42.3	36.3
*Sept 1	100.0	41.0	95.0	63.8	81.8	92.6	59.0	31.2	27.8

* Figures based on data for less than seven days

Table XIV

Evaporation Data from Pine Forest, Obtained with Porous Cup Atmometers

Sta No	1	2	3	4	5	6	7	8	9
Height (M)	1.0	1.0	0.3	2.5		0.3	6.5	11.0	0.3
Date (wk.)	Average daily evaporation in cc. (reduced to standard)								
June 23	*	*	*	*	*	*	*	*	*
June 30	10.4	9.5	7.2	12.5	0.9	5.4	17.7	18.8	
July 7		12.3	10.0	16.9	0.4	† 6.9	21.8	23.7	*
July 14		14.3	12.1	19.6	0.2		27.0	27.2	18.5
July 21	*	13.7	9.6	18.9	0.3		25.5	26.8	18.8
July 28	14.4	13.6	11.7	18.4	0.3		23.8	26.4	16.2
Aug 4		15.4	*	19.2	0.3		25.1	26.8	15.8
Aug 11		7.8	4.4	10.2	0.04		13.0	13.1	‡
Aug 18		6.0	4.3	8.1	0.03		10.5	10.6	
Aug 25		7.5	5.0	10.1	0.04		14.6	15.4	

* The date on which a given atmometer was placed in position, and marks the beginning of the evaporation which was recorded one week later.

† This instrument was moved on July 7 to Station No. 9

‡ This instrument was destroyed, and no further observations were taken at the station

Table XIVa
Location of Stations

- 1 Black atmometer sphere, exposed on specially constructed stand 2 meters from instrument shelter
- 2 White atmometer sphere, exposed with No. 1
- 3 White atmometer sphere, on ground under shrubs, near Nos. 1 and 2
- 4 White atmometer sphere, suspended from lower branch of small hemlock
- 5 White atmometer sphere, placed in an observation cavity dug in the soil, and covered with a grating on which was placed the usual layer of pine needles and other forest floor debris; the sphere was just beneath this mat
- 6 White atmometer sphere, on ground in swampy glade; long grass
- 7 White atmometer sphere, in pine tree
- 8 White atmometer sphere, at level of upper branches
- 9 White atmometer sphere, on ground at western forest margin, among shrubs and weeds, but exposed to wind over short grass area

Table XV
Summer Variations in Light Intensity in Pine Forest, as Measured with a Wynne Exposure Meter August 6-8, 10-13, 15-19, 21-23, 25, 27, 1924
On the Ground

Date	Time	Reading in Sec	Weather Conditions
Aug 6	3:11 P M	80.0	Sun shining through light clouds
Aug 7	2:17 P M	60.0	Clear
Aug 8	2:00 P M	67.0	Clear
Aug 8	2:12 P M	158.0	Sun shining through light clouds
Aug 10	2:09 P M	170.0	Fair; sun shining through light clouds
Aug 11	2:01 P M	180.0	Clear; sun shining through light clouds
Aug 12	2:48 P M	487.5	Cloudy; very dull and raining
Aug 13	1:20 P M	125.0	Fair
Aug 15	1:16 P M	235.0	Clear; diffused light
Aug 16	2:09 P M	281.0	Diffused light
Aug 17	1:46 P M	271.0	Diffused light shining through clouds
Aug 18	1:06 P M	175.0	Fair; sun shining through light clouds
Aug 19	3:22 P M	2100.0	Very dull; raining heavily
Aug 21	2:25 P M	354.5	Dull
Aug 22	1:58 P M	515.0	Very dull
Aug 23	1:44 P M	470.0	Cloudy and dull
Aug 25	2:21 P M	570.0	Cloudy and very dull
Aug 27	2:53 P M	461.0	Cloudy

Table XVI
Summer Variations in Light Intensity in Pine Forest, as Measured with a Wynne Exposure Meter August 6-8, 10-13, 15-19, 21-23, 25, 27, 1924
1.5 meters above Ground

Date	Time	Reading in Sec	Weather Conditions
Aug 6	3:14 P M	33.0	Sun shining through light clouds
Aug 7	2:19 P M	14.5	Clear

Aug 8	2:03 P M	39.0	Clear
Aug 8	2:15 P M	127.5	Sun shining through light clouds
Aug 10	2:13 P M	147.0	Fair; sun shining through light clouds
Aug 11	2:05 P M	162.0	Clear; sun shining through light clouds
Aug 12	2:48 P M	240.0	Cloudy; very dull and raining
Aug 13	1:25 P M	83.0	Fair
Aug 15	1:19 P M	94.0	Clear; diffused light
Aug 16	2:12 P M	89.0	Diffused light
Aug 17	1:51 P M	196.0	Diffused light shining through clouds
Aug 18	1:10 P M	143.0	Fair; sun shining through light clouds
Aug 19	3:32 P M	420.0	Very dull; raining heavily
Aug 21	2:37 P M	211.5	Dull
Aug 22	2:02 P M	220.0	Very dull
Aug 23	1:48 P M	114.0	Cloudy and dull
Aug 25	2:31 P M	420.0	Cloudy and very dull
Aug 27	2:09 P M	90.0	Cloudy

Table XVII

Summer Variations in Light Intensity in Pine Forest, as Measured with a Wynne Exposure Meter August 6-8, 10-13, 15-19, 21-23, 25, 27, 1924

In Open Glade

Date	Time	Reading in Sec	Weather Conditions
Aug 6	3:20 P M	15.0	Sun shining through light clouds
Aug 7	2:23 P M	12.0	Clear
Aug 8	2:06 P M	16.0	Clear
Aug 8	2:18 P M	47.0	Sun shining through light clouds
Aug 10	2:17 P M	25.0	Fair; sun shining through light clouds
Aug 11	2:21 P M	30.0	Clear; sun shining through light clouds
Aug 12	2:52 P M	90.0	Cloudy; very dull and raining
Aug 13	1:28 P M	30.0	Fair
Aug 15	1:23 P M	56.0	Clear; diffused light
Aug 16	2:15 P M	65.0	Diffused light
Aug 17	1:55 P M	39.0	Diffused light shining through clouds
Aug 18	1:12 P M	45.0	Fair; sun shining through light clouds
Aug 19	3:37 P M	90.0	Very dull; raining heavily
Aug 21	2:40 P M	47.0	Dull
Aug 22	2:02 P M	61.0	Very dull
Aug 23	1:48 P M	33.0	Cloudy and dull
Aug 25	2:50 P M	83.0	Cloudy and very dull
Aug 27	2:21 P M	37.0	Cloudy

Table XVIII

Summer Variations in Light Intensity in Grassland Adjoining Pine Forest, as Measured with a Wynne Exposure Meter August 6-8, 10-13, 15-19, 21-23, 25, 27, 1924

On the Ground

Date	Time	Reading in Sec	Weather Conditions
Aug 6	3:27 P M	4.0	Sun shining through light clouds
Aug 7	2:28 P M	3.0	Clear
Aug 8	2:09 P M	3.0	Clear

Aug 8	2:21 P M	3.0	Sun shining through light clouds
Aug 10	2:20 P M	8.0	Fair; sun shining through light clouds
Aug 11	2:24 P M	10.0	Clear; sun shining through light clouds
Aug 12	2:57 P M	13.0	Cloudy; very dull and raining
Aug 13	1:32 P M	6.5	Fair
Aug 15	1:26 P M	7.0	Clear; diffused light
Aug 16	2:17 P M	20.0	Diffused light
Aug 17	1:58 P M	10.0	Diffused light shining through clouds
Aug 18	1:15 P M	9.0	Fair; sun shining through light clouds
Aug 19	3:40 P M	15.0	Very dull; raining heavily
Aug 21	2:42 P M	5.0	Dull
Aug 22	2:07 P M	9.0	Very dull
Aug 23	1:54 P M	10.0	Cloudy and dull
Aug 25	2:53 P M	15.0	Cloudy and very dull
Aug 27	2:23 P M	6.0	Cloudy

Table XIX

Biotic Data

Animal population of coniferous forest, considered by strata and as a whole,
July 7 to Sept. 1, 1924

Date	Soil Coll	Str Ave	Leaf Coll	Str Ave	Herb Coll	Str Ave	Shrub Coll	Str Ave	Total	Per Acre (Thousands)	Per Hectare
Jul 7	1	18	1	9	1	44	1	32	103	1,121	3,039
Jul 21	2	13	2	37	2	14	2	26	90	980	2,656
Jul 28	2	5	2	8	2	95	2	18	126	1,426	3,864
Aug 11	1	16	1	15	1	23	1	42	96	1,045	2,831
Aug 14	1	11	1	21	1	30	1	14	76	827	2,241
Aug 18	1	17	1	34	1	34	1	33	118	1,285	3,482
Aug 21	1	8	2	44	1	15	1	16	83	903	2,447
Aug 25	1	6	1	11	1	79	3	44	140	1,524	4,130
Sept 1	1	4	1	21	1	40	1	41	106	1,154	3,127

Table XX

Biotic Data

Animal population of deciduous forest, considered by strata and as a whole,
October 6, 1924, to March 2, 1925

Week ending	Soil Coll	Str Ave	Leaf Coll	Str Ave	Herb Coll	Str Ave	Shrub Coll	Str Ave	Total	Per Acre (Thousands)	Per Hectare
Oct 6	2	16	3	81	3	28	3	46	183	1,992	5,400
Oct 13	1	68	1	42	1	77	1	41	228	2,482	6,728
Oct 27	1	10	1	48	1	24	1	27	109	1,187	3,216
Nov 3	1	48	2	59	1	7	1	13	127	1,383	3,748
Nov 10	1	11	1	124	1	34	1	5	174	1,894	5,135
Nov 17	1	10	1	74	1	14	1	2	100	1,089	2,951
Nov 24	1	37	1	196	1	7	1	1	241	2,624	7,112
Dec 1	1	20	2	87	1	1	1	0	108	1,176	3,187
Dec 8	1	21	1	165	1	8	1	4	198	2,156	5,843
Dec 22	1	18	1	15	1	0	1	0	33	359	973
Dec 29	1	37	1	28	1	0	1	0	65	707	1,203

Jan 5	1	26	1	78	1	0	1	0	104	1,132	3,059
Jan 12	1	20	1	25	1	0	1	0	45	490	1,328
Jan 19	1	28	1	53	1	0	1	0	81	882	2,388
Jan 26	1	15	1	37	1	0	1	0	52	571	1,549
Feb 2	1	24	1	64	1	0	1	0	88	958	2,597
Feb 9	1	9	1	331	1	0	1	1	343	3,735	10,122
Feb 16	1	23	1	131	1	1	1	0	155	1,687	4,574
Feb 23	1	37	1	260	1	6	1	1	304	3,310	8,971
Mar 2	1	30	1	1	1	0	1	0	31	337	914

Table XXI

Winter Bird Census of Cottonwood (January 5-March 2, 1925)

The forest margin is characterized by presence of thick growths of bushes and is adjacent on three sides to fields of corn. The interior is characterized, throughout the greater part of its extent, by absence both of bushes dense enough to afford shelter and of low branching trees.

In the third column of the following lists M indicates *forest margin*; I indicates *interior*. Species are listed in order of abundance

I. Species Always Present

Name	Estimated Number	Location	Stratum	Remarks
Slate-colored junco (<i>Junco hyemalis</i>)	15	M(I)	Bushes, ground; trees rarely	In flocks, often with tree sparrows
Tree Sparrow				In flocks of juncos
Spizella monticola	10	M	Bushes, ground	
Tufted titmouse (<i>Baeolophus bicolor</i>)	8	I(M)	Tree tops, bushes rarely	Often in flocks of 3 to 5
Blue jay (<i>Cyanocitta cristata</i>)	5	I(M)	Trees oftenest, bushes, ground	Very conspicuous, often in flight
Northern flicker (<i>Colaptes auratus luteus</i>)	5	I,M	Trees	Often in flight
Cardinal (<i>Cardinalis cardinalis</i>)	5♂ 2 ♀ 3	I,M	Trees, bushes	
Downy woodpecker (<i>Dryobates pubescens medianus</i>)	3♂ 1	I,M	Trees	
Hairy woodpecker (<i>Dryobates villosus</i>)	2♂ 1	I,M	Trees	
Red-bellied woodpecker (<i>Centurus carolinus</i>)	1	I	Trees	Conspicuous until last week of Jan. Not seen later

Table XXII

Biotic Data

Winter Bird Census of Cottonwood

The individuals of the first two species listed doubtless changed from day to day, as flocks of juncos and tree sparrows were seen frequently crossing the fields to and from the forest. The numbers of column two represent an estimate of the number of individuals

which could practically always be found by hunting throughout approximately the same parts of the forest. The numbers given are based on the daily records but are an estimate, inasmuch as it was never possible, on one day, to study all parts of the forest with equal thoroughness; also it was difficult to be absolutely certain, in the case of such birds as the titmice and the blue jays, how much allowance to make for "repeaters" in the day's record.

The first three species listed appeared occasionally in much larger flocks. Blue jays and northern flickers were more numerous than the census indicates on a few warm days in February, when they formed small flocks (each with its own species).

Name	Species Frequently Present			Remarks
	Estimated Number	Location	Stratum	
American crow (<i>Corvus brachyrhynchos</i>)	5	I	Above trees	In flight
Chickadee (<i>Penthestes atricapillus</i>)	2	M(I)	Bushes, trees	With juncos, usually at margin
Hawks (probably Buteo, at least 2 species)	1	M,I	Above and between trees (Trees)	In flight usually, tree-tops rarely

Table XXIII

Biotic Data
Winter Bird Census of Cottonwood
Species Occasionally Present

Name	Estimated Number	Location.	Stratum	Remarks
Bob-white (<i>Colinus virginianus</i>)	6	I	Ground	Under fallen, leafy trees. Only in very cold weather
Mourning dove (<i>Zenaidura macroura carolinensis</i>)	4	M	Ground, low branches	Once only
English sparrow (<i>Passer domesticus</i>)	4	M	Tree	Once only, though abundant at farmyard opposite
Redpoll (<i>Acanthis linaria linaria</i>)	2 ♀	M	Bushes, ground	Once only in flock with juncos and tree sparrows. (Probably more common.)
Goldfinch (<i>Astragalinus tristis</i>)	10	M	Above trees	In flight, across edge of forest. Once only
Golden crowned kinglet (<i>Regulus satrapa</i>)	1	I	Ground	Once only
Migrant shrike (<i>Lanius ludovicianus</i>) (var. <i>migrans</i>)	1	M	Tree	Once only
Bronzed grackle (<i>Quiscalus quiscula aeneus</i>)	1		Above trees	In flight across forest. Once only
White-breasted nuthatch (<i>Sitta carolinensis</i>)	1			Once only heard

Table XXIV
 Biotic Data
 Winter Bird Census of Cottonwood
 Spring Migrants

Name	Estimated Number	Location	Stratum	Earliest Date	Remarks
Robin (<i>Planesticus migratorius</i>)	2 to 25	I,M	Trees, ground; above trees	Feb 16	The larger number in flocks. Often in flight
Rusty blackbird (<i>Euphagus carolinus</i>) (♀ 2)	6 to 18	I,M	Trees, bushes, ground	Feb 27	In flocks
Red-winged blackbird (<i>Agelaius phoeniceus</i>)	1 or 2	M	Trees, bushes	Mar 2	With flocks of rusty blackbirds
Bluebird (<i>Sialia sialis</i>)				Feb 8	Once only in forest until after three weeks of cold weather with which winter study closed.

Some of the birds of the list above, instead of being strictly migrants, may have been individuals which had wintered in this latitude in sheltered retreats from which they appeared on favorable days. A few also were probably early summer residents, as in the case of the robins who, after their first appearance, were always present to the number of two or three in the forest.

XXV

Biotic Data

Winter Birds of Cottonwood, January, 1925

The following list states the number of individuals of each species seen on the date given.

January	5	12	19	21	23	24	26	29	31
Quail (<i>Colinus virginianus</i>)	—	—	—	—	6 or 8	—	—	—	—
Mourning Dove (<i>Zenaidura</i>)	—	—	—	—	—	—	—	—	4
Hawk (large)	—	1	2	—	1	—	—	1	1
(<i>Buteo borealis</i>)									
(<i>Buteo lineatus</i>) probably both									
Hairy woodpecker (<i>Dryobates villosus</i>)	—	—	—	—	—	1 ♀	1	—	1
Downy woodpecker (<i>Dryobates pubescens medianus</i>)	—	—	3	—	2	2	1	1	—
Red-bellied woodpecker (<i>Centurus carolinus</i>)	1	—	1	1	1	—	—	—	—
Flicker (<i>Colaptes auratus luteus</i>)	—	—	4	6	4	1	—	—	5
Blue jay (<i>Cyanocitta cristata</i>)	3	3	4	3	2	2	2	3	3
Crow (<i>Corvus brachyrhynchos</i>)	2	—	3	5	—	—	5	9	7
Bronzed Grackle (<i>Quiscalus quiscula aeneus</i>)	—	—	1	—	—	—	—	—	—
Tree sparrow (<i>Spizella monticola</i>)	—	—	—	10	10	—	—	—	2
Junco (<i>Junco hyemalis</i>)	—	—	15	5	—	—	—	—	5
Cardinal (<i>Cardinalis cardinalis</i>)	—	1	3 ♀	1 ♀	2 (1 ♀)	—	—	—	3 (1 ♀)

Migrant shrike (<i>Lanius ludovicianus migrans</i>).....	—	—	—	—	—	1	—	—	—
Tufted titmouse (<i>Baeolophus bicolor</i>)	4	—	4	5	3	8	3	5	2
Chickadee (<i>Penthestes atricapillus</i>)..	1	—	—	—	—	—	—	—	—
Golden-crowned kinglet (<i>Regulus satrapa</i>).....	1	—	—	—	—	—	—	—	—
English sparrow (<i>Passer domesticus</i>)..	—	—	—	—	—	—	—	4	—

Birds of Cottonwood, February 2 to March 2 (Inclusive)

The following list states the number of individuals of each species estimated to be present on the given date.

	F2	6	8	9	13	16	23	27	M2
Hawk (large) (<i>Buteo</i> sp.).....	1	—	1	—	—	—	—	1	1 or 2
Hairy woodpecker (<i>Dryobates villosus</i>).....	—	—	—	1	1♂	1	—	—	—
Downy woodpecker (<i>Dryobates pubescens medianus</i>).....	2♂	—	—	1	3♂	1♂	3♂	—	2♂
Flicker (<i>Colaptes auratus luteus</i>)... 8	3	—	6	5	1	—	—	1	—
Blue jay (<i>Cyanocitta cristata</i>)..... 5	3	—	7	3	4	4	5	5	5
Crow (<i>Corvus brachyrhynchos</i>).....	—	5	—	4	9	3	6	2	4
Red-winged blackbird (<i>Agelaius phoeniceus</i>).....	—	—	—	—	—	—	—	—	1 or 2
Rusty blackbird (<i>Euphagus carolinus</i>).....	—	—	—	—	—	—	—	18	6♀
Redpoll (<i>Acanthis linaria linaria</i>)..	—	—	—	—	—	—	2♀	—	—
Goldfinch (<i>Astragalinus tristis</i>)... 10	—	—	—	—	—	—	—	—	10
Tree sparrow (<i>Spizella monticola</i>)..	10	—	—	—	—	—	20	—	3
Slate-colored junco (<i>Junco hyemalis</i>).....	52	10	—	20	10	8	10	10	18
Cardinal (<i>Cardinalis cardinalis</i>)... 2	5	3♀	—	—	—	—	2	1♀	2
White-breasted nuthatch (<i>Sitta carolinensis</i>).....	—	—	1(heard only)			—	—	—	—
Tufted titmouse (<i>Baeolophus bicolor</i>).....	7	5	—	20	6	8	12	9	3
Chickadee (<i>Penthestes stricapillus</i>)—	—	—	—	2	2	—	—	2	2
Robin (<i>Planesticus migratorius</i>)...—	—	—	—	—	—	2	3	15	26
Bluebird (<i>Sialia sialis</i>).....	—	—	1(Species report only)						

PLATE I

EXPLANATION OF PLATE I

1. Station C, at an elevation of 5,080 feet on the Table-land of Mount Ktaadn. The characteristic vegetation consists of various grasses and sedges.
2. Station D. Krummholz.
3. Station F. Pond-bog habitat; Pamola Pond, 2,700 feet elevation.



PLATE II

EXPLANATION OF PLATE II

4. Interior of coniferous forest at Orono, Maine, showing the exposure of instruments. The instrument shelter contained a thermograph and a hygrograph, which were thus raised to a height of 11 m above the surface of the ground. An atmometer may be seen in a bracket on the shelter and another hanging from the shelter, 6 m above the ground.
5. The deciduous forest habitat at Urbana, Illinois, as it appeared during much of the winter study.



PLATE III

EXPLANATION OF PLATE III

Map of Upper Regions of Mount Ktaadn

(After sketch map by Parker B. Field, published by the Appalachian Mountain Club.)

Fig. 6. Ecological stations as follows:

- Station A—Rock Animal Community
- Station C—Tundra Animal Community
- Station D—Krummholz Animal Community
- Station E-2—Upper Climax Forest Animal Community
- Station E—Lower Climax Forest Animal Community
- Station F—Pond-bog Animal Community.

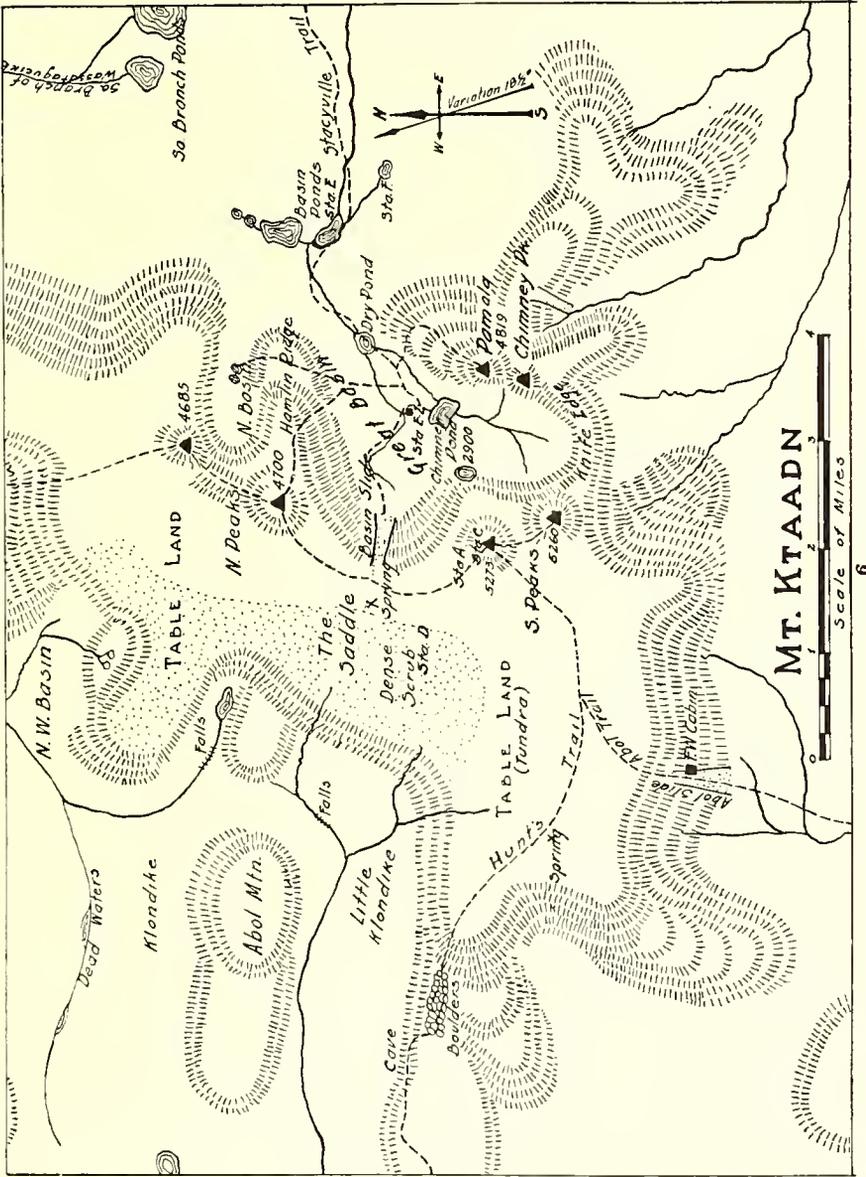
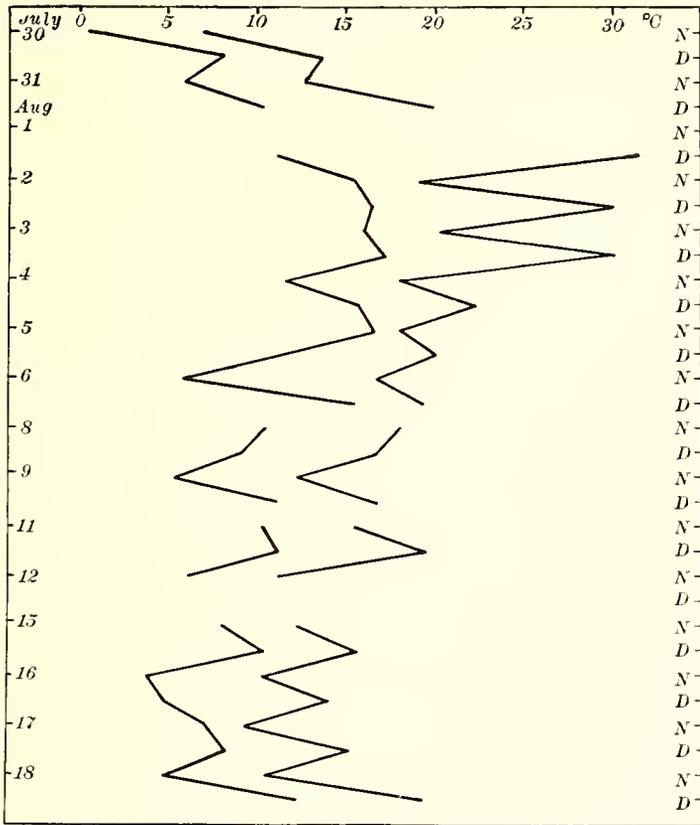


PLATE IV

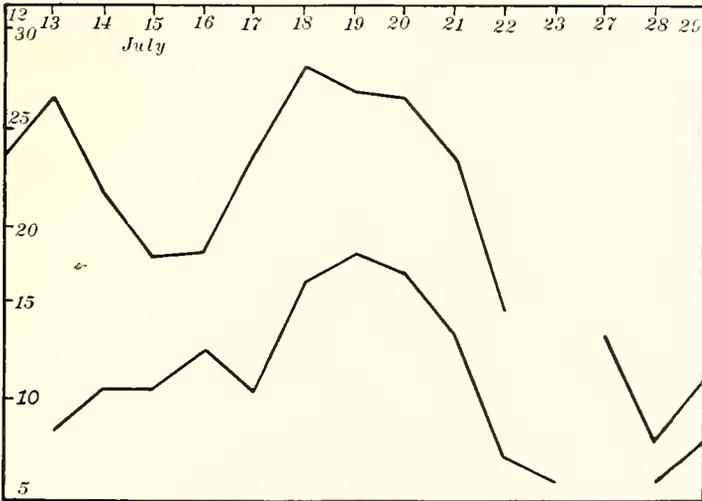
EXPLANATION OF PLATE IV

7. Maximum and minimum temperatures at Chinney Pond on Mt. Ktaadn. D=day, N=night.
8. Maximum and minimum daily temperatures at Basin Pond on Mount Ktaadn.
9. Hythergraphs of localities under consideration.

The horizontal scale shows precipitation in inches, the vertical temperature in degrees Centigrade. The broken curve represents the conditions of precipitation and temperature at Ft. Chimo, Ungava. The graph which is ruled horizontally is for Orona, Maine. That which is ruled vertically is for Mt. Washington, New Hampshire.



7



8

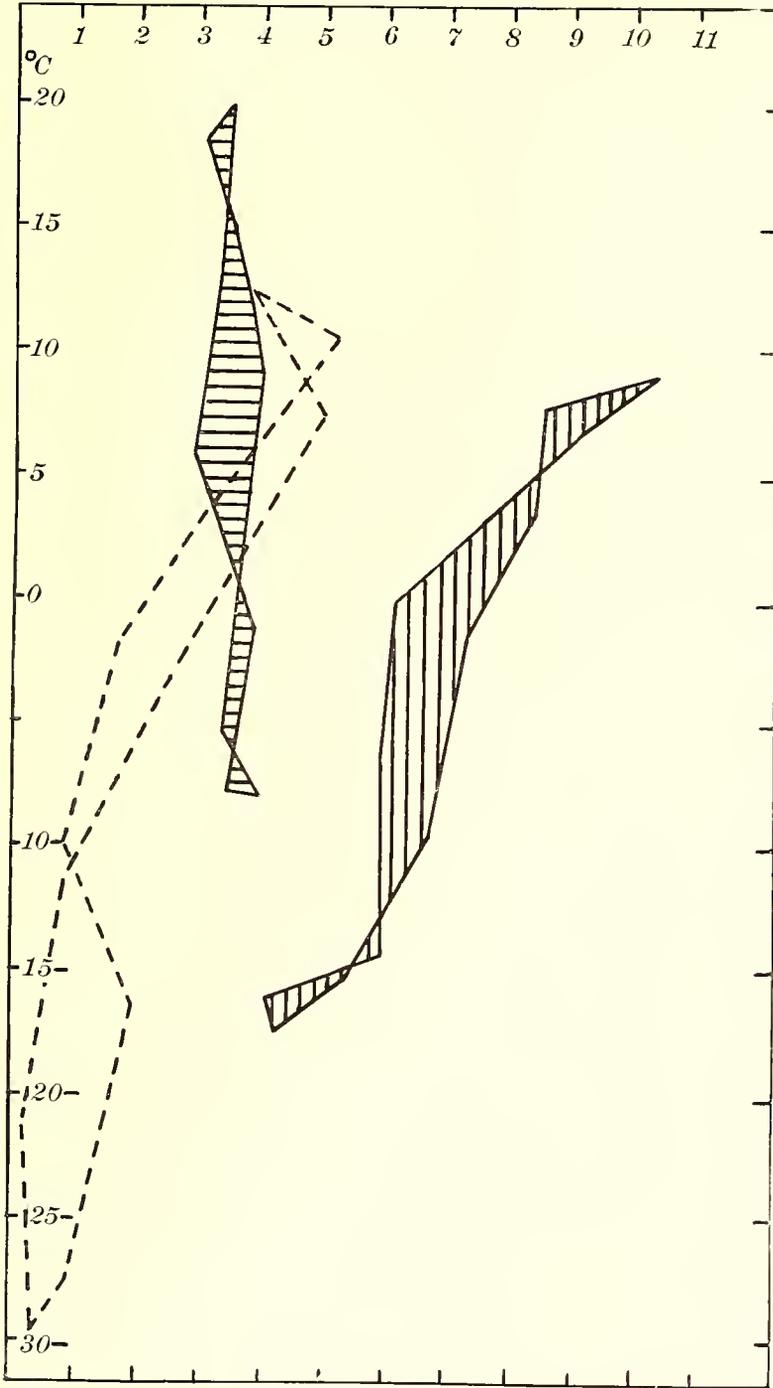
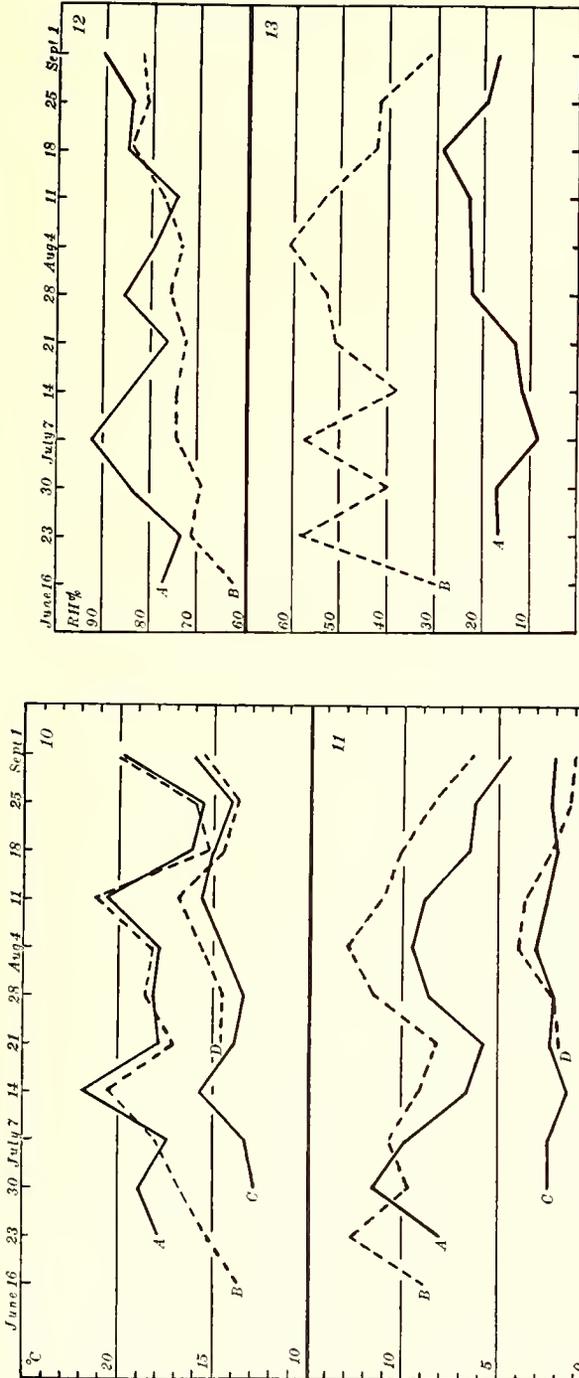


PLATE V

EXPLANATION OF PLATE V

10. Weekly mean temperatures at various strata of the coniferous forest habitat.
 A=Temperature 0.6 m above the ground.
 B=Temperature 11 m above the ground.
 C=Temperature in the ground, under the mat of dead leaves.
 D=Temperature in the mat of dead leaves.
 All temperatures are centigrade degrees, with a base at 10°, and horizontal rulings at 15°, 20° and 25°, respectively. Each Centigrade degree is indicated by smaller divisions on the lateral margins.
 The mean temperatures for the weeks ending June 16, 23, and 30, July 7, 14, 21 and 28, August 4, 11, 18 and 25, and September 1, are indicated by the labels and divisions at the upper and lower margins. The records for some of the strata were not begun until the study had been progressing some time.
11. Weekly mean variations of temperatures at various strata of the coniferous forest habitat.
 A=Variation in temperature 0.6 m above ground.
 B=Variation in temperature 11 m above ground.
 C=Variation in temperature in ground, under dead leaf stratum.
 D=Variation in temperature in dead leaf stratum.
 Notations similar to those used in 1. The base-line is at 0°C; horizontal rulings indicate 5°, 10° and 15°C.
- Humidity Data
12. Weekly mean relative humidity at two levels in the coniferous forest habitat: 0.6 m (A) and 11 m (B) above the ground.
 Divisions on the upper and lower margins indicate the weekly intervals. Horizontal rulings are placed at each 10% of relative humidity, with a base-line drawn at 60% and the top line representing 100% relative humidity.
13. Weekly mean variations in relative humidity at two levels in the coniferous forest habitat: 0.6 (A) and 11 m (B) above ground.
 The base-line is 0% relative humidity, and the horizontal lines above stand for additional increments of 10% relative humidity up to 70%.



BLAKE

PLATE V

PLATE VI

EXPLANATION OF PLATE VI

Evaporation Data from Pine Forest

14. Evaporation from porous cup atmometers at stations 2, 3, 4, 5, 7 and 8, in mean Daily Evaporation per week.
The vertical scale is divided into increments of 1 cc, with horizontal lines drawn at 5, 10, 15, 20 and 25 cc. The vertical scale is divided according to weeks. Each curve is numbered according to the station where it was recorded.
15. Diagram showing the comparative amount of evaporation, in terms of the daily mean, spherical porous cup atmometers at eight stations (No. 2 to No. 9) in the habitat. The data covers the Nine Week Period.
The scale is divided into vertical increments, showing a range of evaporation of from 0 cc to 21 cc, expressed in terms of the daily mean for the period of study, each division representing 1 cc. The columns represent the various stations, to correspond with which they are numbered.

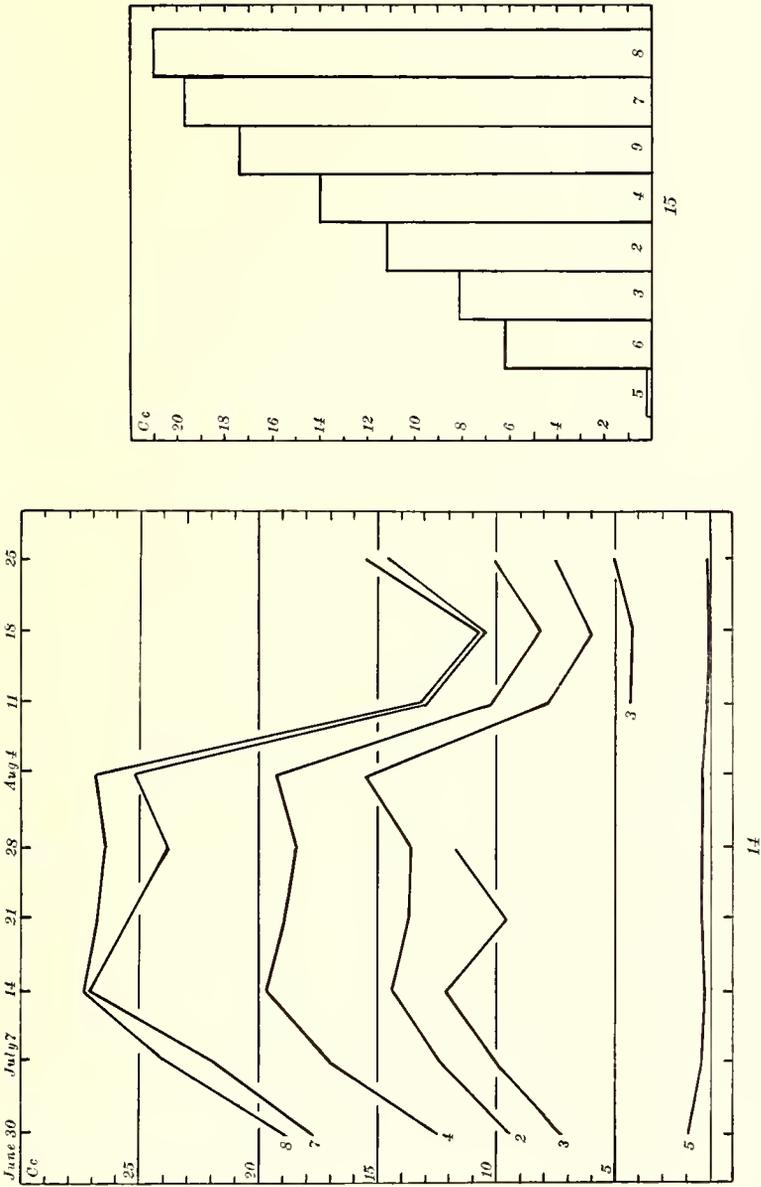


PLATE VII

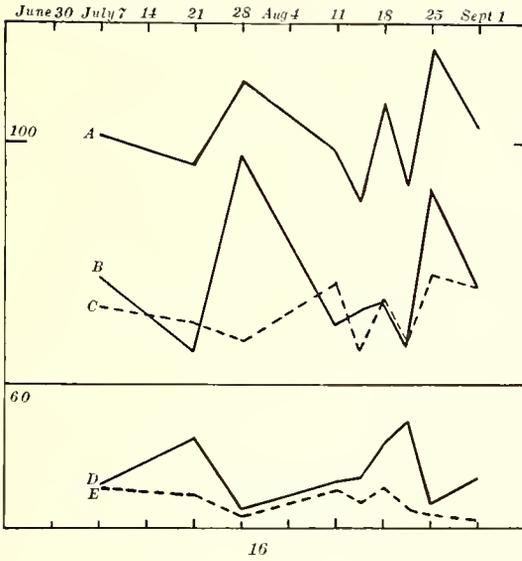
EXPLANATION OF PLATE VII

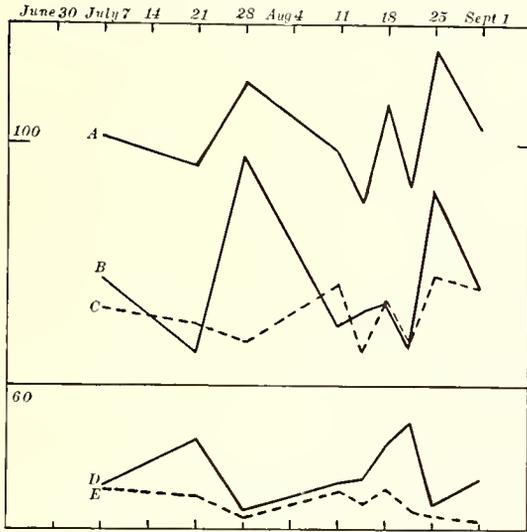
Biotic Data

16. Animal population, as a whole and according to strata, in coniferous forest, July 7 to September 1, 1914.

The divisions along the upper and lower margins represent the weeks, as in the plates on temperature and humidity. The divisions along the lateral margin indicate ten animals taken in collecting.

A—Total population; B—Population of herb stratum; C—Population of shrub stratum; D—Population of leaf stratum; E—Population of soil stratum.





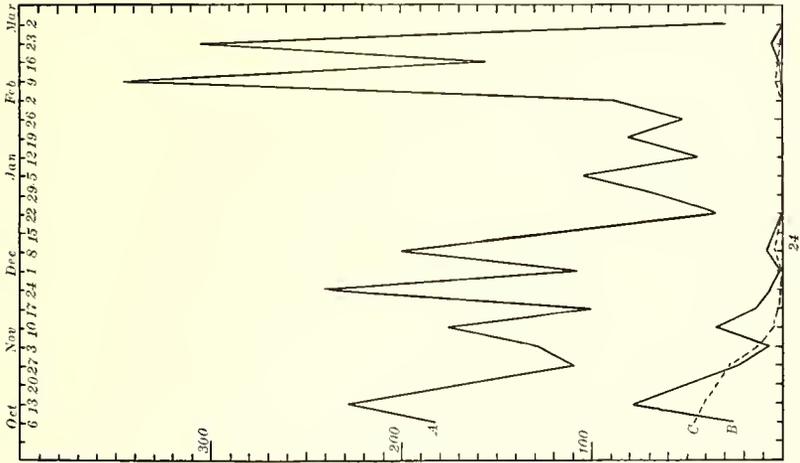
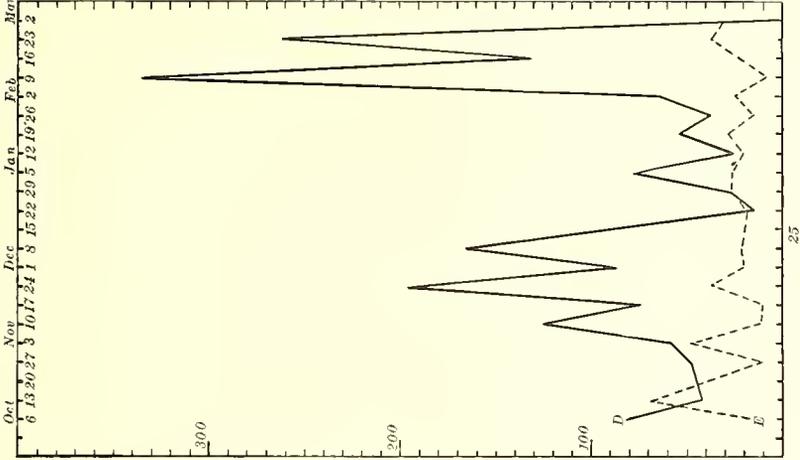


PLATE VIII

EXPLANATION OF PLATE VIII

Resident Population of the Lowest Strata

17. Resident population of the lowest strata
 - A. *Helodrilus caliginosus* trapezoides (Dugès)
 - B. *Tomocerus flavescens* Tullberg var. *separatus* Folsom.
 - b. Herb stratum
 - c. Leaf stratum
 - d. Soil stratum
18. Summer Population of Arachnida
 - a. *Leiobunum politum* Weed.
 - b. *Linyphia* sp. (juvenile)
 - c. *Tetragnatha* sp. (juvenile)

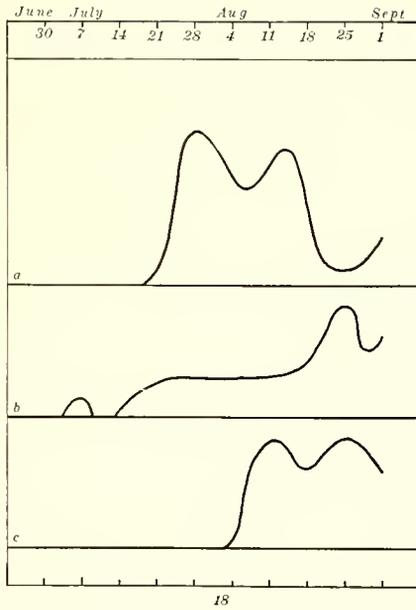
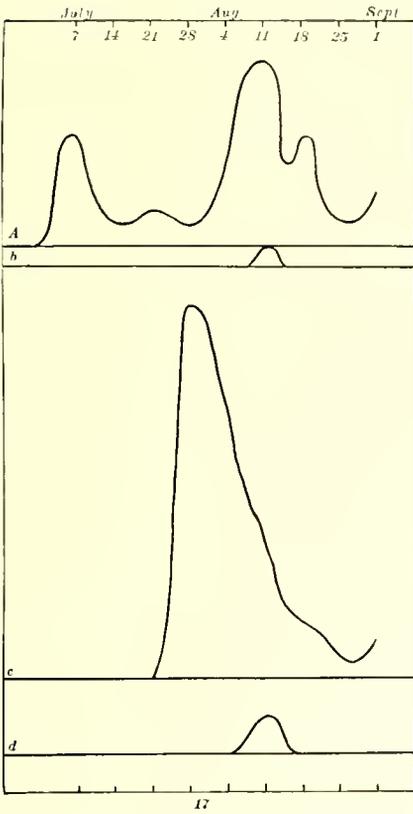


PLATE IX

EXPLANATION OF PLATE IX

19. Summer Population of Homoptera
A *Clastoptera obtusa* (Say)
a. Shrub stratum
b. Herb stratum
B *Graphocephala coccinea* (Forst.)
a. Shrub stratum
b. Herbstratum
20. Summer and Stratal Populations of Homoptera and Hemiptera
A *Macrosiphum coryli* Davis
B *Nabis* sp. (juvenile)
C *Dicyphus famelicus* (Uhl.)
a. Shrub
b. Herb
D *Diaphnidia pellucida* Uhl.

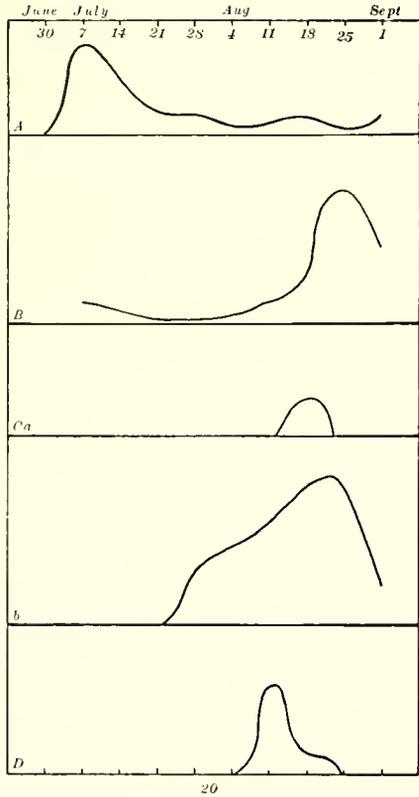
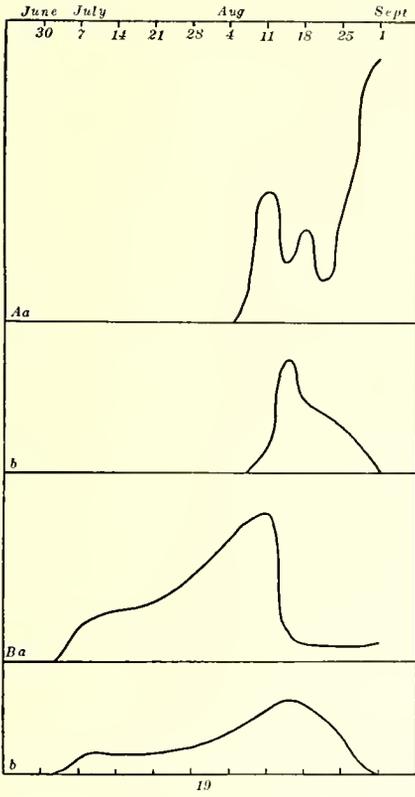


PLATE X

EXPLANATION OF PLATE X

21. Weekly mean temperatures at various strata of the deciduous forest habitat: 15 cm below the surface of the ground, 0.6 m and 11 m above the surface.
All temperatures are Centigrade degrees, with a base at -15° , and horizontal rulings at -10° , -5° , 0° , 5° , 10° , respectively. Each Centigrade degree is indicated by smaller divisions on the margins.
The mean temperatures for the weeks ending November 17 and 24, December 1, 8, 15, 22 and 29, January 5, 12, 19 and 26, February 2, 9, 16 and 23, and March 2 and 9, are indicated by the labels and divisions on the longer margins. A break of one week, that of January 12, occurs in the record taken at a height of 11 m.
A = Temperature .6 m above ground.
B = Temperature 11 m above ground.
C = Temperature 15 cm below ground.
22. Weekly mean variations of temperatures at various strata of the deciduous forest habitat: 15 cm below the surface of the ground, 0.6 m and 11 m above the surface. Scheme of representation same as in preceding plate. The base-line is at 0°C .; horizontal rulings indicate 5° , 10° , 15° , 20° and 25°c .
A = Variation in temperature .6 m above ground.
B = Variation in temperature 11 m above ground.
C = Variation in temperature 15 cm below ground.
23. Weekly mean relative humidity and weekly mean variations in relative humidity 0.6 m above ground in the deciduous forest habitat.
Divisions on the upper and lower margins indicate the weekly intervals. Horizontal rulings are placed at each 10% relative humidity, with base-lines drawn at 40% for the weekly mean relative humidity, and at 0% for the weekly mean variations in relative humidity.
A = Weekly mean relative humidity
B = Weekly mean variations in relative humidity.

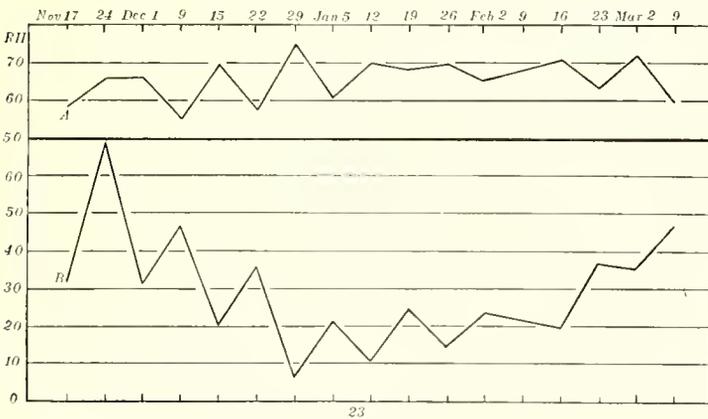
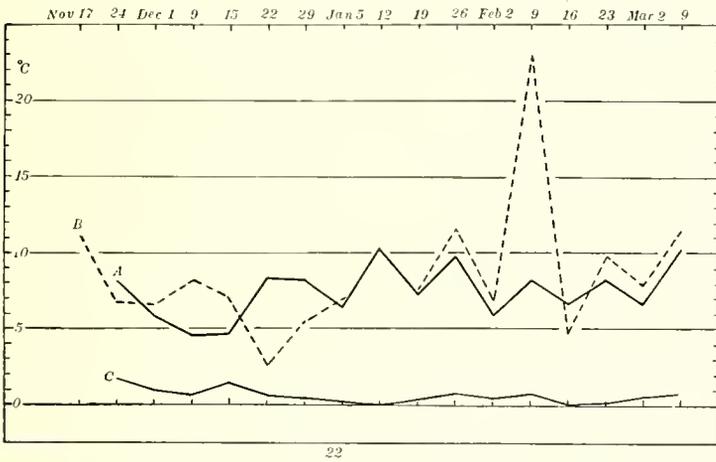
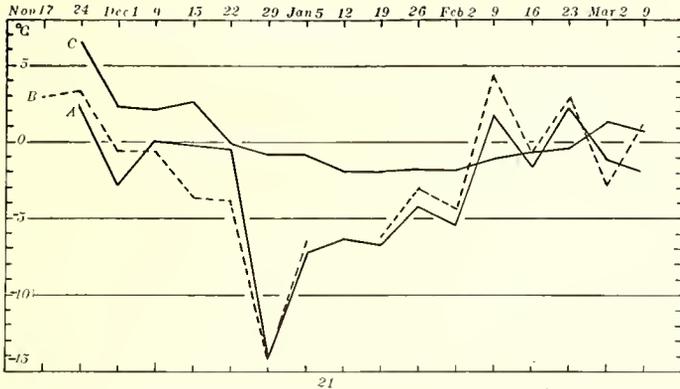


PLATE XI

EXPLANATION OF PLATE XI

Biotic Data

24. Animal population, as a whole and by the two upper strata considered, in deciduous forest, October 6, 1924, to March 2, 1925.

The divisions along the upper and lower margins represent the weeks, as indicated.

The divisions along the lateral margins represent ten animals taken in collecting.

A=Total population.

B=Population of herb stratum.

C=Population of shrub stratum.

25. Animal population of the two lower strata deciduous forest, October 6, 1924, to March 2, 1925.

The divisions along the upper and lower margins represent the weeks, as indicated.

The divisions along the lateral margins represent ten animals taken in collecting.

D=Population of leaf stratum.

E=Population of soil stratum.

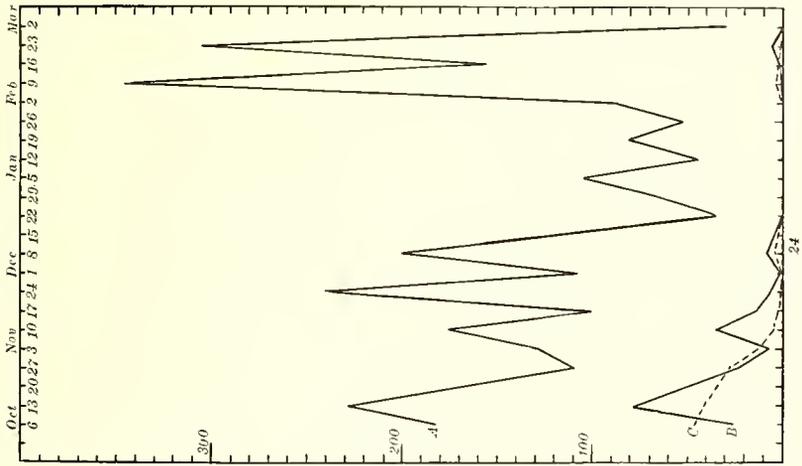
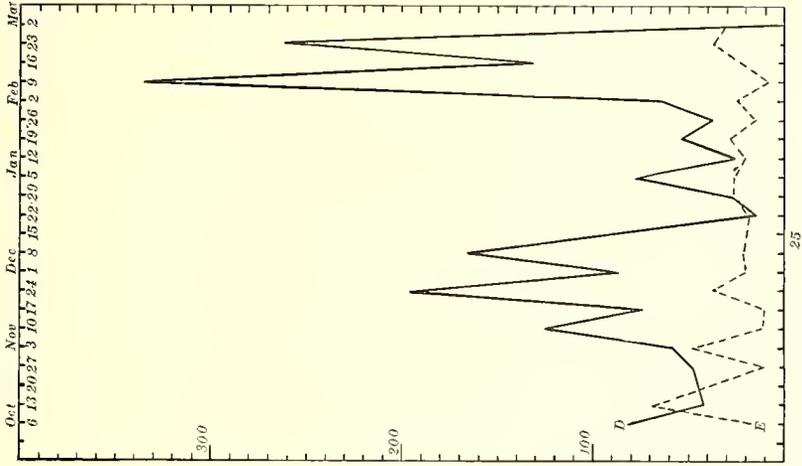


PLATE XII

EXPLANATION OF PLATE XII

26. Winter Populations of Spiders and Mollusks
- A *Linyphia phrygiana* C. Koch
- B *Dictyna volupis* Keyserling
- a. } Shrub and herb strata
- b. }
- c. Leaf stratum
- C *Anyphaena rubra* Emer. (juvenile)
- a. Shrub stratum
- b. Herb stratum
- c. Leaf stratum
- D *Carychium exile* H. C. Lea
- E *Zonitoides arborea* (Say)
- F *Gastrocopta tappaniana* (C. B. Adams)
- G *Zonitoides minuscula* (Binney)
- H *Vitrea indentata* (Say)
- c. Leaf stratum
- d. Soil stratum
- I *Carychium exiguum* (Say)

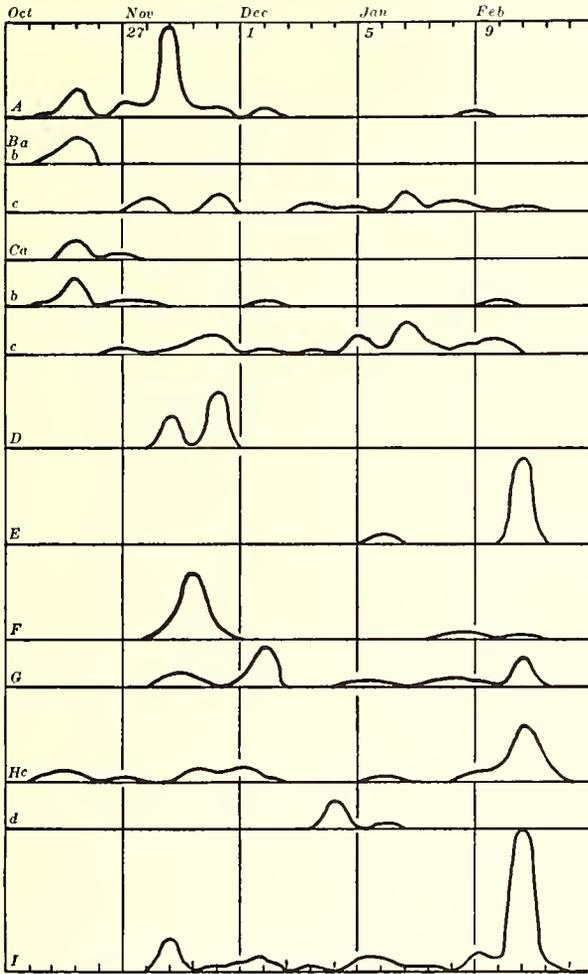


PLATE XIII

EXPLANATION OF PLATE XIII

27. Winter Populations of Various Insects.
- A *Cantharis* sp. (larva)
 - B *Meracantha contracta* (Beauv.) (larva)
 - C *Phyllotreta sinuata* (Steph.)
 - D *Tipula* sp. (larva)
 - c. Leaf stratum
 - d. Soil stratum
 - E *Nabis ferus* (L.)
 - a. Shrub stratum
 - b. Herb stratum
 - c. Leaf stratum
 - d. Soil stratum
 - F *Lygus pratensis oblineatus* (Say)
 - a. Shrub stratum
 - b. Herb stratum
 - c. Leaf stratum
 - d. Soil stratum

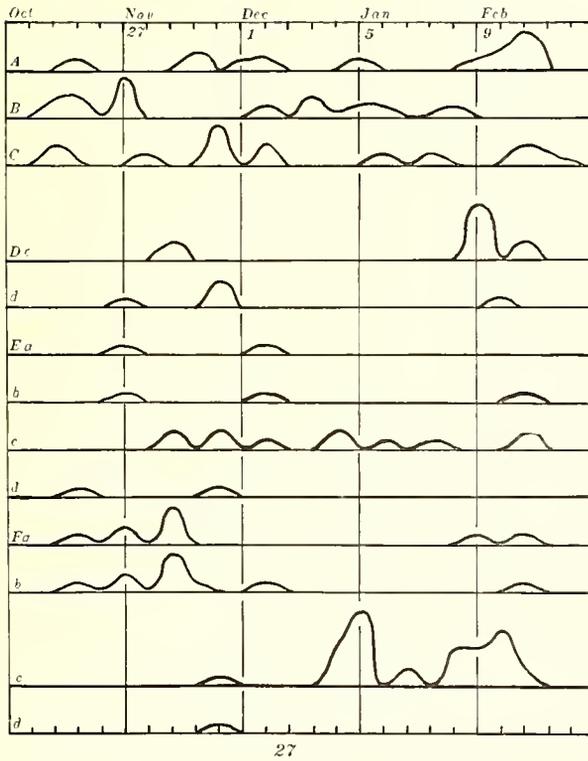


PLATE XIV

EXPLANATION OF PLATE XIV

28. Winter Populations of Beetles
- A *Epitrix brevis* Sz.
 - a. Shrub stratum
 - b. Herb stratum
 - c. Leaf stratum
 - d. Soil stratum
 - B *Ptilodactyla serricollis* (Say)
 - C *Nitidula rufipes* (L.)
 - D *Telephanus velox* Hald.
 - b. Herb stratum
 - c. Leaf stratum
 - d. Soil stratum
 - E *Malthodes* sp. (larva)

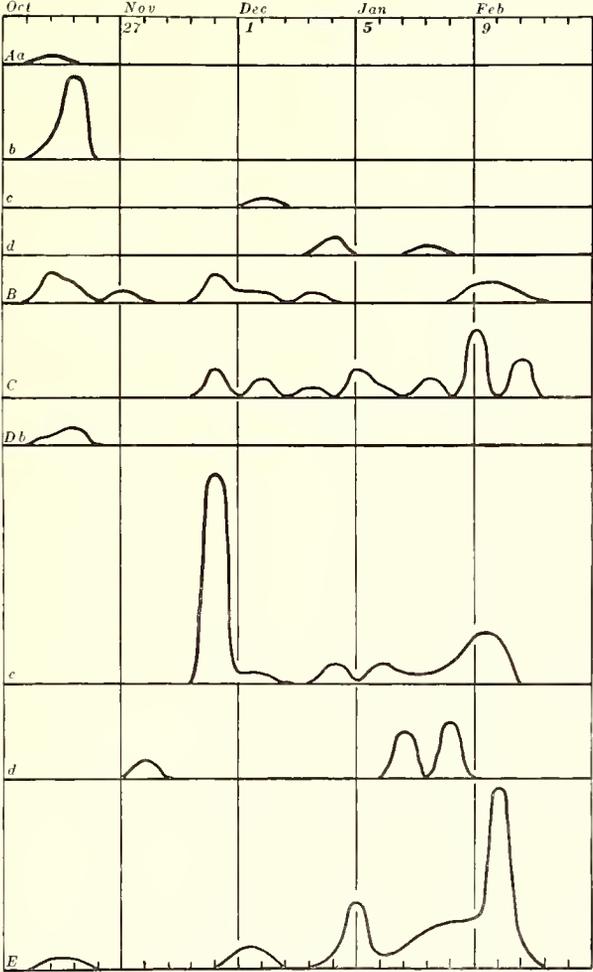


PLATE XV

EXPLANATION OF PLATE XV

29. Winter Population of Collembola
- A *Onychiurus fimetarius* (L.)
 - B *Onychiurus armatus* Tullberg
 - C *Isotoma* sp.
 - c. Leaf stratum
 - d. Soil stratum
 - D *Onychiurus subtenuis* Folsom.
30. Winter Populations of Collembola and Enchytraeidae
- A *Tomocerus flavescens* Tullberg var. *americanus* Schott
 - b. Herb stratum
 - c. Leaf stratum
 - d. Soil stratum
 - B *Enchytraeidae*
 - c. Leaf stratum
 - d. Soil stratum

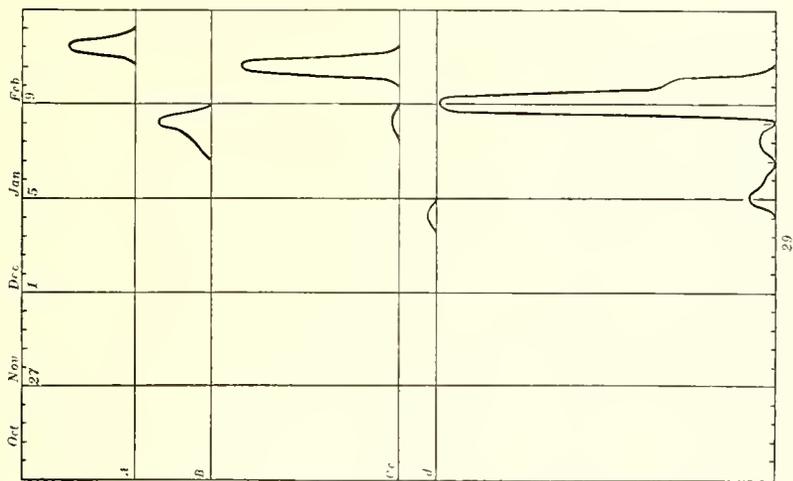
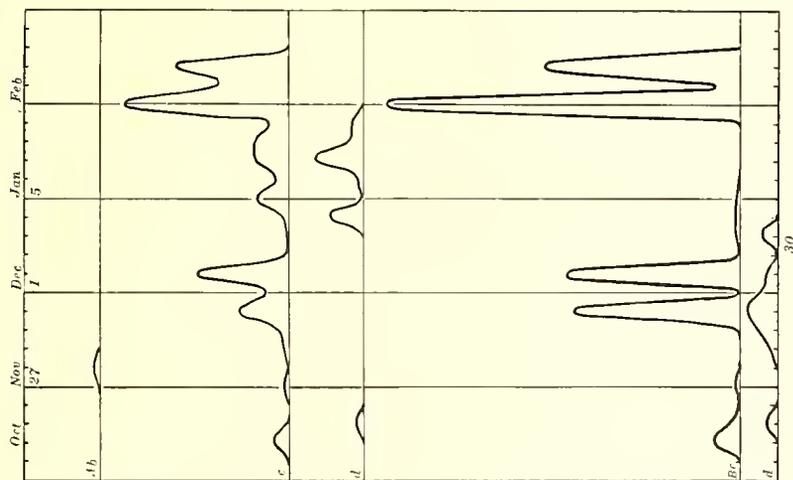
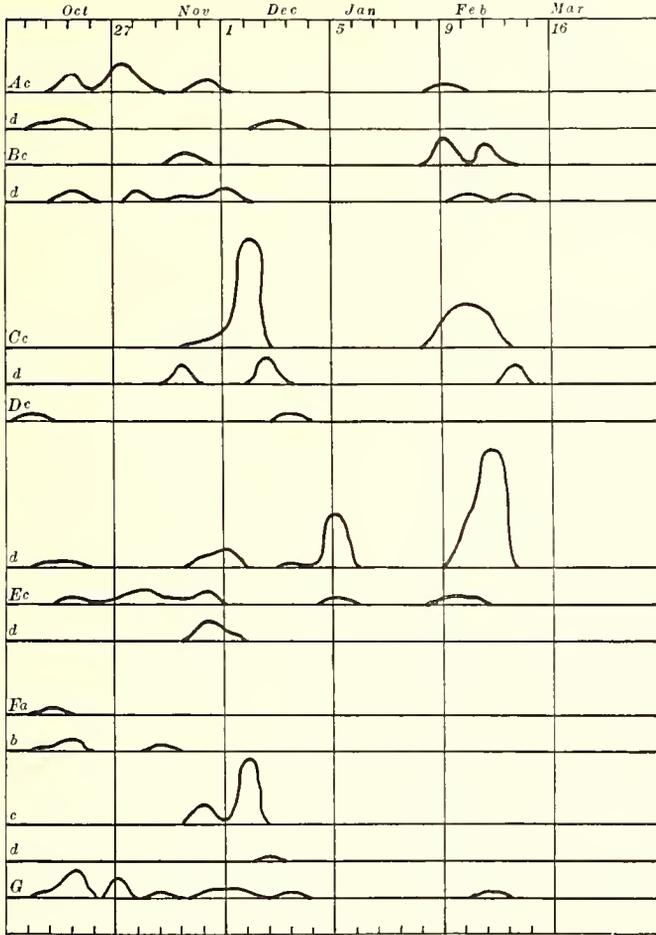


PLATE XVI

EXPLANATION OF PLATE XVI

31. Winter Populations of Myriapods and Diptera
- A *Linotaenia chionophila* (Wood)
 - c. Leaf stratum
 - d. Soil stratum
 - B *Pokabius bilabiatus* (Wood)
 - c. Leaf stratum
 - d. Soil stratum
 - C *Cleiodogona caesioannulata* (Wood)
 - c. Leaf stratum
 - d. Soil stratum
 - D *Fontaria virginiensis* Dru
 - c. Leaf stratum
 - d. Soil stratum
 - E *Scytonotus granulatus* (Say)
 - c. Leaf stratum
 - d. Soil stratum
 - F *Leptocera* sp.
 - a. Shrub stratum
 - b. Herb stratum
 - c. Leaf stratum
 - d. Soil stratum
 - G *Fannia* sp. (juvenile)



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