THE BIRD POPULATION OF AN ELM-MAPLE FOREST WITH SPECIAL REFERENCE TO ASPECTION, TERRITORIALISM, AND COACTIONS*

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INTRODUCTION

Biologists recognize that both animals and plants are important in all communities and constitute an inseparable unit in their structure. Throughout the world, both vertebrate and invertebrate animals belong to various major plant and animal communities which include deserts, prairies, coniferous and deciduous forests, etc. Ecologists call these largest plant-animal communities "biomes" or "biotic formations." They are divided into "associations" which include some wide-ranging species among the dominants and important influents; these constitute the elements of unity in the climax portions of the biome. The associations are interrupted by seral stages which, under natural conditions, develop toward the climax.

Some of the earlier workers perceived distinct "habitat" preferences among birds. Judd (1902) propounded "habitat" preferences and associated them under the following headings: birds that nest in the open fields, birds that depend on covers, birds of less limited distribution and birds of varied distribution. He made no correlations as to the relationships of birds within a given locality but stated that there was a "habitat" preference among the birds of a limited farm area in Maryland which he had studied. Another early paper that discussed this preference in detail was that of Forbes (1907). By his bird census, taken across the corn-belt of central Illinois in early autumn, he pointed out the existence of a feeding ground preference which was influenced by the dominant crops in the area covered—corn, pasture and stubble. Forbes was able to determine statistically the preference for different crops and the aggregation of species in them. Adams (1908) was one of the first to evaluate the position of birds within a biotic community. His correlations were drawn from a grouping of the birds according to plant succession. There was no discussion of the birds from the standpoint of community relationships. Pitelka (1941) illustrates the coincidence of biotic communities with bird distribution. This is the first attempt to develop this viewpoint and offers the ornithologist an alternative to the life zone concept.

There are numerous individual life histories recorded in the literature, but little attention has been given to the interaction of birds with other members of a community. Williams (1936), in a report on a beech-maple climax community, demonstrated that avian populations are a factor in community dynamics. The present study presents further evidence confirming this thesis. During the past fifteen years several investigations have been carried on in an elm-maple forest (the William Trelease Woods, formerly University Woods, five miles northeast of Urbana) that belongs to the University of Illinois. The previous researches determined the characteristic species which make up the animal community in such a forest, and included a record of their life-habits and a study of their environment as it affected their existence. McDougall (1922) grouped the plants of this forest according to their significance. Weese (1924) made a study of the animals during 1921-1922. Blake's analyses of the 1924-1925 winter population of the animals was published in 1926. In 1925-1926, Smith (Davidson) (1928) studied the climax and developmental stages of the forest. Blake (1931) made a comparison of the 1924-1925 animal communities with those described by Smith (Davidson) and Weese. In the meantime Smith-Davidson (1930) reported on the tree-layer society and, later, on the effect of seasonal variation of weather upon the population of animals in the succession of a deciduous forest. Rice (1939) and Kanatzar (1935) studied the invertebrate population for the periods 1933-1935 and 1935-1936, respectively. From 1938-1940, Koestner (1939) studied the mammals of Trelease Woods. He writes that his actual catches for 1938-1939 totaled 54 fox squirrels and 43 rabbits, and for 1939-1940, 65 squirrels and 73 rabbits. Lindeborg (1941) observed the fluctuation in abundance of Peromyscus and Blarina in Trelease Woods. During the fall of 1937 and 1938 he noted a sharp increase that dropped off during the spring of each year.

Observations begun by the author in 1933 at the Trelease Woods are being continued indefinitely as a research program, or until enough data have been accumulated to give significant and accurate indication of the population trends. The writer's investigations continued from the fall of 1933 until June of 1936. For uniformity of comparison, however, only 1934 and 1935 are herein considered.

The writer wishes to express his sincere appreciation to Dr. V. E. Shelford, under whose direction this investigation was carried out, for his friendly advice and encouragement. Thanks are also due to Miss Lucile Rice who made many of the stomach analyses of birds from the elm-maple forest and permitted the use of her insect population studies of Trelease Woods; to Mr. W. E. Clyde Todd and Dr. S. C. Kendeigh for helpful suggestions; to Mr. C. L. Kanatzar for the compilation of weather data; to Mr. E. J. Koestner who read the paper in manuscript form; and to Mrs. Twomey, Mr. R. D. Hamilton, Miss Helen Jacobs and many other friends.

DESCRIPTION OF COMMUNITY STUDIED

Trelease Woods, located in the park-land region of east central Illinois, covers approximately 22 hectares with about 20 hectares of actual forest. The county

topograpical map shows the 690- and 706-foot contour lines passing through the woods. There is a difference in level between the highest and lowest points of about 16 feet, which gives a slightly rolling aspect.

The soil is the yellow-gray silt loam characteristic of upland forest, the limits of which are but little beyond the present border of the woods to the north and east (Hopkins *et al.* 1918). The drainage in the forest is poor because of the slight slope and impervious subsoil. In the early spring the low spots are always filled with water or are extremely moist. If rain is abundant, the water may stand for several weeks. Thus, throughout a wet season, the forest floor is saturated with moisture, and during the entire year the low ground remains moist. The distribution of the vegetation reflects variation in soil moisture as shown by the more dense growth in the sub-climax areas. The nearest stream is a tributary of the Salt Fork (of the Vermilion River), which flows eastward about four hundred yards south of the forest.

The area lies within the red oak-maple ecotone between the beech-maple and oak-hickory associations. The map of the woods made by McDougall (1922) shows only 13 per cent of the plots without maple trees. At the present time, however, even these contain many sizable maple seedlings. In view of these facts, and for convenience of general discussion, the entire woods will be treated as climax. The division of the woods into climax and late sub-climax portions is clearly illustrated on the map (Fig. 1) and is further substantiated by the breeding areas selected by the different species of birds (Fig. 6). The plant constituents have been described by McDougall (1922) and by Marberry, *et al.* (1936). Of the total tree population, approximately 29 per cent is sugar maple (*Acer saccharum* Marshall) and 22 per cent is American elm (*Ulmus americana* L.) and red elm (*Ulmus fulva* Michx.). Red oak (*Quercus borealis* Michx. var. *maxima* Ashe) is prominent in the climax portion. Other trees found in the woods are the white or American ash (*Fraxinus americana* L.) the blue ash (*F. quadrangulata* Michx.), the basswood or American linden (*Tilia americana* L.) and the blue beech (*Carpinus caroliniana* Walt.). There are occasional trees of other species sparsely scattered throughout.

The shrubs are not uniformly distributed. They are densest on the intermediate ground between the high and low places. There is a long strip of shrubs along the west side extending inward 25 to 45 meters. This strip varies in width; across the north end, it is 24 to 30 meters wide, while at the southern edge, it widens from 45 to 90 meters, probably on account of light conditions. The prevalent shrub is the pawpaw (*Asimina triloba* Dunal), which usually grows from one to three meters but sometimes attains a height of ten meters. The spice bush (*Lindera benzoin* (L.) Blume), which varies from one to two meters in height, is second in abundance. The remaining shrub-sized plants are largely tree seedlings.

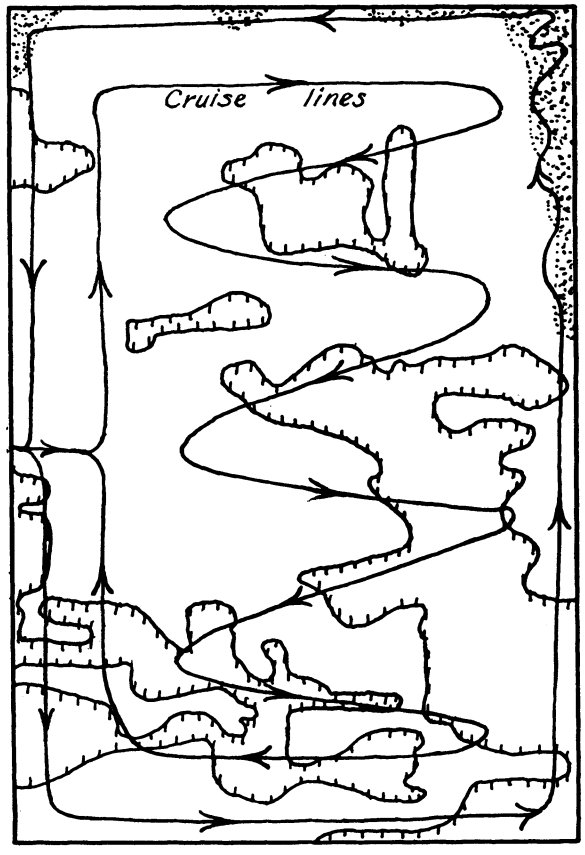


FIG. 1. Climax areas and cruising routes. The lines pointing inward mark the red oak-maple climax. Stippling shows unwooded areas. The remainder of the area is late sub-climax. Cruising route is indicated by line with arrows.

The herb seasonal groups are vernal, aestival and serotinal. The wild-ginger (*Asarum reflexum* Bickn.) and the water leaf (*Hydrophyllum canadense* L. and *H. appendiculatum* Michx.) flower in spring but remain green for the remainder of the summer and wilt after the killing frosts. The dutchman's breeches (*Dicentra cucullaria* (L.) Bernh.), spring beauty (*Claytonia virginica* L.), jack-in-the-pulpit (*Arisaema atrorubens* (ait.) Bl.) and many others are also characteristic vernal plants. During the aestival and serotinal periods the wood nettle (*Laportea canadensis* (L.) Gaud.) is very abundant, often attaining a height of over four feet. It occurs in dense groupings, which may cover almost a hectare. At this time of the year other common herbs are the touch-me-nots (*Impatiens pallida* Nutt. and *I. biflora* Walt.).

Four to six centimeters of decaying leaves and other debris cover the moist ground layer of the forest floor. According to Weese (1924) this area was heavily pastured previous to 1918; some of the hardwoods (*Juglans nigra* L.) were cut *circa* 1895. For about 22 years the forest has remained undisturbed, and the woody plants have almost come back to their normal conditions.

The area studied is completely surrounded by cultivated fields, and the nearest woods is one-fourth mile to the southwest and a half mile south. As a result of this isolation, agricultural and prairie insects are abundant in the woods (Metcalf & Flint 1939) and maintain a much more important position in the community than they would in a larger natural unit.

METHODS OF STUDY

OBSERVATION

Motile animals, whether invertebrate or vertebrate, are difficult to observe, chiefly because of their movements, and different methods must be used for the various groups. For this research, the following system was adopted:

1. Careful estimations of the bird populations were made twice each week throughout the period of study, both for the forest and forest edge. The forest edge is defined as that area in which seedlings, shrubs, vines and herbs form a dense cover at the margin of the main forest—reaching neither into nor out of the forest proper more than 60 meters.

The observer entered the main west gate (Fig. 1) and walked east 60 meters into the woods. He then walked north along the west, and east along the north side, but kept within 60 meters of the edge of the woods or the inner margin of the shrub strip. A general southward path was next followed, crossing and recrossing the woods at least six times until a point 60 meters from the south edge was reached. A path along the south side was taken to within 60 meters of the west edge and along the west side to the gate. This completed the forest observations. For the forest edge, the center path was followed with deviations into the forest edge as far as 30 meters. The general direction followed was again from the main gate but south along the west edge and across the south end, up the east side with an irregular route along the margin of the north half of the east edge, then across the north end and down the west side to the gate. This procedure was carried out each time a census was taken. Several checks were made throughout the study when classes of 25 to 30 students cruised the woods, and the numbers of birds noted on these trips compared favorably with the author's counts.

It was necessary to employ a more nearly detailed method for estimating numbers of migratory individuals. A complete census of the forest edge was always made, but for the forest proper, a sampling plan was used. For instance, at each census a plot (30 meters square) was chosen in some part of the woods and a careful count made of all birds within this area. Similarly, additional plots were selected far enough away so that the observer's earlier activities did not interfere with the movements of the birds. These counts served as a basis for the calculation of the numbers present in the whole forest.

The main winter population was found along the east forest edge and was sometimes difficult to count accurately because the flocks kept moving out in front as the observer proceeded through the woods. In order to take a census, the observer walked along the east edge, starting at the southeast corner, and worked steadily northward. As the northeast corner was approached, the birds that had been moving ahead flushed from cover at the north end. They would then fly up and move back south, passing overhead. Thus the individual members of each species were easily ascertained.

2. Observations in the forest were not always made at the same hour of day. Conditions were studied at sunrise, noon, afternoon, and evening. Likewise, observations were made during heavy rains and snows to determine whether or not the animals would react differently under these more severe weather conditions.

3. During the summer residence of the birds, from May to September, observations were made nearly every day.

4. Emphasis was placed on special phases of animal activities; birds were studied while they were feeding, incubating or carrying on territorial activities.

5. A close watch was kept for any sign of the presence of predators.

6. Specimens were taken for stomach analyses.

METEOROLOGICAL RECORDS

As an aid in the study of the animals of the elm-maple community, meteorological records (including soil and air temperatures and relative humidity) were kept. The instruments for recording these data were enclosed in a standard weather bureau type instrument shelter, located about 30 meters in from the west forest edge in the north portion of quadrat 76 (McDougall 1922: 204). The instruments were at the level of the low shrub stratum.

A recording hygrothermograph was used to obtain records of the air temperature and relative humidity. The humidity readings were checked weekly with a sling psychrometer. Standard maximum-minimum thermometers were used as a check upon the accuracy of the hygrothermograph.

A soil thermograph also was located within the shelter box and continuously recorded the temperature at a two-inch depth in the soil. The sensitive element was placed just underneath the surface of the soil, which was covered with leaf mat and other debris.

From the records made, monthly means were computed and used in the correlation of movements of vertebrate and invertebrate populations with weather conditions.

It was necessary to obtain other weather data from the records of the Urbana Station of the United States Weather Bureau, located on the campus of the University of Illinois, Urbana, Illinois. Inasmuch as any existing differences between the altitude of the two locations, or the exposure at the two stations were not great enough to introduce any appreciable variation between the means of the Urbana

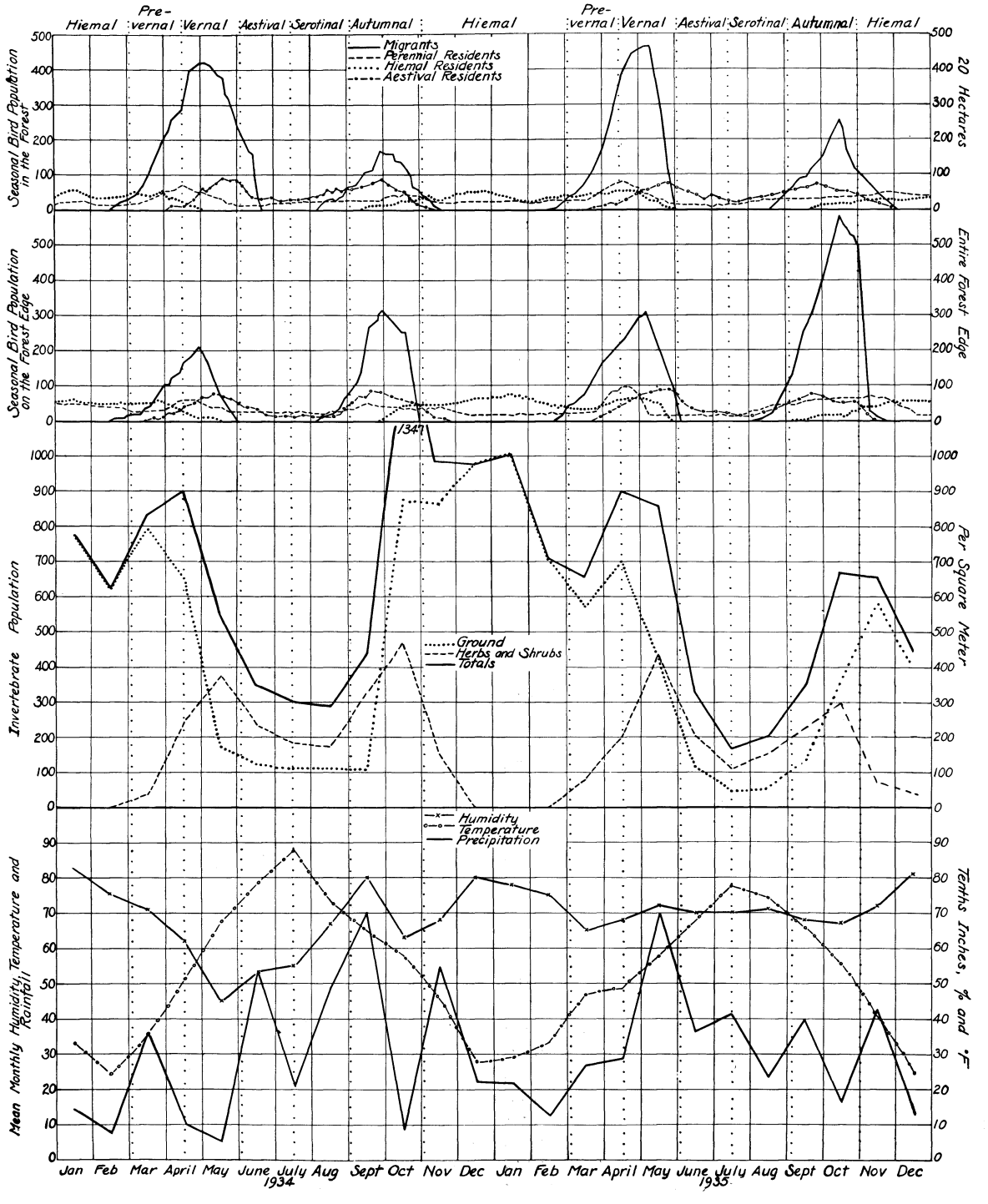


FIG. 2. Correlation of bird and insect populations with seasons and weather. From top to bottom: seasonal populations of the migrants, aestival, hiemal, and perennial residents estimated separately for forest and forest edge; total insect population, total number of insects on shrubs, and in soil; precipitation in inches of rain per month; mean monthly temperature in degrees F, and mean monthly per cent humidity.

Station and those of the woods station, temperature averages and other data of the Urbana station were assumed to be equivalent to those of the woods station.

CLIMATOLOGICAL DATA

The hiemal and perennial avian populations exhibited fluctuations from season to season, especially on account of local movements. In order to interpret these changes correctly, weather data were carefully examined. In most cases the local movements of a species of bird are governed by the direction of the prevailing winds and, in part, by the available food supply. In those instances in which the food of the particular species of bird is largely insects, it is necessary to evaluate weather conditions which cause the fluctuations in available insect population. These weather factors are: air and soil temperatures, relative humidity, precipitation and the direction of prevailing winds. Comparisons of seasonal differences in the invertebrate and bird populations and monthly means for the years involved are presented in tabular and graphic form (Fig. 2, Table 1).

ASPECTION

The biotic seasons are characterized by a decline to a minimum of individuals of one seasonal group and the beginning of the appearance of another. In seasonal community study, biotic seasons are referred to as hiemal, prevernal, vernal, aestival, serotinal, and autumnal aspects (Weaver & Clements (1929); McDougall (1931); Clements & Shelford (1939)). Smith (Davidson) (1928) used these terms in describing seasonal communities in a deciduous forest succession. The latter diagrammatically depicted the more common invertebrates in the various societies. Birds were mentioned in the seasonals, but only the junco and the tree sparrow were listed as belonging to the hiemal society. Smith-Davidson (1932) also pointed out the abundance of certain spiders which occurred during various biotic seasons.

The use of the biotic seasonal groupings was found to be of value in discussing the activities of birds; along with insects and other invertebrates, they appear to follow the pattern of the seasonal phenomena of any given locality, although the dates vary from locality to locality and from year to year. The following dates are typical of the elm-maple forest for 1934 and 1935.

Hiemal Aspect.....November 1 to March 1
Prevernal Aspect.....March 1 to April 15
Vernal Aspect.....April 15 to June 1
Aestival Aspect.....June 1 to July 15
Serotinal Aspect.....July 15 to September 1
Autumnal Aspect.....September 1 to November 1

HIEMAL ASPECT

This period is one of cold winds, snow and rain. It is a season of minimum bird population, made up of the tree sparrow, slate-colored junco, brown creeper, red-tailed hawk, and perennial residents. Although the insects are in hibernation, some display a certain degree of activity, especially on warm days when they come to the surface of the ground stratum. This insect activity is responsible in part for the erratic movement of the hiemal residents (Fig. 2, Table 1). Throughout the hiemal period the avian population remains fairly uniform, although there is a noticeable increase during the latter part of the period (February) because of population movement from the surrounding areas coincident with the start of the insect migration from beneath the leaves of the ground stratum.

TABLE 1 A. Fluctuations in bird populations. Totals per month. Young birds are counted as soon as independent of parents.

1934	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Humidity, Relative	81.3	77.2	72.1	61.6	46.8	56.5	57.3	69.7	80.5	55.5	73.3	51.5
Mean Temperature, °F.	32.5	24.6	35.4	53.2	70.5	60.8	83.5	74.9	64.5	57.9	65.7	27.8
Migrants: Forest	....	30	50	375	400	150	....	25	140	130	50	
Migrants: Forest Edge	....	20	50	200	150	10	....	40	350	375	20	
Permanent Residents: Forest	20	18	30	50	40	20	20	25	30	40	35	30
Permanent Residents: Forest Edge	50	45	30	55	50	30	30	30	50	45	45	35
Summer Seasonals	....	....	....	....	....	156	156					
Winter Seasonals: Forest	50	45	40	35	10	....	....	....	15	30	35	40
Winter Seasonals: Forest Edge	50	40	40	50	25	....	....	....	....	30	40	50
TOTAL POPULATION	170	198	340	765	675	366	206	120	585	660	225	155
1935												
Humidity, Relative	77.1	76.6	74.6	69.0	73.3	70.5	70.3	70.5	70.4	76.1	78.7	79.7
Mean Temperature, °F.	29.0	32.9	46.4	50.1	58.1	69.4	79.1	74.8	67.3	53.7	40.1	24.9
Migrants: Forest	....	30	100	450	350	350	....	50	100	250	75	
Migrants: Forest Edge	....	20	175	320	200	....	....	150	425	450	50	
Permanent Residents: Forest	30	30	35	60	40	20	18	30	30	30	40	30
Permanent Residents: Forest Edge	20	30	35	100	20	20	20	50	50	60	60	25
Summer Seasonals	....	....	....	....	....	136	136					
Winter Seasonals: Forest	30	30	30	40	20	....	....	....	10	20	30	30
Winter Seasonals: Forest Edge	55	50	40	50	30	....	....	....	15	25	50	50
TOTAL POPULATION	135	190	415	1020	630	523	174	230	630	835	305	135

Prevailing wind direction exerts an influence on the hiemal bird population in that the winds are principally from the north and northwest. The birds seeking the more sheltered localities are invariably found scattered over the east and south forest edges and often 40 or 50 meters back into the forest. Hiemal residents are absent from the middle of May until the middle of August.

Prevernal Aspect

The appearance of numerous early Diptera and various beetles marks the beginning of the prevernal period. Leafhoppers and other hibernating insects come to the surface and begin their vertical movement into the shrubs; increasing numbers of robins scratch over the duff of the forest floor in search of adult and larval insects; bluebirds begin to catch flies; tufted titmice and cardinals commence calling; woodpeckers start their drumming; and the first northward migratory birds, the most prominent of which are the fox sparrow, golden-crowned kinglet, crow, cowbird and hermit thrush, begin filtering in. Toward the end of the prevernal period, there is a definite impetus in the activity of the birds as they begin pouring in from the south. Green shoots sprout up through the drab cover of dead leaves, new buds are bursting, and the insects have moved into the shrubs and have started to migrate toward the edge of the forest.

Vernal Aspect

The vernal aspect is one of intense activity. Dutchman's breeches (*Dicentra cucullaria* (L.) Bernh.) and spring beauty (*Claytonia virginica* L.) are scattered in profusion over the forest floor. The new foliage of the shrubs and trees soon covers the forest. A host of seasonal birds swell the forest population to its maximum numbers (Table 1, Fig. 1) and simultaneously, the greatest number of insects appear. Warblers are everywhere; sparrows seek the dense tangle of the forest edge for food or shelter from hawks. These seasonals appear in the following diminishing order of abundance: white-throated sparrow, ruby-crowned kinglet, myrtle warbler, yellow-bellied sapsucker, Cooper hawk, Tennessee warbler, chipping sparrow, warbling vireo, Baltimore oriole, yellow warbler, Cape May warbler, prothonotary warbler. Many of the perennial birds are building nests. The vernal period ends with the passage of the northward migrants and the last movements of the agricultural and prairie hibernating insects out of the forest.

Aestival Aspect

An abundance of nesting birds characterizes the aestival period. The indigo bunting, red-eyed vireo, crested flycatcher and wood pewee establish territories. The period changes from one of song to silence as the feeding of the nestlings takes more and more of the adults' time. Spiders as well as numerous flies that are not found at other times of the year are abundant in the herb and shrub stratum. Weese (1924) designates this period by a decrease in the total invertebrate population due to the absence of migratory insect forms.

Serotinal Aspect

The young birds leave their nests, almost *en masse,* marking the opening of the serotinal period. The territories are no longer retained, and the birds travel in family groups. The cardinal, tufted titmouse, red-headed woodpecker, downy woodpecker, red-eyed vireo, crested flycatcher, and wood thrush wander throughout the forest. In August a dispersal into the surrounding areas (beyond the area under discussion) causes a sudden decrease in the avian population, a serotinal phenomenon (Fig. 2, 3). By late August the first migrants from the north, the blackburnian warblers, appear but spend most of their time in the forest. These are followed by the main warbler mi-

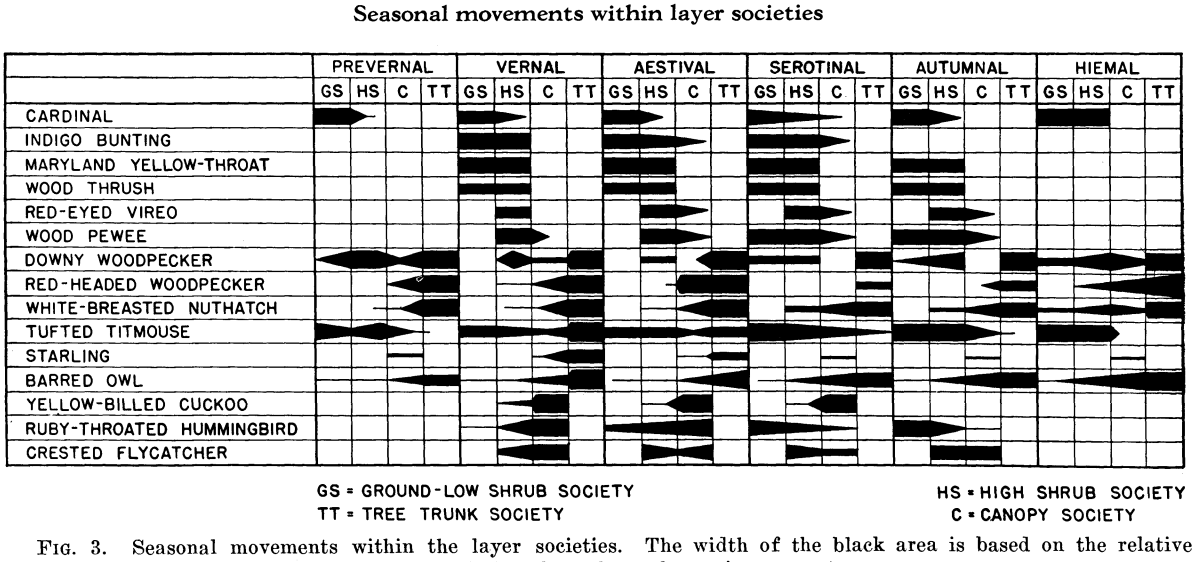


FIG. 3. Seasonal movements within the layer societies. The width of the black area is based on the relative time spent by each species in the layer societies throughout the various aspects.

gration. The summer residents disappear. The numbers of southward migrating birds gradually increase. Weese (1924) found that many additional insect types, the lantern-flies, *Acanalonia conica, Ormenis pruinosa,* and *Ormenis septentrionalis,* appeared in the herb stratum during this period.

Autumnal Aspect

The most striking phenomenon of the autumnal period is that of movement both in the insects and birds. The daily range of temperature, particularly the sudden fall of night temperatures and the shortening of the daylight hours, is no doubt partly responsible for the increased activity. The forest margin and agricultural invertebrates move inward from the forest edge and downward to the forest floor (Weese, 1924). The sudden jump in the avian southward seasonals to a maximum number in late September and early October occurs as waves of these birds meet the insect maximum on the forest edge (Fig. 2). The abundance of weed seeds and fruits on the forest edge at this time also plays an important role in causing this concentration. During both years, 1934 and 1935, the autumnal migration reached its height during the last week of September and then fell off rapidly.

The following list of seasonal birds includes the most abundant and common species in the order of their appearance from September 1 to October 1: blackburnian warbler, Tennessee warbler, black-poll warbler, warbling vireo, slate-colored junco, tree sparrow, fox sparrow, ruby-crowned kinglet, song sparrow, hermit thrush, white-throated sparrow, rusty blackbird, robin, olive-backed thrush, gray-cheeked thrush.

Discussion of Aspection

The elm-maple community in the deciduous forest area is broken into distinct seasonal aspects. The movements and appearance of groups of birds and insects tend to be correlated with the seasonal variations of the plant matrix. The general avian population, a highly specialized and mobile group, exerts a pressure from coaction that changes with the biotic seasons. The seasonal or migratory birds take an enormous toll of the various invertebrates that characterize the aspects. This influence is greatest during the vernal and autumnal periods. The birds that remain in the community as summer residents are principally insectivorous and require great numbers of insects for food during the aestival aspect and an even greater abundance during the serotinal period because of young birds. The returning seasonals are in part late serotinal, but principally autumnal. With the rapid expansion in the seasonals during the autumnal aspect, there is a corresponding increase in the insect populations, as well as the appearance of seeds and fruits. Many of the birds at this season reverse their food habits wholly or in part by eating seeds and fruits instead of a completely insectivorous diet. The perennial avian population is relatively stable in numbers and species. Their role in coaction is easily absorbed within the community under normal circumstances. The minimum of activity is during the hiemal aspect when only the perennials and hiemal avian residents are present.

AVIAN POPULATIONS

The term population implies a known number of identified individuals living in an area. All biological censusing strives to approach this implied ideal. In the case of nesting birds, investigators make use of the observable phenomena of mating, of nest building, and of the feeding of the young, to identify individuals. The writer believes that, for the nesting season, he has arrived at the number of birds of each nesting species, and thereby the total number of birds in the woods, with a good degree of accuracy.

However, outside the nesting period where a type of strip cruising was employed no claims of accuracy can be made. The identity of individuals is entirely obscure and thus no real knowledge of the character and magnitude of the population is obtainable by this method. Color banding or other method of marking individuals was not used because it is far beyond the capacity of a single investigator, or perhaps of many investigators, when applied to such an extensive area.

Suggestions of the deficiencies of the method may be seen in the increases and decreases in populations which are evident. For example, the permanent residents show concurrent increases and decreases in the forest and forest edge, suggesting for the migration period that individuals of the species are present as "permanent" residents, but some additional individuals migrate into the area while en route north and thus increase the total. It further suggests for other periods that there is migration to and from adjacent woodlands, etc. Further comparison of the forest and forest edge numbers suggests rapid movement from one to the other during the counting process so that the same individuals may have been counted more than once, but there is no way to ascertain how many individuals are counted twice or more. The writer does not know how many of the individuals counted had regular or permanent headquarters in the woods under consideration, how many were out visiting other areas, or how many were visiting in the area of study from nearby woods. During the migration period it was not possible to know which individuals are en route as distinguished from those that stay throughout the year. The counts are concerned only with individuals recognized as belonging to a particular species. The writer is convinced however that the figures obtained constitute a reliable index of a population probably somewhat smaller than the figures indicate.

Seasonal Changes in Avian Population

Fluctuations in population of the various aspects are demonstrated (Figs. 2, 3) for 1934 and 1935. The shifting population of the forest is compared diagrammatically with special reference to seasonals, hiemal residents, aestival residents, and perennial residents. There is a noticeable fluctuation in the bi-weekly average number of birds.

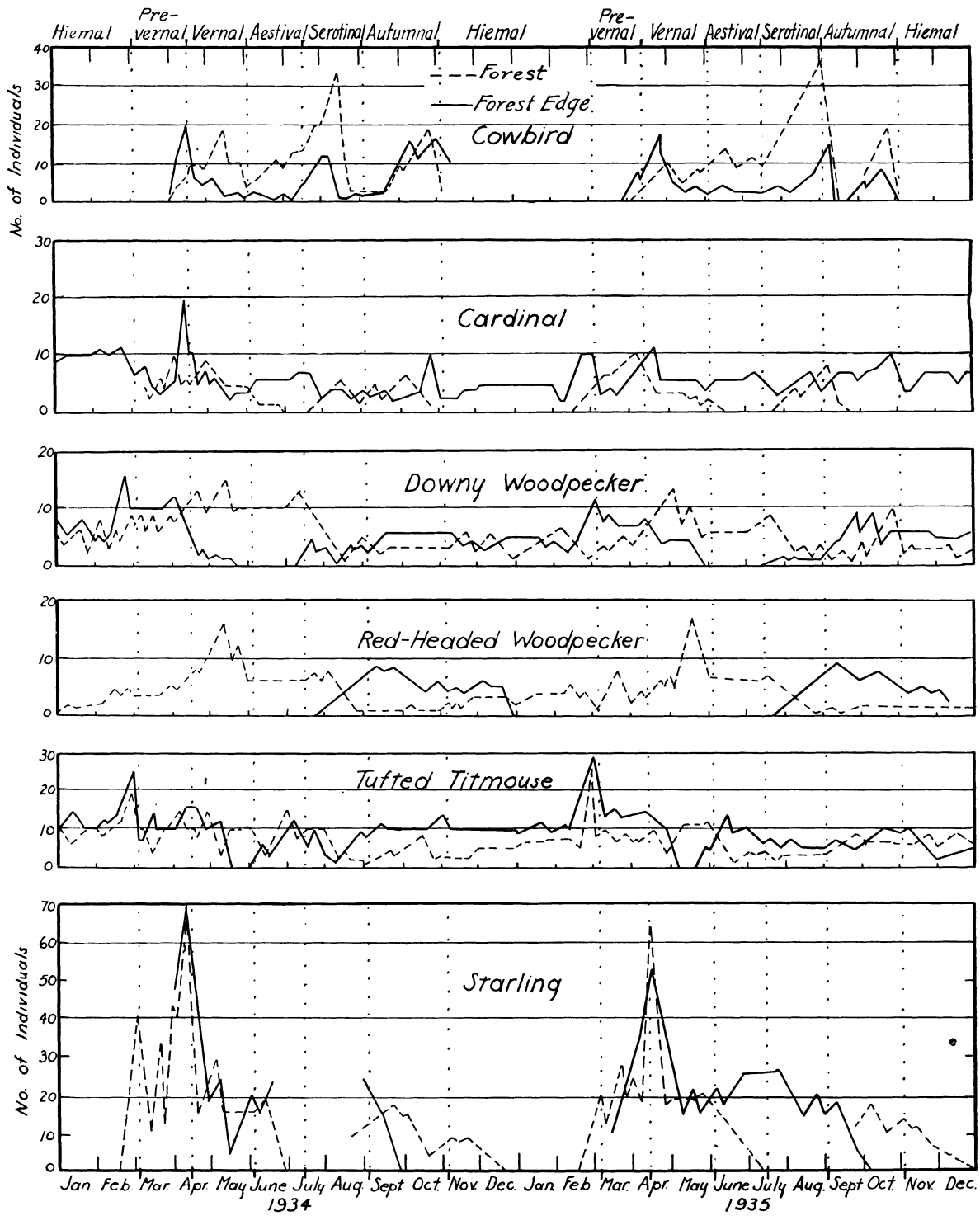


FIG. 4. Number of birds using the forest and forest edge throughout the year. Some birds evidently moved back and forth between forest and forest edge while the count was being made and are included more than once in the number recorded. Preferences for the two different kinds of cover are indicated. This and the following figure show primarily that certain species are forest-edge birds part of the year and forest birds the remainder; at certain seasons, the whole population wanders over the forest and forest edge, depending upon the weather, food, cover, etc. Broken line shows numbers observed in the forest. Solid line forest edge.

The variations in the seasonal bird population, apparent even among the perennial residents, are fairly uniform for the two years. Young birds brought about an augmentation in the nesting population during the vernal and serotinal aspects, but in the span of a year, through dispersal and general mortality, this increase is not discernible in the returning population. The charts (Figs. 3, 4) of forest-edge and forest populations were made primarily to show that certain species are forest-edge birds part of the year and belong to the forest during the remainder; while at certain seasons, the whole population wanders over the forest and forest edge, depending upon the weather, food, cover, etc. Thus in the individual species charts, part of the population may be on the edge one day and in the forest the next. Thus the charts cannot be used to determine the total population by simply adding the forest and forest-edge figures. For instance in a wintering population tree sparrows are forest-edge birds while tufted titmice are found both on the forest and forest edge.

Permanent residents are not a stable population in the woods, but have periods of fluctuation in numbers, particularly during time of increase due to young birds. During the hiemal minimum there is increased activity because of lower temperatures and subsequent wandering throughout the forest in search of food. Permanent residents are made up of birds that are both forest and forest-edge dwellers and, as a result, the total population curve for the permanent residents tends to be approximately the same for both the forest and forest edge.

Variation in the total annual population, as well as fluctuation in the various aspects from year to year, is bound to occur so that conclusions based on only two years must be evaluated with a consideration for the specific local factors as they affect the community. An analysis of Table 1, and Figure 2 shows that the vernal peaks for the seasonals are greater in the forest than on the forest edge both in 1934 and 1935.

Two graphs incorporated into Figure 2 show the total monthly precipitation and the mean monthly temperatures. There was a total precipitation of 35.15 inches in 1934 and 37.21 inches in 1935. The daily mean temperature for a 24-hour period is obtained by applying the formula:

$$\frac{7\text{ A.M.} + 2\text{ P.M.} + 2 \times 7\text{ P.M.}}{4}$$

Vernal migration peaks were reached at 65° F. in 1934 and at 61° F. in 1935. Smith (1917), who carried on observations from 1903 to 1922 in the same general locality, declares that the greatest migratory activity in spring occurred at times when the weather maps showed areas of low barometric pressures approaching from the West, with the south winds and rising temperatures which normally accompany them.

The abundance of insects and birds may be correlated with the occurrence of rain and subsequent plant growth during the vernal and aestival aspects. These two periods of 1934 were dry. In 1935 the heaviest rain for the year fell in May; from June to the first weeks of August, frequent rains also were recorded. This produced a luxuriant plant growth that in turn afforded a more adequate cover within the community and a subsequent enlargement of the general food supply.

TABLE 1 B. Number of pairs of breeding birds. * permanent residents.

	1934	1935
Cooper Hawk	0	1
Mourning dove	0	2
Yellow-billed Cuckoo	2	1
Barred Owl*	1	1
Hummingbird	1	1
Flicker	1	1
Red-headed Woodpecker	4	2
Hairy Woodpecker*	1	1
Downy Woodpecker*	5	4
Crested Flycatcher	5	4
Wood Pewee	3	4
Crow*	2	5
Tufted Titmouse*	5	4
White-breasted Nuthatch*	1	0
House Wren	3	4
Catbird	1	1
Brown Thrasher	1	1
Wood Thrush	3	3
Starling	8	10
Red-eyed Vireo	8	4
Yellow-throat	2	1
Cardinal*	3	3
Indigo Bunting	22	21
Goldfinch	2	..
Field Sparrow	2	2
Song Sparrow	1	1
TOTAL (excluding cowbird)	87	82

Insects affect the local and seasonal movements of the bird population to a pronounced degree, but insects are at the same time physiologically controlled by the precise climatic and biotic seasonal phenomena that stimulate the physiological mechanism of the birds. The biotic balance of excess populations is apparent throughout the period of observation. The birds (seasonals, aestival residents, hiemal residents and perennials) follow the pattern of aspection. A rise in temperature during the hiemal period brings many insects out of hibernation, and in response the birds shift their feeding territories to the area of greatest food abundance. Another example of this balance is illustrated by the sharp advance in the sparrow and warbler population and the prevalence of small predatory hawks during the vernal and hiemal migration periods. Figure 2 shows that the general insect populations of the soil, herb and shrub stratums shift during the various aspects (Rice, ms.). The graph is based on sweepings of shrubs and herbs, $1m^2$ for each sweeping, and the population of the soil invertebrates was determined on those taken on a $0.1m^2$ area. The specimens were collected by the sampling method over the entire forest. Soil samples in December, January, February, and March show the abundance of hibernating species and also indicate a seasonal population change that corresponds to the general insect movements. During the remainder of the year, after the emergence of the winter populations, the soil contains a fairly constant

number. A comparison of the two years shows a relatively uniform population and consistent seasonal movements. The 1935 herb and shrub population is much larger than in 1934. This increase accompanies the more luxuriant herb growth in 1935, caused by the wetter vernal and aestival periods.

Weese (1924) emphasizes the marked biotic seasonal coordination of the community components: "The most striking phenomena of the entire period covered by the collections were the hibernating reactions of the autumn, involving a migration inward from the forest margin and downward to the forest floor and the migration in the opposite sense in the spring. The principal inciting factors of the former seemed to be the fall in temperature and the great daily range of temperature of the early autumnal period. The latter was likewise a response to the changing temperature conditions of the forest, supplemented, perhaps, by changing moisture and light conditions. The fact that many species react alike and at the same time to the same stimulus or combination of stimuli shows a great degree of similar adjustment to the climatic rhythm of the temperate savannah on the part of the characteristic insects of the region."

SEASONAL MOVEMENTS

In addition to the seasonal changes of bird populations caused by long migrations, there are local, seasonal movements that illustrate the importance of species within the community. These movements, especially between forest and forest edge, agree with the correlations already made in relation to general insect oscillations and avian population movements. The following observations of the most abundant species in the elm-maple forest are evaluated as to their seasonal societies within the community.

The cardinal *(Richmondena cardinalis cardinalis)* can be found almost entirely along the forest edge (Fig. 3) where there is an abundance of food—seeds, berries and insects. From October to the middle of November there is a tendancy toward redistribution, for the birds travel from one wooded section to another. By the first week of December they become more settled and remain comparatively so for the remainder of the winter. With the advent of the prevernal aspect in March, cardinals are noted in the forest proper as often as on the forest edge. In the vernal period they are found on the forest edge, but as the nesting period advances, they move into the dense cover just inside the edge and into the forest proper. Here they begin nidification, and from then until the first of August they are, for the most part, forest inhabitants. During the period of feeding the young, the cardinals are on the ground a great deal. A large percentage of their food consists of midge larvae, pentatomids, numerous beetles and lepidopterous larvae secured from the ground and low shrub layer. During the latter part of July there is a slight rise in the cardinal population, but by August a drop occurs. Until after the fall migration, they range over the entire forest and forest edge. Then, from late serotinal and on throughout the hiemal and prevernal periods, they again become forest-edge dwellers.

The spring migration of the indigo bunting *(Passerina cyanea)* starts during the first week of May and reaches its peak about May 20 or a little later (Fig. 5). Although primarily a forest bird at this time, a few (mostly males) frequent the forest edge. During the peak, flocks of 10 to 25 buntings are found on the forest floor—generally in the dense underbrush. By the first week of June the numbers decrease and the majority of those that remain become forest-edge inhabitants. A sudden gain in the population (due to the appearance of young birds) takes place from July 10 to 30, but after the first week of August there is a dispersal of the young to the surrounding areas, although the adults are still common throughout August. In 1934, however, nests with young which may have been second broods were found as late as August 15 to 18. They disappear early in September on their autumnal migration.

Upon arrival in the elm-maple forest in early May, the Maryland yellow-throat *(Geothlypis trichas trichas)* is very shy and difficult to approach. Although never abundant in the community, almost continuous singing shows their presence. During the spring and fall migrations, as many as twelve individuals were recorded. Only two pairs in 1934 and one pair in 1935 nested on the forest edge. Throughout their entire summer residence, from early vernal to the late autumnal aspects, these birds are forest-edge inhabitants, seeking a feeding ground as well as concealment for themselves and their nests in the heaviest tangle of the ground-low shrub society.

The wood thrush *(Hylocichla mustelina)* begins to arrive during the first week of May (Fig. 5) and is distributed over the whole forest. By early June, when the thrush migration reaches its peak, the birds show a preference for the forest edge where they can secure an abundance of food. In a few days, however, there is a decided change in their habitat preference. The males begin to sing, and the mated pairs choose definite territories along the west side of the forest—about 60 meters in from the forest edge. Three pairs selected nesting sites at intervals of 150 meters (Fig. 6, No. A) in an area of abundant pawpaw and spice bush, where they remained and confined their feeding activities throughout the aestival aspect. Between July 20 and 28, there was a gain (due to young birds) followed by a drop with the shifting of the new population into other woods. Near the end of August the migration of individuals from farther north was responsible for a steady rise in population which reached the autumnal migration peak by mid-September.

The red-eyed vireo *(Vireo olivaceus)* appears in small numbers throughout the forest during the first week of May (Fig. 5). By May 10 the birds move into the forest, and, except for an occasional hunt for food on the forest edge, they remain almost entirely in the forest proper. They feed on leaf-hoppers, midges, lepidopterous larvae, lacewings and numerous other insects in the dense lower shrub layer

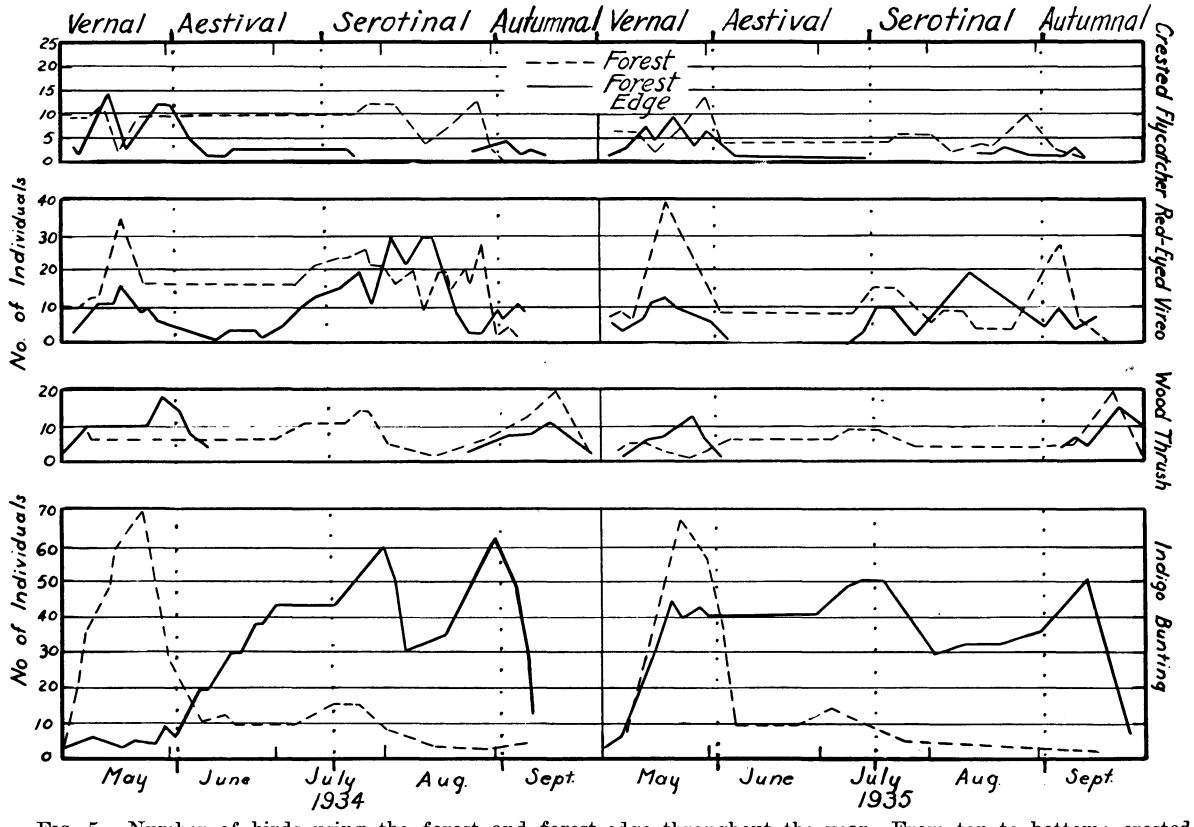


FIG. 5. Number of birds using the forest and forest edge throughout the year. From top to bottom: crested flycatcher, red-eyed vireo, wood thrush, and indigo bunting. For further description, see Fig. 4.

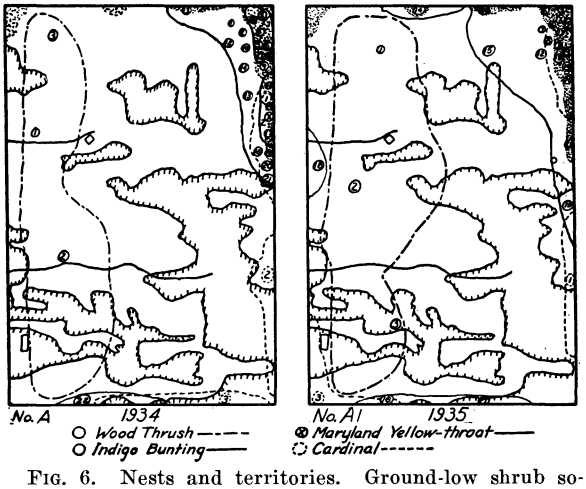


FIG. 6. Nests and territories. Ground-low shrub society. A, 1934; A_1, 1935. Lines pointing inward mark the climax communities of the forest. Irregularities of the forest edge are indicated by stippling.

and up in the forest canopy. By the end of July they again become wanderers and frequent the forest edge as much as the forest. During the first week of September, the vireos are found chiefly in the forest, where their food is in greatest abundance, and finally, by the middle of September, they begin their southward migration.

Except for the warmer days, the downy woodpecker *(Dryobates pubescens medianus)* is a forest-edge dweller throughout the greater part of the hiemal period (Fig. 4). A change in movements begins about the last week of February, and by the first of March, there is a high peak caused by the transfer of scattered winter populations into the woods. From the latter part of the prevernal period, the birds remain on the forest edge in fairly constant numbers. About the first of May the woodpeckers become forest dwellers. Mating occurs and the pairs establish territories. Young birds augment the population during the later vernal interval, and all remain strictly forest inhabitants until the middle of the aestival period when there is a general dispersal into outlying areas.

The tufted titmouse *(Baeolophus bicolor)* is generally regarded as a forest-edge bird (Fig. 4). With the approach of winter, the population drops to about half because of dispersion to other localities. Throughout the hiemal period this bird spreads out over the whole forest. From May to the middle of June, it remains almost entirely in the forest, where pairs build their nests and raise their young in old woodpecker holes. From the middle of June throughout July, the young birds travel about with the parents, both in the forest and on the edge, in search of food. After the breeding season in late spring, the titmice become seclusive, and the singing becomes less vigorous and frequent as the summer progresses. This

concurs with the findings of Gillespie (1930), who says that, throughout the late spring, summer and early fall, titmice tend to disappear, denoting a period of retirement during nesting and subsequent molt.

The starling *(Sturnus vulgaris vulgaris)* leaves the forest in September, becoming very gregarious throughout the hiemal aspect. During this period large flocks fly over the cultivated fields and feed on grain and ground beetles, as shown by stomach analyses. On bright sunny days the few individuals that remain in the forest occupy branches of some tall dead tree, where they sun themselves and imitate songs of native birds and calls of barnyard fowls. They spend the colder days and cold nights in the hay-lofts of neighboring barns. As March approaches, more starlings appear in the forest. The largest concentrations coincide with sudden drops of temperature. These spasmodic changes in temperature seem to be a stimulus for intense breeding activity which usually lasts for about two days. Then only the breeding pairs remain in the forest. After the eggs are laid, few starlings are seen either in the forest or on the edge (Fig. 4). From the middle of May until the first week of June, they spend the greater part of their time going from the forest to the nearby fields for food. When the young are able to fly (about June 20), the birds move to the forest edge; by the middle of August almost all go into the open fields.

From the middle of December until the first week of July, the red-headed woodpecker *(Melanerpes erythrocephalus)* seldom is seen outside of the forest (Fig. 4). The winter population includes but three or four individuals. In May, additional birds move in from outlying wintering territories. With the approach of the breeding and nesting season in June, there is another slump in the population. By July, when the young appear, there is an increase, and, at the same time, a movement toward the forest edge. This movement is due to a change in their feeding coactions, for now the woodpeckers could be seen flying from some favorite telephone pole, fence-post or dead tree, catching insects on the wing. At this time the young, although almost fully grown, are fed prodigiously by the parents. From then until the middle of December, the woodpeckers become wanderers and are found in the forest, at the forest edge, and also at a distance from wooded areas. After December 15 they move into the forest, and the winter population becomes established.

The white-breasted nuthatch *(Sitta carolinensis carolinensis)* is a permanent resident of the forest and spends most of its time creeping over the trunks and branches of the larger trees. In 1934 two pairs spent the winter in the woods, but in 1935 only one pair was observed. As the prevernal period approached, the nuthatches became more active and one or two additional males appeared. The breeding period terminated with only one pair choosing a nesting site. Their activities were restricted to a limited area in the woods (Fig. 8, No. C). By the early aestival period, the young left the nest and roamed throughout the forest with the adults. The family group of five individuals stayed together until the late autumnal period, when the young left the woods. The adults remained and established their hiemal quarters.

The crested flycatcher *(Myiarchus crinitus boreus)* appears during the first week of May (Fig. 5). The birds wander extensively over the forest and spend much of the time far up in the heavy forest canopy on the forest edge. They also come close to the ground on the lower shrubs, where they are able to catch the abundant flying insects. As the nesting period progresses, the flycatchers gradually become less numerous on the forest edge, and for the remainder of their stay, they are found almost exclusively in the high canopy of the forest proper. The birds leave the forest and begin their autumnal migration during the last week of August.

During the first week of June, the yellow-billed cuckoo *(Coccyzus americanus americanus)* arrives, usually in pairs, and immediately occupies the forest canopy. In 1934 two pairs nested in the woods, while only one pair was present in 1935. They are strictly summer residents and leave the forest early in September. Throughout their residence, they restrict their activities to the forest and its canopy and are never seen on the lower forest edge.

As the autumnal period approaches, the cowbird *(Molothrus ater ater)* is noticed more on the forest edge; some are seen in the forest but do not feed there to any great extent (Fig.4). Toward the middle of October there is a rise in population that lasts about ten days and is due to the autumnal migration. The cowbirds practically vanish from the forest by the end of October. They are not observed from the middle of November to the first week of April, but the vernal migration brings a wave of cowbirds that follow the movements of the insects from the forest to the forest edge. From May to August cowbirds are scarce on the forest edge. The breeding population (15 to 20 individuals) travels throughout the forest in bands of three or four females with one or two males. By the middle of June young birds begin to add to their numbers. The increase continues until August, when there is a slump as the immatures and adults move from the forest to the open corn fields and pastures. For the next two months few cowbirds are seen in the forest, but as the autumnal migration wave approaches, many birds occupy the tall trees of the forest edge.

DISCUSSION OF SEASONAL MOVEMENTS

The individual species may be divided into two distinct groups—perennial residents and summer visitors. The perennial residents, such as the cardinal, downy woodpecker and red-headed woodpecker, show a seasonal preference for either the forest or the forest edge (Fig. 4). The downy and red-headed woodpeckers are usually regarded as forest inhabitants, but during the serotinal, autumnal and early hiemal periods, the red-headed woodpecker ranges out to the forest edge. The downy woodpecker, un-

like the red-headed woodpecker, is a wanderer. Consequently it is found as much on the forest edge as in the forest, except during the breeding season, vernal and aestival periods, when it is almost wholly confined to the forest. The tufted titmouse is even a greater wanderer than the downy woodpecker, yet it remains in the seclusion of the forest during the vernal nesting period. The cardinal, a forest-edge bird, enters the forest during the vernal and aestival periods. The starlings are distinctive in relation to the movements of the other perennial residents in that they occur irregularly both in the forest and forest edge throughout the year. They are forest dwellers during their nesting season from March to June, but continue to move outside for food. In early April the appearance of large numbers of starlings in the forest after a rapid drop in temperature, demonstrates the effectiveness of sudden temperature changes upon the breeding activities of the species.

The second class of birds consists of summer residents—all of which are migratory. The crested flycatcher, red-eyed vireo and wood thrush, which are, for the greater part of their residence, forest inhabitants, display a preference for the forest edge during the vernal and early autumnal periods (Fig. 5). The indigo bunting, primarily a forest-edge bird, exhibits a preference for the forest during the vernal period, and some individuals even remain in the forest to nest. The cowbird is more of a wanderer over the whole forest and forest edge, especially during the nesting period (Fig. 4).

The seasonal movements of the birds are comparatively consistent for both 1934 and 1935. There are no broad deviations, although slight fluctuations in numbers of individuals do occur. Specific species respond, in general, to similar seasonal environmental variations.

TERRITORY

The term "territory," as used in this study, is in agreement with the use of the term as defined by Howard (1920), Palmgren (1932), Lack & Lambert (1933), Mayr (1935), Tinbergen (1939), Crawford (1939), Noble (1939), and Nice (1941). These investigators all regard this avian activity from the standpoint of an individual species rather than as a community phenomenon. Howard (1920) discusses territory in relation to reproduction, warfare between species, and defense of chosen sites. Noble (1939) gives the most simple and straightforward explanation, ". . . territory is any defended area. . . ." To explain the varied and intricate complex of avian behavior, Nice (1941) distinguishes six types of territory which deviate slightly from those proposed by Mayr (1935): mating, nesting and feeding ground for young; mating and nesting, but not feeding ground; mating station only; territory restricted to narrow surroundings of nest; winter territories; and roosting territories. The present study indicates that these designations are not rigid and are subject to modifications that depend upon the particular species in question with regard to locality, community preference, and aspection. Individual species within the community are considered in relation to their particular habitats and territorial preferences throughout the various aspects of a community. In its broad sense, then, territory may be defined as a seasonal community phenomenon which tends to bring the influx of an avian population into the aspects of a biotic community. Not only is there a seasonal change or aspection in the deciduous forest biotic community, but the forest is stratified into distinct layer societies that follow the seasonal change of the plant matrix and animal influents. Birds, highly specialized influents of the community, belong to one or more layer societies, that depend upon the seasonal aspect (Fig. 2).

In the following detailed discussion of territories, the birds of the elm-maple forest are grouped under (a) ground-low shrub society—cardinal, wood thrush, Maryland yellow-throat, indigo bunting; (b) high shrub society—red-eyed vireo, wood pewee; (c) tree trunk society—downy woodpecker, red-headed woodpecker, white-breasted nuthatch, tufted titmouse, starling, barred owl; (d) upper canopy society—yellow-billed cuckoo, ruby-throated hummingbird, crested flycatcher. These categories are based on the choice of the nesting site of the particular species at a time of relative stability within the community.

GROUND-LOW SHRUB SOCIETY

The birds in this society are inhabitants of the dense undergrowth both in the forest and on the forest edge. Here they establish territories, build nests and continually search for food, gleaning insects, snails, etc., from the foliage or scratching for larvae among the debris of the forest floor. Their territories are well defined and overlap very little. Few other nesting species except the cowbird and tufted titmouse penetrate into this society.

The cardinal *(Richmondena cardinalis cardinalis)*, a perennial resident in the forest and forest edge, formed a winter range which served as a common feeding ground on the east forest edge and inward for a distance of 30 meters. By the end of the hiemal period in February, the males began to sing, and there was a general intensification of activity. From this time until the vernal period in May when they began to breed, the birds moved into the forest for short intervals, probably because of the insects coming out of hibernation. As the prevernal period ended and the vernal commenced, the males sang continuously. It soon became apparent that individual males were singing from one locality, and the females were building nests in the same areas. At this early establishment of the territories around the singing posts, the males became aggressive and drove the sparrows, buntings and warblers away from their immediate territories. The nesting territories extended into the forest on an average of only 3 meters, but they followed along its length for distances of 60 to 90 meters. The birds showed no tendency to wander beyond their established territories and consequently there was no interference with other cardinals. After the hatching of the young, a preference

for the forest edge was indicated (Fig. 6, Nos. A, A1). The young left the nests by the middle of June, and this circumstance prevented conflict in the territories with later nesting birds such as the indigo bunting. The territories were abandoned quickly, and there was a shift of the population into the forest. Again in the late serotinal period, the cardinals returned to the forest edge, while the young left the vicinity.

The wood thrush *(Hylocichla mustelina)* arrived in May, in small migratory flocks which never exceeded 10 individuals, and moved about over the whole forest, showing no preference for any particular part. As the aestival period approached, there was a change in activity, and those individuals that chose to nest farther north moved on. At first the songs of the males were heard from various parts of the forest. Then as June advanced, territories were established, and individuals were heard singing more consistently from one locality. In the meantime, the females began the construction of the nests, while males alternately sang and aided. The location of the nests is plotted in Figure 6, No. A. There was never a sign of overlapping of the extremities in the range of any two pairs within the strip of forest undergrowth that constituted the individual territories, and they chose approximately the same territories both years. As the young began to hatch, the adults were more active and traveled in all directions in search of food. After the young left the nests, the males retained their old singing positions. A dispersal of the young out of the forest was noticed in August. Only a few individuals remained until the late serotinal and early autumnal periods, when the migrants began to move into the forest. As during the vernal migration, this interval was characterized by a general wandering over the whole forest. The greater abundance of insects in the undergrowth of the forest edge made it even a greater attraction at this time than during the spring migration.

The Maryland yellow-throat *(Geothlypis trichas trichas)*, strictly a forest-edge bird, was found only along the east side of the woods. Because of the wary habits of the birds, it was difficult to observe their activities minutely. Throughout May there was little indication that they had chosen territories. Males sang continually, but not always from the same localities. They shifted as the migrants passed through the woods. By the first of June the two remaining pairs had chosen nesting sites. The song of the male was used as an index of an established territory. Each was located on the forest edge and was separated by at least 40 meters. The actual boundaries were not well defined until the young were being fed, when it could be seen that the territories were marked out by the limits of the feeding ranges (Fig. 6, No. A1). These territories overlapped those of the indigo bunting and cardinal, but there was never any evidence of competition between the nesting species. In no case, however, would the buntings, yellow-throats or cardinals tolerate a close approach of another bird to their nests. Thus there was a distinction between the territory and the nesting site among the members of the ground-low shrub society. After the young left the nest (first week of July), they stayed with the adults as family groups during the remainder of the aestival and throughout the major portion of the serotinal period. Nesting territories were abandoned on the arrival of the first migrants in late August, and at that time family groups could not be differentiated. The migrants, as well as the resident birds and their young, kept within the east forest edge until they moved south.

The indigo bunting *(Passerina cyanea)* showed tendencies toward territorial selection which were limited to the defense of the areas around the singing posts during the mating and breeding period in early June. After the nests were built and the eggs laid, the males continued to retain their original singing posts, which, in all cases, were within three to five meters of the nest. After the young hatched, it became apparent that the whole nesting population used a large feeding range, the limits of which took in all of the nests (Fig. 6, No. A). The buntings, which formed a social group, were unlike the other forest nesting species in their territorial behavior, at least insofar as feeding was concerned. Howard (1920) says that buntings [*Emberiza schoeniclus*] desert their territories temporarily and collect in flocks on the newly sown fields of grain. He observed that they established a territory in the early part of the season, but when food became scarce, they were forced to range out to places where there was an abundance of food.

HIGH SHRUB SOCIETY

This society supported only two species of nesting birds, the red-eyed vireo and the wood pewee, but many of the birds from other societies expanded their territories slightly into this community. The cardinal, indigo bunting and tufted titmouse established secondary singing posts and, along with the downy woodpecker and wood thrush, gleaned insect food from this layer.

The selection of territories by the red-eyed vireo *(Vireo olivaceus)* was a rather passive affair, carried out by the male. When the migration reached its maximum early in May, there was a great deal of chasing between males and females, often with three or four birds taking part. Finally, when only the breeding population remained, the birds mated. It was easy to locate the individual nesting pairs by the singing males (Fig. 7, No. B). Each male retained a singing post in the upper canopy throughout the summer. The vireos were decidedly solitary in their nesting habits. No two pairs nested close to each other but were well spaced over the forest. They occupied the middle layer or high shrub society which extended from three meters above the ground to just below the canopy (about 12 meters), thus giving them a wide choice of nesting sites. The outer limits of the territories were not clearly ascertained until after the young had hatched. Most of the food was obtained from the vegetation relatively close to the nest. The young left the nests by the first of

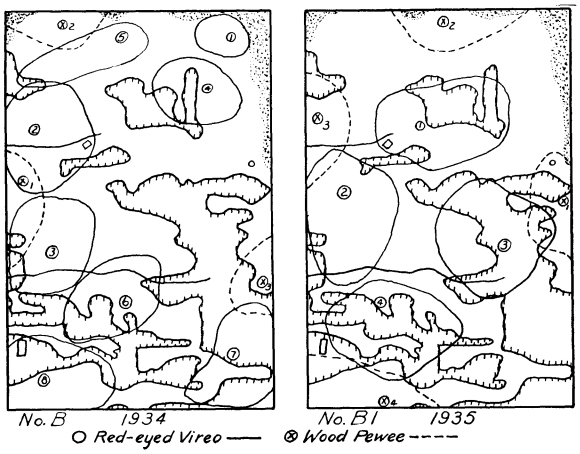


FIG. 7. Nests and territories. High shrub society. B, 1934; B_1, 1935. See Fig. 6.

July and became very seclusive in the dense foliage. By the serotinal period they dispersed, leaving only the adults.

Almost as soon as the migrants left, the wood pewee *(Myiochanes virens)* chose its territory. This flycatcher was easily located because of its activity and continual singing as it fed along the edge of the forest. Territories, which were never large and always extended to the forest edge, were established even before the nests were built (Fig. 7, No. B1; Table 2). The birds seldom traveled more than 100 yards from the vicinity of the nests. One or the other of the adults habitually alighted on some dead branch overhanging the forest edge, or on a fence, and from such perches flew out and caught passing insects. When the young hatched at the end of the first week of July, vigorous feeding activities did not alter the territories. The adults continued to occupy the same perches or remained within a few meters of them. After young left the nests, family groups moved along the edge of the forest without any indication of territory. Family groups gradually broke up between the first of August and their departure in September. It was common to see individual birds catching flying insects and showing no apparent interest in others of their own species. This behavior is characteristic of most flycatchers with the approach of the migration period.

TREE TRUNK SOCIETY

This community is not a true layer society for it includes an area from the base of the trees to the upper branches. Because of their structural specialization, the downy woodpecker, red-headed woodpecker and white-breasted nuthatch comprise this distinct community. The only competitors are such birds as the tufted titmouse, starling and crested flycatcher. These birds use old woodpecker holes for nests and establish territories which reach into one or more of the recognized layer societies.

By the first week of May the downy woodpecker *(Dryobates pubescens medianus)* became a forest dweller. During a brief interval between April 28 and May, the downies were heard throughout the

TABLE 2. Territory size within the layer societies.

	1934			1935		
Ground-Low Shrub Society	Average size of individual territories in hectares	Available area in hectares per pair	Number of pairs	Average size of individual territories in hectares	Available area in hectares per pair	Number of pairs
Indigo Bunting	.23	1.1	22	.24	1.1	21
Wood Thrush	2.7	7.0	3	2.7	7.0	3
Cardinal	3.3	7.0	3	3.3	7.0	3
Maryland Yellow-throat	1.5	11.0	2	3.0	22.0	1
High Shrub Society						
Red-eyed Vireo	2.3	3.0	8	4.5	6.0	4
Wood Pewee	3.3	8.0	3	2.5	2.4	4
Canopy Society						
Crested Flycatcher	4.4	4.8	5	5.5	6.0	4
Yellow-billed Cuckoo	11.0	11.0	2	22.0	22.0	1
Tree Trunk Society						
Downy Woodpecker	4.4	4.8	5	5.5	6.0	4
Red-headed Woodpecker	5.5	6.0	4	11.0	11.0	2
White-breasted Nuthatch	22.0	22.0	1	....	....	.
Barred Owl	22.0	22.0	1	22.0	22.0	1
Tufted Titmouse	4.8	4.8	5	6.0	6.0	4
Total pairs		73			62	
Hectares per pair of total population		.30			.32	
Acres per pair of total population		.74			.79	

daylight hours, but there was no evidence that territories had been established. Two males were often seen pursuing a single female. The birds were found mated on May 10, and each pair had its separate territory. Nesting holes were constructed in dead portions of large limbs or tree trunks. Pairs were distributed evenly over the forest with individual nests widely separated. In 1934 there were five nests, while in 1935 there were only four. There was no overlapping of nesting territories. They were comparatively uniform in size and did not comprise the full extent of the forest area, although in 1935 they were slightly larger than in 1934 (Fig. 8, No. C; Table 2). With the hatching of the young in early June, the adults became more active but seldom flew more than 50 meters from the nest in search of food. On an average, the young were fed every 3.05 minutes by one or the other of the parents. The male left the nest in one direction; the female in the opposite, and the directions shifted from day to day. Territories were abandoned as soon as the young left the nest. The adults took the young into the dense foliage of the canopy and left them while they went in search of food. The young were able to take care of themselves by the late aestival period, after which time they left the woods. The adults remained and moved to the forest edge. There was never any indication of winter ranges. Singly or in small groups of three or four, the birds traveled over the forest and forest edge according to changing weather conditions.

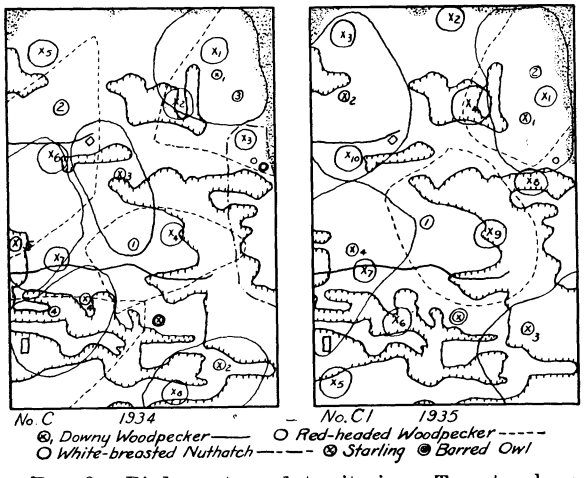


FIG. 8. Birds nests and territories. Tree trunk society.

In at least one instance the red-headed woodpecker *(Melanerpes erythrocephalus)* showed pronounced territoral inclinations. In 1934 a pair of woodpeckers (Fig. 8, No. C1, nest 2) selected a tall, dead sycamore in the center of the woods, which, from the number of old holes present, had been a favorite nesting site. A pair of crested flycatchers had built their nest in one of these holes, and the female was sitting on her five eggs. On June 23, 1934, while censusing the woods, the writer heard a great commotion in the direction of the crested flycatchers' nest. Two red-headed woodpeckers, a male and a female, were busy fighting off the flycatchers and at the same time going into the flycatchers' nest, throwing out the feathers and, finally, the eggs. By the end of an hour the flycatchers were ejected from their nest. The following day the red-heads, rather than take the hole which the flycatchers had used, proceeded to build a new one directly below the flycatcher nest. They completed the nesting hole on the third day, June 27, and a brood of four red-headed woodpeckers left the nest on July 28. In 1934 four pairs nested in the woods. In 1935 the two nesting pairs occupied the same nesting sites as did numbers 1 and 3 in 1934, but the 1935 territories were larger. By the time the young were able to come to the entrance of the nesting holes, the parents had extended their territories to the limits indicated in Fig. 8, No. C1; Table 2. These territories were retained for a short time after the young left the nest. They were broken by the first of August, and the families moved to the forest edge. The adults continued to feed the young until the middle of August, even though they were fully grown. While the young rested on a fence post, the adults caught flies, grasshoppers, and hymenopterous insects. The wintering birds wandered throughout the forest, singly or in pairs.

A pair of the white-breasted nuthatches *(Sitta carolinensis carolinensis)* spent the winter in the elm-maple forest during 1934. Their winter feeding range comprised the entire woods. Throughout the hiemal period the birds spent over half their time in the locality which was to be their nesting site. This conforms with the studies of Butts (1931) who found that all nests of the white-breasted nuthatch were within five hundred yards of the place where the birds had been captured during the winter. The nests were built within or near these ranges, and, in general, the nesting territories and winter ranges coincided fairly well. In the elm-maple forest, the birds began to show a more active interest in each other and frequently appeared together as the prevernal period approached. Their wanderings throughout the forest became less noticeable toward the end of this aspect. At the beginning of the vernal period two additional males arrived, and intense activity was exhibited during the following few days as mating began. Eventually, the two extra males left, and the pair of resident nuthatches chose a nesting site in a large elm. Between May 20 and 25 both birds participated in the nest building, chipping out wood on the under side of a dead limb. The male stayed close to the nest until the young hatched on June 10. In the subsequent feeding activities there were suggestions of a restricted territory (Fig. 8, No. C; Table 2). The adults did not travel far for food; they seemed to procure it in suffiicent quantities from the surrounding trees. Butts (1931) reported that although the birds which he observed traveled considerable distances from the nests, they also obtained an abundance of food close to the actual nesting sites. In the present study the young were found to leave

the nest on June 30, and the family group, consisting of four young and the two parents, remained in the vicinity of the nesting territory until the middle of July. Throughout this time the adults carefully watched and fed the young. Then the young disappeared, and the adults established their hiemal range. Butts (1931) mentioned that he did not succeed in banding any young but noticed that a number of young appeared at a neighboring station a half mile away, where they remained all winter. Whittle (1926) found that the young left the parents or, perhaps, were driven away, in July.

Figure 9, No. C2 represents the territories established by nine pair of tufted titmice *(Baeolophus bicolor)*—five in 1934 and four in 1935. These territories were discovered early in the mating season, during the last of April and the first week of May.

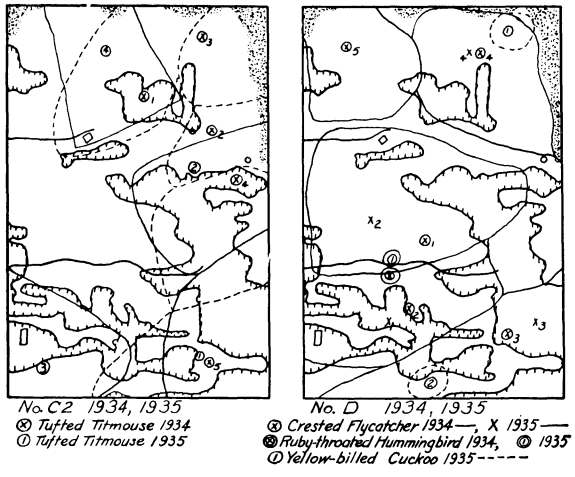


FIG. 9. Birds nests and territories. Tree trunk society. C, 1934; C_1, 1935. See Fig. 6.

The singing birds were invariably heard from the same localities, and the mated pairs were seen at the same places each day. The nests were located by observing the movements of both birds when together, or when one was carrying nesting material. When the young hatched out, the actual limits of the territories were ascertained by watching the movements of the adults as they left the nests for food. The distances traveled were plotted on a map, and by the time the young were able to leave the nests, the limits of these territories were well defined (Fig. 9, No. C2; Table 2). No two territories overlapped. They were well spaced over the forest, and the birds always stayed within their territorial limits. There was no apparent competition with other breeding species, for the time of nesting was several weeks earlier. On an average, the nests were located 15 or more feet above the ground, and the feeding activities were confined to the higher shrubs and upper tree canopy. By August there was a dispersal of some family groups out of the forest while the remaining birds roamed over the whole forest. During the two years studied, the titmouse population tended to remain fairly uniform, although it was not so large from late serotinal to the prevernal aspect as during the rest of the year. During the hiemal period there was no evidence of a limited winter range. The birds wandered over the whole forest in bands of four or five (probably family groups). Their movements were governed by changes in weather conditions. With a rise in temperature, they moved into the forest, and with a drop, they shifted to the east forest edge. During the winters of a four-year period, Gillespie (1930) found that tufted titmice traveled in small bands, suggesting family groups, and occupied definite and limited areas which never overlapped.

The starling *(Sturnus vulgaris vulgaris)* wandered freely over the forest proper, but had a limited territory around the immediate nesting site. The essential nesting requirement was an old woodpecker hole or a natural cavity. Two pairs of starlings never nested in the same dead tree, no matter how many holes were in it, and thus indicated their preference for isolation at this time. Other birds were tolerated close to the nesting tree but were not permitted to alight on it. Upon one occasion an eastern bluebird's partially finished nest was destroyed by a pair of starlings which later occupied the same hole and successfully raised their own family. Eight nests were located in 1934 and ten in 1935 (Fig. 8, No. C1). As the young hatched, the starlings became more aggressive and attempted to drive off any intruders—bird or mammal. They all had young by May 20 and moved out to the forest edge and open fields where they scratched over the ground in search of beetle larvae, spiders, earthworms, lepidopterous larvae and other soft-bodied insect types. While the nesting territory was distinct, the feeding range was not well defined and covered a wide area. The starlings might then be considered merely as visitors in the forest for about five or six weeks during which time they received shelter for the raising of their young.

The barred owl *(Strix varia varia)* spent most of its time in the woods, and, since there were few other large birds of prey, the owl took in the whole forest and its edge as a feeding range and as territory during the breeding season. The pair was seldom seen together except during the mating season. At all other times they were within calling distance, but displayed only a passive interest in each other. This indicates that they probably were mated for the year and that they renewed their activity just before the nesting period.

UPPER CANOPY SOCIETY

This community is used by numerous birds for gathering food, protection from enemies, shelter, and also, by a few, for the establishment of nesting territories. The yellow-billed cuckoo, ruby-throated hummingbird, and crested flycatcher made up the nesting population.

The yellow-billed cuckoo *(Coccyzus americanus americanus)* was one of the last birds to arrive. Cuckoos appeared in early June and remained almost exclusively in the upper canopy. There, in the dense crown of the forest, they hunted insect larvae, running along the branches but seldom flying more than

a few yards. The male of each pair began calling from specific localities in the upper canopy before the nest was built. The three nests observed were all over ten feet from the ground in the high shrubs. The territories defended by the males were principally from the immediate nesting site to the limits of the individual singing posts in the upper canopy. Since the greater part of their activity was confined to the upper canopy, they are here treated as belonging to this society. The male cuckoo became much disturbed at the close approach of any other bird and drove the intruder from the vicinity of the nest. On the other hand, the feeding range could not be included as a part of the territory for it covered the whole forest canopy and was not defended.

A pair of ruby-throated hummingbirds *(Archilochus colubris)* arrived about the first of July and immediately constructed a nest. In 1934 the nest was 25 feet up in a pawpaw in the center of the woods; in 1935 a pair nested 40 feet up in a large maple tree, out on the farthest tip of a branch (Fig. 9, No. D). The birds avoided the west and northwest forest edges for the east, northeast, and south edges which were abundant with trumpet weed and numerous other flowering plants. For the most part, the birds stayed in the tops of the higher shrubs and forest canopy from whence they darted down to the dense foliage of the forest edge. The hummingbirds had well-established territories, especially in relation to nests. No other bird, regardless of its size, was permitted to approach within ten meters. Even the female was belligerent and did not allow another bird to fly by when there were young in the nest. It was not uncommon to see her chasing off a red-headed woodpecker or even a crow. The chief mode of attack was to fly at the intruder and buzz about the back of its head, a procedure which was most annoying to the trespasser. The female did the incubating, feeding, and caring for the young. The feeding range, which covered the greater part of the woods, was not so well defined as the territory.

The crested flycatcher *(Myiarchus crinitus boreus)* arrived singly or in pairs in early May and wandered over the forest and its edge in search of insects in the higher shrubs and canopy. On only a few occasions were birds seen catching flying insects in the low shrubs. Soon mating calls came consistently from definite localities, and by the first week of June, territories were established. The nests occupied were in the old holes of the red-headed woodpecker or flicker, 40 to 50 feet from the ground. The only competition over nesting holes was with the red-headed woodpecker. A pair of these birds chose to nest in the same tree already tenanted by a pair of flycatchers. As mentioned earlier, the battle terminated in the woodpeckers throwing the nest and eggs out of the hole and then constructing a new nest below that of the flycatchers'.

Five territories were established in 1934 and four in 1935 (Fig. 9. No. D). They were comparatively large, each covering about one-fifth to one-fourth of the forest canopy (Table 2). Nests 1, 2, and 3 in 1935 were close to the actual nesting sites of 1, 2, and 3 of 1934, and the birds occupied approximately the same territories. Nest 4 in 1934 was again used in 1935. The young hatched by the middle of June in both years and left their nesting holes in early July. The territories were broken as the birds scattered throughout the forest.

The cowbird *(Molothrus ater ater)* showed no signs of territorial selection. The birds ranged in small groups, generally three or four females and one or two males, throughout the forest and forest edge. The females spent much of their time locating other birds' nests in which to deposit their eggs. The selection of females was accompanied by some combat among the male birds, but there was no evidence shown that cowbirds select and protect a territory. Friedmann (1929) found that *Molothrus ater ater* does not have a territory. Likewise, Nice (1933 b), in speaking of the cowbird, points out: "I have banded a number of breeding adults of this species near our home; in 1931 one female was seen on her summer range as late as September 13, and the next year even until October 3. These birds are entirely friendly to one another throughout the summer; two females, one banded and the other not, regularly roamed about together in a 30-acre tract, and two others, again one banded and the other not, did likewise on another 30-acre tract further north. A banded male consorted with all these females and with still another banded female still further to the north; there were also a number of unbanded males that lived in the same region. Of course, cowbirds do not feed young, nor do they repell [sic] rivals to ensure their offspring less competition. *Molothrus ater* cannot be said to have a 'territory,' when it never defends it."

SEASONAL SOCIETIES

Toward the end of the serotinal period and the beginning of the autumnal migration, the layer societies were no longer apparent (Fig. 3). With the development of the young birds, there was a dispersal of the general breeding populations, followed somewhat closely by the arrival of the first migrants. At this time the birds wandered throughout the forest. The autumnal migration peak was greatest on the forest edge, where it coincided with the newly concentrated masses of agricultural and prairie insects.

The east half of the forest, and especially the east and south forest edges, constituted the major area covered by the winter ranges of the hiemal and perennial birds. There were no particular territorial boundaries between species or individuals other than the structural limitations of the birds in the community. The ground cover of the forest edge was the most pronounced layer. The heavy mat of dead leaves and the dense undergrowth of shrubs and herbs afforded an excellent place of shelter and food for tree sparrows, juncos, cardinals, Carolina wrens, tufted titmice, robins and song sparrows. Usually in flocks of five to fifty, the birds fed extensively on seeds, berries, and insects scratched from the ground

cover of leaves. Actually, then, groups of birds rather than individuals chose the feeding ranges which were very flexible, shifting with changes in the weather and available food supply. Since no combat was involved, there was no evidence of a defended territory.

The robin was an influent in the ground society from the middle of January to the end of March. Both in 1934 and 1935, a flock of about 40 robins appeared in the south third of the forest by January 20. They spent the greater part of their time on the ground, scratching among the dead leaves. By the end of February, the whole south third of the forest looked as if a flock of chickens had been scratching over the forest floor. Throughout the stay of the robins, 12 stomach contents were examined at intervals and found to contain large numbers of white Bibio larvae. One stomach contained 40 larvae, another 35—representing 92 per cent of their entire food. In addition to these larvae, the stomachs contained Coleoptera, Carabidae, Hemiptera, Arachnida and small amounts of vegetable food. Assuming that the 40 robins each consumed 40 Bibio larvae per day, approximately 96,000 of these larvae were accounted for in the two months. Bibio larvae disappeared in the forest by the end of March and none was found in the numerous soil samples examined. Forbes (1880) described a similar incident during February and March at Normal, Illinois. In one stomach, he found 175 Bibio larvae, which further brings out the preference of robins for this type of insect.

The food of the tufted titmice was diversified. Their activities on the ground and shrub layers were somewhat indefinite so that they did not interfere to any extent with other birds. Since their numbers were comparatively large (10 to 14 individuals), and because of their permanency in the forest, they should be regarded as minor influents.

The tree sparrows and juncos occupied a somewhat separate niche on the east and south forest edge which afforded them shelter and an ample supply of weed and grass seeds. These minor influents, in flocks of 50 to 100, were found consistently throughout the hiemal period. The effect of the one pair of Carolina wrens was negligible.

The principal occupants of the tree trunk society were the downy, hairy, red-headed and red-bellied woodpeckers, the white-breasted nuthatch, brown creeper and tufted titmouse. These birds did not indicate very specific ranges within the forest and showed changes with wind exposure. Frequent west and northwest winds drove them to the east forest edge. Food was not a factor, for on calm days, when the atmospheric temperature was fairly uniform, the birds of this society scattered over the whole woods—the nuthatches, creepers and titmice looking over the surface of the bark, and the woodpeckers chipping out rotten and dead stumps in search of beetle larvae.

During both the northward and southward migrations, there was no particular stratification. In the spring, the migrant birds moved through the forest and along its edges in waves that increased in magnitude as the peak was reached and then gradually decreased to a minimum as the breeding birds became stable with the selection of territories in one or more of the recognized layers.

NESTING STATISTICS

A study to determine the percentage survival of the young was made of three species; the indigo bunting, red-eyed vireo, and wood thrush. The final percentage values are only relative for in order to establish a survival rate, it would be necessary to evaluate critically a much larger area over a period of years.

The most destructive enemy of the indigo bunting is the cowbird. Its parasitic habit of laying eggs in other bird's nests is well known, but the effect which this has upon the increase of other birds is not so well understood. Tables 3 and 4 disclose that 112 bunting eggs and 22 cowbird eggs were laid in the 41 buntings' nests built in 1934 and 1935. The growth curves (Fig. 11) indicate that, at the time of hatching, the cowbird has a distinct advantage in size and weight over the bunting. The growth of the cowbird is very rapid, for it is able to monopolize most of the food, and in consequence, the other young birds are either pushed out of the nest or trampled to death. Figure 11a shows the normal development of three buntings. In a nest occupied by three buntings and one cowbird (Fig. 11b) one bunting was pushed out the second day after hatching; the other two were able to withstand the competition until they left the nest. In another nest three buntings and two cowbirds hatched (Fig. 11c). One bunting was pushed out by the end of the first five days; another was ejected on the eighth day and the third on the eleventh day. The two cowbirds thrived normally and on the thirteenth day crowded themselves out of the nest, but they had advanced enough to hop about among the shrubs.

The effect of the cowbird is significant. In 1934 (Table 3) 57.0% of the buntings and 53.8% of the cowbirds successfully left the nests. In 1935 it was 59.0% of the buntings compared to 100% of the cowbirds (Table 4). In 1934, 23.8% of the buntings were destroyed by the cowbirds as against 31.7% in 1935.

Other enemies of buntings were few indeed. Cats destroyed 22% of the bunting young in 1934 and were responsible for 8.8% of the mortality in 1935. No estimates could be made of the numbers of birds killed after leaving the nests. In 1934, 12.3% of the eggs were destroyed by snakes (*Lampropeltis* sp.), but in 1935 none was molested in this way. Twenty-two per cent of the nests were abandoned in 1934 and 36.8% in 1935. The cause of these desertions was undetermined. The nests were completed, but no eggs laid. Whether the adults met with misfortune or merely built additional nests was never established.

Figure 11 (a, b, c) shows the rate of growth of young indigo buntings and cowbirds during the first ten to twelve days after hatching. The growth curves are steep, showing an average daily growth of about

TABLE 3. Nesting statistics of the indigo bunting, 1934.

Nest Number	Number of Bunting eggs	Number of Buntings hatched	Number of Cowbird eggs	Number of Cowbirds hatched	Young Buntings destroyed by Cowbird young	Eggs taken by snakes	Young taken by cats	Nests deserted	Buntings that successfully left nest	Cowbirds that successfully left nest
1....	4	0	..	..	..	4	..	..	..	..
2....	4	3	..	..	..	..	3	..	..	..
3....	2	0	..	..	..	..	..	..	..	..
4....	3	3	1	1	1	..	..	..	2	1
5....	3	3	..	..	..	..	..	..	3	..
6....	..	..	..	..	..	..	..	1	..	..
7....	3	3	..	..	..	..	..	..	3	..
8....	4	4	2	0	..	..	..	..	4	..
9....	3	3	..	..	..	..	..	..	2	..
10....	..	..	..	..	..	..	..	1	..	..
11....	..	..	..	..	..	..	..	1	..	..
12....	3	3	..	..	..	..	..	..	3	..
13....	4	0	1	0	..	5	..	..	..	..
14....	3	0	1	0	..	..	..	1	..	..
15....	3	3	2	2	3	..	..	..	..	2
16....	..	..	..	..	..	..	..	1	..	..
17....	3	3	1	1	2	..	..	..	1	1
18....	4	3	1	0	..	..	..	..	3	..
19....	4	4	..	..	..	..	4	..	..	..
20....	4	4	1	1	3	..	..	..	1	1
21....	4	4	1	1	1	..	4	..	..	..
22....	2	2	2	2	..	..	..	..	2	2
Total.	60	42	13	8	10	9	11	5	24	7
Per cent.	..	70%	..	61.5%	23.8%	12.3%	22%	22.7%	57%	53.8%

TABLE 4. Nesting statistics of the indigo bunting, 1935.

Nest Number	Number of Bunting eggs	Number of Buntings hatched	Number of Cowbird eggs	Number of Cowbirds hatched	Young Buntings destroyed by Cowbird young	Young taken by cats	Nests deserted	Buntings that successfully left nest	Cowbirds that successfully left nest
1.....	..	..	..	..	..	..	1	..	..
2.....	..	..	..	..	..	..	1	..	..
3.....	4	4	1	1	2	..	..	2	1
4.....	4	0	..	..	..	..	1	..	..
5.....	5	5	..	..	..	..	..	5	..
6.....	4	4	..	..	..	..	..	4	..
7.....	1	0	..	..	..	..	1	..	..
8.....	4	4	..	..	..	..	..	4	..
9.....	4	4	1	1	3	..	..	1	1
10.....	3	2	2	2	2	..	..	0	2
11.....	2	0	..	..	..	..	1	..	..
12.....	3	3	2	1	1	..	..	2	1
13.....	3	3	1	1	2	..	..	1	1
14.....	4	4	..	..	..	4	..	..	..
15.....	3	3	2	2	3	..	..	0	2
16.....	..	..	..	..	..	..	1	..	..
17.....	4	4	..	..	..	..	..	3	..
18.....	..	..	..	..	..	..	1	..	..
19.....	4	4	..	..	..	..	..	4	..
Total...	52	44	9	8	13	4	7	26	8
Per cent..	..	84.6%	..	88.8%	31.7%	8.8%	36.8%	59.0%	100%

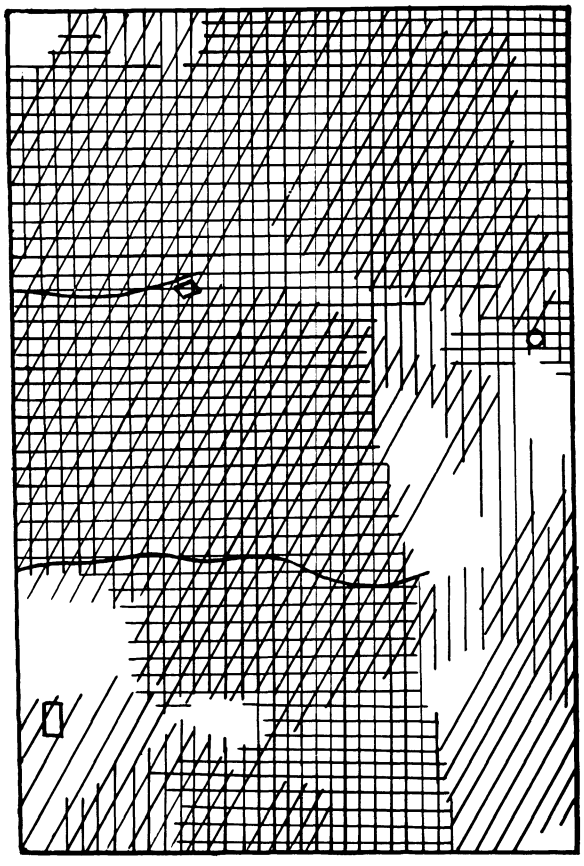


FIG. 10. Vegetation and territory maps. A composite of all nesting territories in the elm-maple forest. Horizontal lines indicate the area covered by territories of birds nesting on the ground and in low shrubs. Oblique lines indicate the area covered by territories of birds nesting in tree trunks. Vertical lines indicate the area covered by territories of birds nesting in high shrubs and the forest canopy. Compare with Figs. 1, 6 to 9. Note avoidance of the climax.

one gram which, in the first day or two, represents an increase of one-half their body weight. Great numbers of insects must be consumed each day to effect this gain. The amount of food eaten by a family of four young buntings during a 12-hour day between 6 A.M. and 6 P.M. was estimated. One or the other of the parent birds brought an average of five insects to the nest every 15 minutes, making a total of 60 insects for each young bird per day, or 960 insects from the time of hatching until leaving the nest. For the 26 buntings that successfully left their nests in 1934 and the 25 in 1935, the consumption for each year totaled roughly 25,000 insects taken from 2.53 hectares (6.25 acres) during the time spent in the nests.

In 1934, three nests of the wood thrush, containing four eggs each, were located (Table 5). A cowbird's egg was found in nest 1 the first day after the thrush had finished laying, but the whole complement of eggs was destroyed by bronzed grackles after the tenth day of incubation. Nest 2 contained four thrush eggs and one cowbird egg. One thrush egg and the cowbird egg failed to hatch. The three young thrushes were successfully raised. All of the eggs in nest 3 hatched and left the nest. During this season 58.3% of the young left the nest successfully, while 33.3% were destroyed by bronzed grackles. Since only three nests are represented, the percentage values should be regarded only as relative values.

Again in 1935 only three pairs of wood thrushes nested in the forest (Table 5). Nests 1 and 3 contained four eggs each, which were successfully hatched and raised. Nest 2 contained three thrush eggs and one cowbird egg. All were hatched and raised. Since the nest was not overcrowded, and the cowbird young was nearly the same size as the thrush young at hatching, all developed at the same rate and left the nest together on the 13th day. The low mortality may be attributed to the larger size of the nest, the fact that it is less exposed than the nests of the forest-edge birds, and to the more seclusive habits of the thrushes.

Eight red-eyed vireo nests were studied in 1934 and four in 1935. The nests were from one to five meters from the ground and always in the dense foliage of pawpaw or young basswood. Nidification began during the first week of June, and by the middle of the month, all of the nests contained eggs. In 1934, there

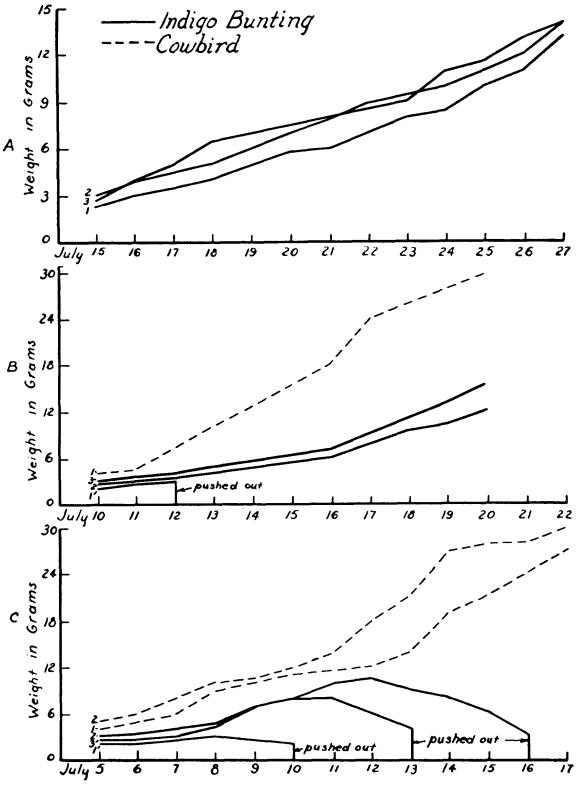


FIG. 11. Growth curves of nestlings. a. Three indigo buntings in normal development. b. The effect of one cowbird in a nest of three indigo buntings. c. The effect of two cowbirds in a nest of three indigo buntings.

were 24 eggs laid in the eight nests with an average of three per nest. Almost as soon as the vireos started to lay, cowbirds deposited eight eggs in six of the nests (Table 6). The eggs began hatching by June 28 in both years. Immediately after the hatching of the last bird, both adults fed the young, displaying no discrimination between their own progeny and those of the cowbirds. Throughout the entire feeding of the young, an insect diet consisting of large numbers of Arachnida, larval and adult Lepidoptera, assassin-bugs, tree hoppers, and chinch-bugs was administered. Stomach analyses revealed that the adults consumed the same kind of food that they fed their young. Herrick (1901) reported that a female was observed feeding raspberries and blackberries to the young on the third day after hatching. The vireos studied by the author were never noticed feeding the young any form of vegetable food.

TABLE 5. Nesting statistics of the wood thrush, 1934 and 1935.

1934

Nest	Number eggs	Eggs hatched	Number Cowbird eggs	Eggs destroyed by grackles	Cowbirds hatched	Thrushes successfully left nest	Cowbirds successfully left nest
1.....	4	0	1	4	0	0	0
2.....	4	3	1	0	0	3	0
3.....	4	4	0	0	0	4	0
Total..	12	7	2	4	0	7	0
		58.3%		33.3%		100%	

1935

Nest	Number eggs	Eggs hatched	Number Cowbird eggs	Cowbirds hatched	Successful Thrushes	Successful Cowbirds
1.....	4	4	0	0	4	0
2.....	3	3	1	1	3	1
3.....	4	4	0	0	4	0
Total...	11	11	1	1	11	1
		100%		100%	100%	100%

Of the 24 vireo eggs, 66 per cent hatched, and of these, 81 per cent of the young birds left the nest (Table 6). On the other hand, 75 per cent of the cowbird eggs hatched, and of these, 100 per cent left the nest. Eighteen per cent of the vireos that hatched were pushed out of the nest by young cowbirds. One vireo nest was deserted.

In 1935 there was a drop in the nesting population; only four pairs of vireos built nests and raised young. Of the 15 eggs laid, 86.6 per cent hatched, but only 53.8 per cent of these left the nest. Cowbirds parasitized all four nests with 100 per cent hatching and 80 per cent of the young leaving the nest. A total of 46 per cent of the red-eyed vireos were directly destroyed through eviction from their nests by the larger cowbird young.

Predation by the cowbird, and to a limited degree,

TABLE 6. Nesting statistics of the red-eyed vireo, 1934.

1934

Nest Number	Vireo eggs laid	Vireo eggs hatched	Cowbird eggs laid	Cowbird eggs hatched	Vireo nests deserted	Young Vireos destroyed by Cowbirds	Vireos that were successfully raised	Cowbirds that were successfully raised
1.....	2	1	2	2	..	..	1	2
2.....	4	3	1	1	..	1	2	1
3.....	3	3	1	0	..	..	3	0
4.....	1	1	2	1	..	1	0	1
5.....	4	0	..	..	1	..	..	..
6.....	2	2	1	1	..	..	2	1
7.....	3	2	1	1	..	1	1	1
8.....	5	4	..	..	..	..	4	..
Total.....	24	16	8	6	1	3	13	6
Percent....	..	66%	..	75%	12.5%	18%	81%	100%

1935

Nest Number	Vireo eggs laid	Vireo eggs hatched	Cowbird eggs laid	Cowbird eggs hatched	Young Vireos destroyed by Cowbirds	Vireos that were successfully raised	Cowbirds that were successfully raised
1.....	4	4	1	1	2	2	1
2.....	5	4	1	1	1	3	1
3.....	3	2	2	2	2	0	1
4.....	3	3	1	1	1	2	1
Total.....	15	13	5	5	6	7	4
Percent...	..	86.6%	..	100%	46%	53.8%	80%

by the domestic house cat and bronzed grackle, was considered to be the primary cause adversely affecting the ultimate success of the passerine fledglings under discussion. Kendeigh (1942) made an analysis of a large number of nesting birds. He regarded a nesting attempt to be successful when at least one bird was raised to the point of leaving the nest, regardless of the other young or eggs. Throughout the territorial studies reported in the present paper, the number of nests for each species observed was relatively small so that only percentage values of species chosen for nesting statistics can be compared with those noted by Kendeigh (Table 7).

TABLE 7. Comparison of nesting success 1934-1935 with 1942.

Species	Elm-Maple Forest		Kendeigh (1942)	
	Number Nests	Percent Success	Number Nests	Percent Success
Red-eyed Vireo	12	75	13	62
Wood Thrush	6	83	16	73
Indigo Bunting	41	43.9	..	..
Bluebird	..	..	142	60
Starling	..	..	21	76
Cardinal	..	..	11	82
Crested Flycatcher	..	..	7	43

These "successes" are naturally subject to variable environmental factors so that any such set of figures must be very critically examined before any semblance of a conclusion can be drawn. An undisturbed community would undoubtedly afford an ample food supply, more cover, and predation would be at a relatively uniform level. Nice (1937) states that in normal years when there is adequate cover and food, the song sparrow population had a high percentage survival rate for nestlings, and predation was at a minimum. In adverse years when survival rate was very low, the decrease was directly accountable to the disturbance of the nesting territory by man, or in some years, by drought or flooding. The unfavorable years were always accompanied by a decrease in available shelter and food supply and an increase in predation. In his study of 1,056 nests of the house wren, Kendeigh (1942) found that the average percentage of eggs which failed to hatch is constant within the temperature range of 58°-70° F. A drop or rise of temperature beyond this range brought about a rise in the percentage of eggs that did not hatch. These observations strongly emphasize the critical effect of temperature and to some extent, humidity, upon the optimum of environmental factors necessary for the survival of a species (Twomey, 1936).

POPULATION DENSITY AND CARRYING CAPACITY

The most suitable method that I know for determining the population density of the woods during the breeding season is to count nesting species and note their territories. Williams (1936) also found this procedure satisfactory. Table 2 shows the nesting population density of the elm-maple forest. During the years 1934 and 1935, there was little difference in the total number of nesting pairs; in 1934 there were 0.3 hectares per pair, and in 1935, 0.32 hectares per pair. The territories were stratified into layer societies but did not cover the total area of each community. In each society there were species limitations (structural adaptations) as well as such environmental limitations as wind velocity, temperature, exposure of nesting sites, cover, food supply, predation, etc., with respect to the amount of available territory.

The distribution of the nesting population indicates an individual species selection of suitable territories. The comparative stability of the total population for each layer society gives some idea of the possible carrying capacity of the elm-maple forest during the nesting period. Errington & Hamerstrom (1936) refer to the winter carrying capacity of the northern bob-white *(Colinus virginianus virginianus)* ". . . as denoting the upper limit of survival possible in a given territory as it exists under the most favorable conditions." Carrying capacity, as applied to the elm-maple forest, designates the number of pairs per hectare of the total nesting population and is comparatively uniform from year to year. There is a normal survival and reproductive rate and no apparent overcrowding of available nesting territories or food ranges.

There are many factors that limit the carrying capacity of any given community. Wind velocity, temperature, exposure of nesting sites, cover, food supply, etc., affect the availability of suitable nesting sites within a community. Over 75% of the nesting territories were in the east two-thirds of the woods. The prevailing winds from the southwest may have been partly responsible for the decrease in nests in the west one-third of the forest. Kendeigh and Baldwin (1937) give the following factors that affect yearly abundance: "first, the number of adults at the beginning of the breeding season; second, the amount of reproduction, measured by the percentage increase in total number of individuals due to the raising of young during the breeding season; and third, the loss in number or mortality of adults and young from the breeding season of one year to the beginning of the breeding season of the next year."

Predation is also an important factor in controlling population densities. The predators in the woods were the barred owl, bronzed grackle, and domestic cat. Parasitism by the cowbird (which may be regarded as a form of predation) was effective in controlling the population increases, and nearly half the population in the forest felt the dint of this agency.

The avian population in the elm-maple forest is subject to great seasonal fluctuations. No two seasons are the same. A study covering a long period of time would, no doubt, bring out more clearly an average population density for each aspect, making it possible to ascertain a carrying capacity for each season of the year in the association.

DISCUSSION OF TERRITORIES

Birds as specialized influents of the elm-maple forest are distinct components of one or more layer societies (Fig. 3). The establishment and stabilization of territories in these layer societies during the mating season is a function of the environment that tends to distribute the population. In a community there is a limit to the area available for nests and territories of any one species of bird. This circumstance, because of cover, food and other factors, automatically sets a maximum population level.

The term "territory" is applied only in the sense of an area that is defended. This, in general, adheres to the concept of the majority of ornithologists who have studied this particular avian reaction. This action is a physiological response or an adjustment which tends to bring the influx of an avian population into the aspects of a biotic community. Previously the behavior of a species was based primarily on its positive reaction to the individuals of its own kind or other species and not as part of the biotic complex.

Defended territories were established about the newly constructed nests and around the singing posts of the males during the breeding season. It was not until the adult birds began feeding young at the nest that the full extent and limitations of each territory became significant in the community.

Territorial space within the community and the resulting apportioning of the food supply during the critical period of a bird's life history (from the beginning of the mating season until the young have left the nest and are able to take care of themselves) should be stressed. In her summary Nice (1933) deduces: "It must be that the food aspect of territory has been overemphasized, and that sex jealously in many cases plays a definite role." Sex jealousy is no doubt apparent in most cases, but may it not be a part of avian activities, the ultimate result of which brings with it stability within the community?

The size in hectares of individual territories is listed and compared with the number of hectares per pair of the total area for the two years (Table 2). It is significant to note that there were more nesting pairs in the woods in 1934 than in 1935. A decrease in the population in 1935 brought an increase in the average size of the individual territories. The stratification of the territories was apparent in the general distribution of the nesting pairs over the forest. There was only a slight overlapping of territories within the layer communities. Nice (1934) emphasized that the song sparrow *(Melospiza melodia beata)* would not allow overcrowding of its nesting territory. She wrote, ". . . each must have approximately two-thirds of an acre for his territory."

In the elm-maple forest there were other factors which affected territorial selection in the community. Figure 10 illustrates a composite of all the nesting territories. Scattered climax areas within the forest were relatively free of nesting territories. The principal nesting population was confined to the late subclimax and forest edge, which afforded more cover than the climax. Those territories falling within the climax belonged to woodpeckers and nuthatches, species that characterized the tree-trunk society. These same species, however, tended to show a feeding preference for the developmental stages of the community.

Each species showed individual variations in choice of territories and subsequent nesting activities. The indigo bunting had territories only insofar as the actual nesting site was concerned, and the breeding population roamed over a common feeding range. The same was true of the wood thrush although it did not show the social tendencies of the indigo bunting. Starlings had limited territories about the nest and had a feeding range that extended beyond the limits of the forest. Birds that defended a feeding range as a part of their territory exhibited a positive reaction against members of the same species. Other species were tolerated over the feeding part of the territory, but under no circumstance were they allowed to approach the actual nesting site.

The population density for the elm-maple forest in 1934 was 0.3 hectares (0.74 acres) per pair and 0.32 hectares (0.79 acres) per pair in 1935 (Table 2), which shows a relative stability in the avian population with the community during the nesting period.

There were both species and environmental limitations in each society in regard to the amount of available territory. Such limitations were: the structural adaptations of species, wind velocity, temperature, exposure of nesting sites, cover, food supply, etc.

Predation was effective in controlling the yearly population increase as well as being a limiting factor on the nesting population.

REACTIONS AND COACTIONS

The final result of a study of a biotic community is an understanding of the ultimate cause and effect that organisms have upon a habitat and the influence which they exert upon each other. The first is termed a "reaction," while the latter is called a "coaction." The complexity of these interactions in many instances tends to overshadow any individual effect, but through the accumulation of these reactions and coactions, the community emphasizes influences that would otherwise be insignificant.

REACTIONS

Reactions exhibited by terrestrial communities are diminished by the effects exerted upon the soil complex and those that modify aerial factors. Because of the relative protection of the forest from wind, the resulting reaction in the accumulation of falling organic material such as leaves, trees, herbaceous and shrub litter, animal remains, excrement and, to a limited degree, owl pellets, share in the formation of soil.

Reactions by disturbing soil are accumulative in a community. The scratching of the forest floor by robins, starlings, titmice, cardinals, sparrows, and juncos are reactions induced by food coactions. The effect produced by these small passerine birds was

not always noticeable, but, nevertheless, during the late hiemal aspect, large flocks of robins, by their scratching reactions, caused an appreciable turn-over of the forest-floor duff. Likewise, the digging of fox squirrels to store acorns, the innumerable mouse and mole tunnels through the upper foot of the forest floor and the extensive burrowings of earthworms and other invertebrate types all add up to a series of reactions resulting in aeration, decomposition, and ultimate accumulation of forest floor soil.

In discussing air reactions, Clements & Shelford (1939: 91) state: "From the very nature of the medium, the reactions of plants upon the air are usually less definite and controlling than upon the soil. Naturally, the chief reason for this lies in the fact that effects are not readily accumulated in a gaseous medium. However, a notable exception exists in respect to light, in which the time element produces results not unlike those of accumulation. The absence of air reactions by animals is noteworthy since the functions that produce their striking reactions in water are almost without effect on land."

The role of reaction in terrestrial communities is primarily that of the directive function in the succession or competition in the development of the habitat. In the early seral stages, plant reaction brings the establishment of invaders. Succession in a sense is but a series of progressive reactions by which communities succeed each other in such a fashion that only those in closest harmony with the climate will survive. Thus one seral habitat will follow another until the ultimate habitat, the climax, is reached and will become permanent for as long as the climate concerned persists.

FOOD COACTIONS

The food coactions of birds of the elm-maple forest are exemplified in Table 8. On a yearly basis the bird population of the associes was found to be 70% insectivorous and 30% vegetarian. The seasonal variation of the diet is the most outstanding feature. It explains many of the local movements of the birds within the community (discussed earlier) and also the role played by birds as influent coactors, whether seasonal or perennial, in the community.

The vernal aspect is one of great fluctuation and change throughout the whole community. This trend is shown in the food coactions. The indigo bunting, cardinal, red-headed woodpecker, white-breasted nuthatch, starling, tufted titmouse, and cowbird show a preference for vegetable matter to the extent of 20 to 60% of their total diets; the remainder is composed of miscellaneous insects of which Coleoptera and Diptera predominate. On the other hand, such insectivorous birds as the red-eyed vireo, wood pewee, and crested flycatcher, along with the wood thrush, which is almost wholly insectivorous, feed on a variety of species, but show a choice for the abundant vernal insects; i.e., Coleoptera and Diptera.

The vernal and autumnal aspects are comparable in that they both show great fluctuation in their respective animal populations. Avian migration occurs during both periods and correlates with seasonal rhythms. In the autumnal period the coactions of the insectivorous birds are directed to the selection of the most abundant seasonal types of insects, which include Lepidoptera, Coleoptera, Diptera, and Hymenoptera. The indigo bunting, wood thrush, cardinal, red-headed woodpecker, white-breasted nuthatch, starling, tufted titmouse, and cowbird show a reversal in their food coactions during the autumnal aspect by feeding on the abundant wild fruits and seeds.

The aestival aspect is marked by greater food selection with reference to individual species and to their relative stability within a community. It is

TABLE 8. Food coactions in the elm-maple forest and its margins. The figures are in % of total individuals for insect groups for the season shown. Stomach contents analyses by Lucile A. Rice.

Species	Number of Stomachs	VERNAL						AESTIVAL							AUTUMNAL								HIEMAL					
		Vegetable	Lepidoptera	Coleoptera	Hemiptera	Diptera	Miscellaneous	Lepidoptera	Coleoptera	Hemiptera	Diptera	Hymenoptera	Orthoptera	Homoptera	Miscellaneous	Lepidoptera	Coleoptera	Hemiptera	Diptera	Hymenoptera	Orthoptera	Homoptera	Vegetable	Miscellaneous	Coleoptera	Lepidoptera	Homoptera	Mice and shrew	Vegetable	Miscellaneous
Indigo Bunting	10	15	25	20	...	40	...	50	10	5	20	5	1	9	...	20	30	...	...	...	40	...	10							
Wood Thrush	6	2	15	16	20	10	37	30	...	10	15	10	...	15	20	15	30	10	5	...	10	...	30							
Maryland Yellow-throat	5	2	...	40	15	10	35	40	30	...	15	...	10	...	5	15	20	5	10	5	20	25								
Cardinal	8	50	...	20	...	...	30	35	20	10	...	...	5	...	30	5	30	...	...	...	...	...	60	5	5	...	...	...	90	5
Red-eyed Vireo	6	...	15	25	10	25	25	50	...	...	20	15	...	2	13	20	15	10	20	15	...	15	...	5						
Wood Pewee	4	...	5	10	...	35	50	15	...	...	40	25	10	...	10	10	20	...	50	20										
Downy Woodpecker	8	...	...	70	...	...	30	15	50	...	...	5	...	...	30	...	90	...	...	...	...	10	...	...	80	...	8	...	2	10
Red-headed Woodpecker	6	50	...	15	...	...	35	35	20	...	10	10	...	...	25	...	15	...	5	25	10	...	45	...	20	...	...	...	70	10
White-breasted Nuthatch	7	50	20	10	...	10	10	25	10	...	30	...	...	20	15	...	20	...	15	...	...	20	40	5	2	3	15	...	60	20
Barred Owl	30pl	(85% mice)						(75% mice, 10% birds)								(90% mice and shrew)									(95% mice and shrew)					
Starling	15	50	20	20	...	5	5	20	30	...	15	5	5	...	25	...	2	...	...	...	...	...	95	3	(absent)					
Tufted Titmouse	10	20	10	10	5	15	40	25	10	...	18	...	...	...	40	10	20	...	15	5	...	...	40	10	20	...	...	...	60	20
Crested Flycatcher	5	...	5	20	30	30	15	20	...	10	50	10	...	...	10	15	...	5	40	25	5	...	10							
Yellow-billed Cuckoo	10	...	...	...	...	...	...	80	2	...	10	5	...	...	3	70	5	10	...	5	10									
Ruby-throated Hummingbird	1	...	...	...	...	...	...	...	...	...	20	...	...	...	80															
Cowbird	4	60	10	...	...	...	30	...	...	...	...	...	...	...	...	...	9	...	...	...	...	...	81	10						

pl pellets.

characterized by territorial coactions (competition for suitable mates, nest building, and territorial space within the community for the care and feeding of the young as well as the adults) which illustrate the aestival community relationships of the Aves. This has been fully discussed in relation to territory and layer societies. The young are fed chiefly on the abundant soft-bodied types that contain a high water content such as Lepidoptera and Diptera. Table 8 shows that food selection is prevalent because 15 to 80% of the total food for both young and adults was composed of Lepidoptera and Diptera. It is interesting to note here that, in the analyses, vegetable material was lacking.

The hiemal aspect presents a distinct change in community relationships. All insect life is at a minimum in both activity and numbers. The avian population is likewise reduced to a few species such as the cardinal, red-headed woodpecker, white-breasted nuthatch, and tufted titmouse. These species reverse their food coactions to vegetable diets which are supplemented by only the most abundant and most easily found invertebrate types which include Coleoptera, Homoptera, miscellaneous Arachnida, millipeds, and centipedes. The downy woodpecker retains its food coactions by feeding exclusively upon invertebrates.

The barred owl was the only predator present throughout the year. Because of its role as a coactee in the check on the abundance of mice, shrews and, to a certain extent, on other birds, it may be regarded as a major perennial influent in the associes. Barred owl pellets were surprisingly few in number in any one place. But, because of their presence at various sections throughout the forest, one might be led to believe that their nightly hunting was accompanied by much activity. Roosting holes were used only for shelter during the daylight hours. The pellets in all cases showed that 95 per cent of the total food for the year was made up of the wood mouse, *Peromyscus leucopus noveboracensis* (Fischer), and the short-tailed shrew, *Blarina brevicauda* (Say). The discovery of indigo bunting and warbler feathers in the pellets (especially during May and June) may account for one or two disappearances of indigo bunting young. In all cases the nests were slightly torn, and the adults had vanished. Williams (1936) reported similar findings. Fisher (1893) recorded that the barred owl was also an eater of insects.

In an investigation of the food of several owls in central Illinois, Cahn & Kemp (1930) made a study of the barred owl pellets collected in Brownfield Woods, Illinois, and Turkey Run State Park, Indiana, during the winter of 1925. Brownfield Woods, which resembles Trelease Woods, lies one and one-half miles northwest of Trelease Woods and is also owned by the University of Illinois. Of the 58 pellets collected, 79 per cent of the total food consisted of mammals. *Microtus ochrogaster* (Wagner) (not found in the forest) and *Peromyscus leucopus noveboracensis* (Fischer) made up 55% of the total. The cottontail (*Sylvilagus floridanus mearnsii* (Allen)) contributed 15%, the northern gray squirrel (*Sciurus carolinensis leucotis* Gmelin) 6% and the opossum (*Didelphis virginiana* Kerr) 3%. Of the bird remains, the following were found in the pellets: woodpecker, 3%; eastern robin *(Turdus m. migratorius)* 6%; eastern crow *(Corvus b. brachyrhynchos)* 3%; eastern mourning dove *(Zenaidura macroura carolinensis)* 3%; and domestic fowl (remains in 5 pellets), 3%. The remaining 3% of the food was made up of the common leopard frog (*Rana pipiens* Schreber).

Stomach analyses of the birds under observation were compared with those reported by earlier investigators (Table 9). The food coactions for the total year had to be estimated since, in most cases, the contents of a large number of stomachs were given with no reference to time or place. A comparison with Table 8 shows a fairly uniform correspondence with the total yearly foods of the birds in question.

FOOD NEXES

The overlapping of nesting territories might engender the assumption that there is an appreciative amount of competition for suitable territories which provide food. Even within a given society, however, the apparent overlapping of territories did not necessarily bring about competition between species because of particular physiological adaptations. An example may be cited in the case of the downy woodpecker and the red-headed woodpecker. During the aestival period, the downy woodpeckers were most active in the smaller trees and high shrubs, and in the hiemal aspect, in the standing weed stalks. The red-headed woodpeckers visited the larger trees while in the forest, and on leaving, during the serotinal, autumnal and part of the hiemal period, invaded the surrounding fields, where they changed their coactive activities. They were seen, for instance, catching flying insects instead of working into trees for their food, bringing out the variation in physiological adaptations of two members of the same group.

The tufted titmouse was a competitive coactee of the white-breasted nuthatch and brown creeper during the hiemal period. Even then, the tufted titmouse used two hectares per individual, whereas the white-breasted nuthatch and brown creeper used only one hectare per individual.

The flycatchers were entirely insectivorous coactees in that they caught mostly flying insects. Their only competitors, and they were of little consequence because of the greater abundance of insects and other food during these periods, were some of the warblers, including the Myrtle warbler *(Dendroica coronata)*, redstart *(Setophaga ruticilla)* and others during the spring and fall migrations.

A general survey of the avian populations shows that each species belongs to an individual society, either a specific layer society during the nesting season or a more general community during the other seasons of the year—based on the abundance and availability of the food supply and upon the climatic factors, wind exposure, temperature and snow. By means of food charts, a comparison has been made of the aestival and hiemal food nexe.

Figure 12 clearly shows the dependency of the birds

TABLE 9. Some reports of stomach analyses in the literature.

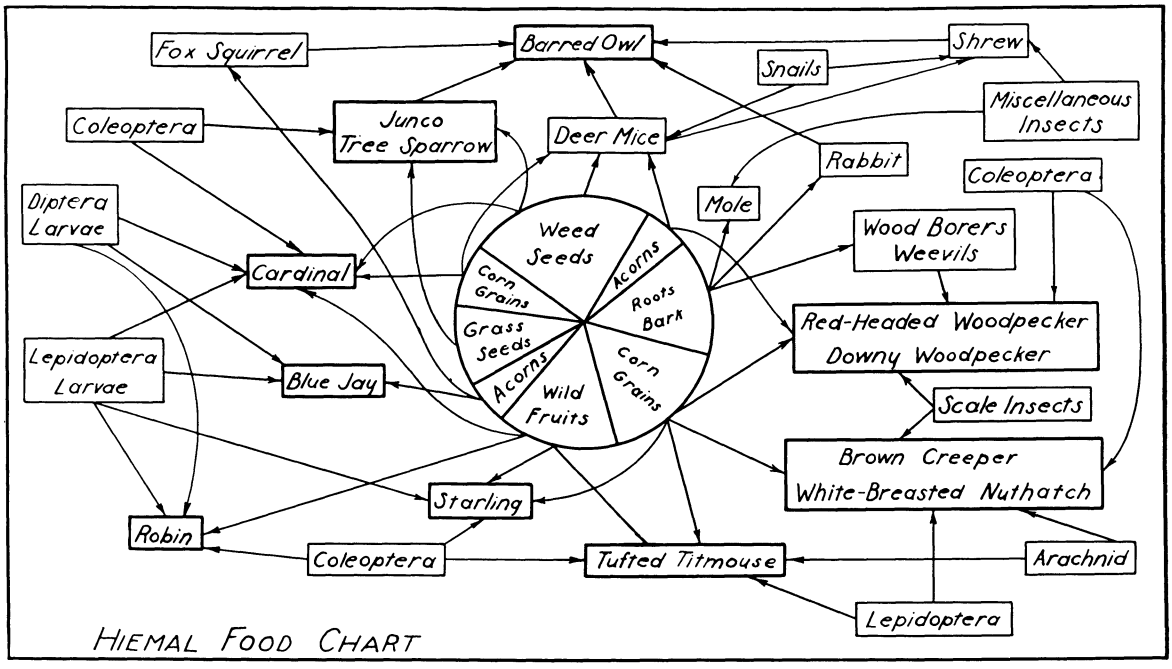
Species	Number of stomachs	General Yearly Food Percentage												Author
		Vegetable	Lepidoptera	Coleoptera	Hemiptera	Diptera	Hymenoptera	Orthoptera	Homoptera	Arachnida	Miscellaneous	Mice and Shrew	Birds	
Indigo Bunting	18	.....	67	29	.....	.....	trace	.....	.....	.....	.....	.....	.....	Forbes 1883
Wood Thrush	41	64	12	17	3	trace	9	trace	.....	.....	.....	.....	.....	Henderson 1927
Maryland Yellow-Throat	3	.....	80	8	5	4	.....	.....	.....	.....	.....	.....	.....	Forbes 1883
Cardinal	498	71	5	10	4	.....	.9	6	.....	.....	.....	.....	.....	Henderson 1927
Red-eyed Vireo	569	14	32	.....	15	.....	10	.....	.....	.....	28	.....	.....	Henderson 1927
Wood Pewee	359	1	12	14	5	29	28	3	.....	2	2	.....	.....	Henderson 1927
Downy Woodpecker	723	13	.....	30	.....	.....	21	.....	.....	.....	26	.....	.....	Henderson 1927
Red-headed Woodpecker	443	66	.....	20	.....	.....	6	3	.....	.....	.....	.....	.....	Henderson 1927
White-breasted Nuthatch	34	41	.....	.....	.....	.....	.....	.....	.....	.....	52	.....	.....	Henderson 1927
Barred Owl	.....	.....	(24	other	mam	als)	.....	.....	.....	.....	.....	55	18	Cahn 1930
Starling	2157	43	.....	.....	.....	.....	.....	.....	.....	.....	57	.....	.....	Henderson 1927
Tufted Titmouse	?	34	(sum	mer d	iet)	.....	.....	.....	.....	.....	67	.....	.....	Gillespie 1930
Crested Flycatcher	265	6	21	16	.....	.....	2	15	.....	.....	39	.....	.....	Henderson 1927
Yellow-billed Cuckoo	155	.....	50	.....	.....	.....	.....	.....	.....	.....	50	.....	.....	Weed and Dearborn 1903
R. Throated Hummingbird	59	6	(94	% an	imal)	.....	.....	.....	.....	.....	.....	.....	.....	Henderson 1927
Cowbird	544	77	(23	% an	imal)	.....	.....	.....	.....	.....	.....	.....	.....	Henderson 1927

upon the plants within the community during the hiemal period. The invertebrates are, for the most part, in hibernation, or are wintering as eggs or larvae and are inactive. They are eaten principally by such birds as the robin, tufted titmouse, cardinal, and starling. These birds expose numerous hibernating adult and larval invertebrate types by scratching up the duff of the forest floor, creating a surface reaction that was initiated by a feeding coaction. The remaining groups, which include the woodpeckers, brown creepers and white-breasted nuthatches, glean Arachnida, scale insects, and Coleoptera from the surface of the trees; or as in the case of the woodpeckers, institute a reaction by digging into rotten wood—another instance of stimulation by a food coaction.

There is not sufficient invertebrate life in the hiemal period to warrant complete animal diets for the birds. As indicated in the hiemal food chart, all except the brown creeper (which is insectivorous) depend to a great extent upon plant materials. The junco and tree sparrow feed largely upon grass and weed seeds. Wild fruits and grains are eaten by the cardinal, robin, starling, tufted titmouse, and even the red-headed woodpecker and white-breasted nuthatch. These hiemal food coactions of birds are in part responsible for the sowing of such plants as trumpet weed, cherry, virginia creeper, and many others that are early members of forest succession. Of the other coactees of the food chain, the fox squirrel, rabbit and deer mouse feed on bark, roots and acorns. These animals in turn undergo the predatory coaction of the barred owl.

The aestival food nexe illustrated in Figure 12 is almost a reversal of the hiemal food nexe. In the aestival period, the insects come out of hibernation and move to their separate niches in the community. The food of these various insect types is primarily plants and plant products. The mammals (rabbits, fox squirrels, and deer mice) feed on much the same plant materials during this period as they do during the hiemal period except for the addition of green leaves. As in the hiemal period, these animals are preyed upon by the barred owl. The insects utilize the plants as their chief source of food: lepidopterous larvae live on the green leaves; Diptera, Homoptera, and Hymenoptera find food in the leaves, sap, and juices of plants and flowers; Coleoptera feed chiefly on dead organic decay, leaves and also on other insect types. Birds, in turn, feed upon masses of insect forms, both adult and larval. The Maryland yellow-throat, red-eyed vireo, wood thrush, and tufted titmouse feed on the adults and larvae of Diptera, Lepidoptera, Homoptera, Coleoptera, Hymenoptera, and Arachnida. The downy woodpecker, red-headed woodpecker, and white-breasted nuthatch live on such forms as Lepidoptera, Diptera, and wood borers. The flycatchers concentrate on the flying types, mostly Diptera, Hemiptera, Orthoptera, and Coleoptera.

When studied from the seasonal aspect, the nexes within the community indicate a decided cycle. In the elm-maple associes, the avian population, as a whole, does not depend upon any one specialized type of food throughout the year, but rather it tends to choose the most abundant type, whether it be plant or animal. This adaptability of the birds to their food requirement is the factor which most easily explains the instability of an avian population. Fluctuations in numbers of the avian population are at times extreme; considerable fluctuation is exhibited even in the hiemal population. Avian population, then, must be considered as an important influent element which varies its effects on the community in accord with the seasonal phenomena.



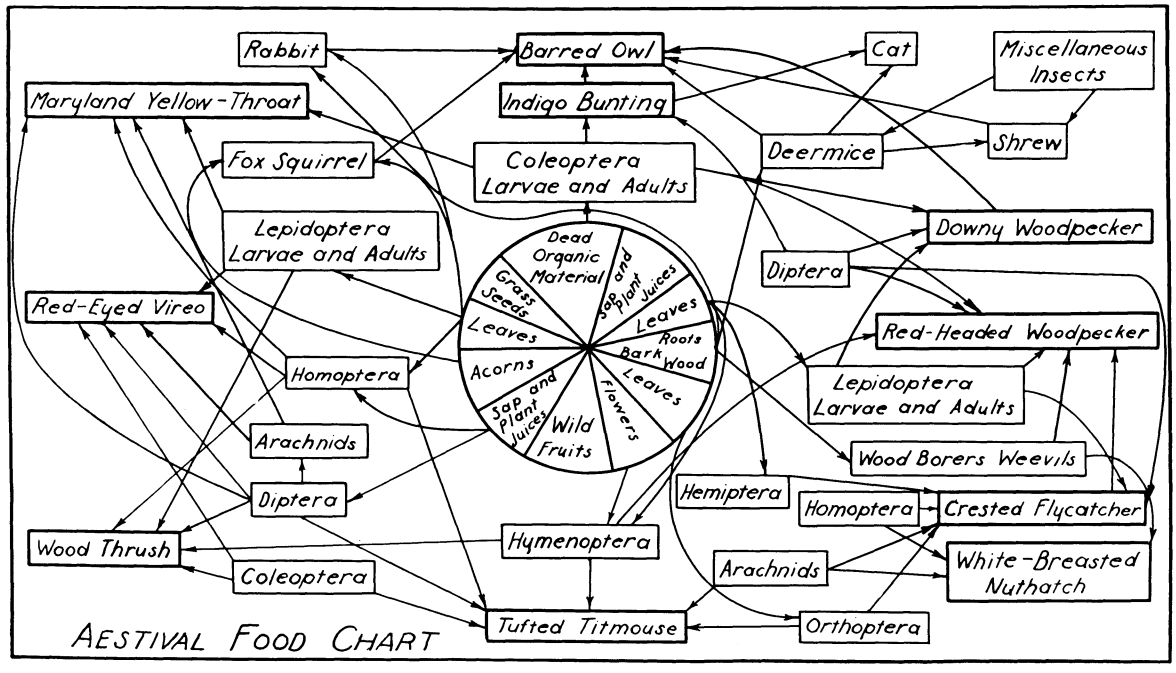


FIG. 12. Food cycle charts for hiemal and aestival periods.

SEASONAL LIST OF BIRDS

The common and scientific names and the order of listing are those adopted by the American Ornithologists' Union Check List of North American Birds, Fourth Edition, 1931. A total of 105 species were recorded for the elm-maple forest.

Perennial Residents

Eastern Bob-white.....*Colinus virginianus virginianus* (Linnaeus)
Northern Barred Owl.....*Strix varia varia* Barton
Northern Flicker.....*Colaptes auratus luteus* Bangs
Red-bellied Woodpecker...*Centurus carolinus* (Linnaeus)
Red-headed Woodpecker...*Melanerpes erythrocephalus* (Linnaeus)
Eastern Hairy Woodpecker.*Dryobates villosus villosus* (Linnaeus)
Northern Downy Woodpecker.....*Dryobates pubescens medianus* (Swainson)
Northern Blue Jay.....*Cyanocitta cristata cristata* (Linnaeus)
Eastern Crow.....*Corvus brachyrhynchos brachyrhynchos* Brehm
Tufted Titmouse.....*Baeolophus bicolor* (Linnaeus)
White-breasted Nuthatch..*Sitta carolinensis carolinensis* Latham
Carolina Wren.....*Thryothorus ludovicianus ludovicianus* (Latham)

Starling ..... *Sturnus vulgaris vulgaris* Linnaeus
Eastern Cardinal ..... *Richmondena cardinalis cardinalis* (Linnaeus)
Red-eyed Towhee ..... *Pipilo erythrophthalmus erythrophthalmus* (Linnaeus)

Hiemal Residents

Eastern Red-tailed Hawk .. *Buteo borealis borealis* (Gmelin)
Northern Red-shouldered Hawk ..... *Buteo lineatus lineatus* (Gmelin)
American Rough-legged Hawk ..... *Buteo lagopus s.johannis* (Gmelin)
Ring-necked Pheasant ..... *Phasianus colchicus torquatus* Gmelin
Northern Blue Jay ..... *Cynaocitta cristata cristata* (Linnaeus)
Brown Creeper ..... *Certhia familiaris americana* Bonaparte
Winter Wren ..... *Nannus hiemalis hiemalis* (Vieillot)
Eastern Robbin ..... *Turdus migratorius migratorius* Linnaeus
Eastern Golden-crowned Kinglet ..... *Regulus satrapa satrapa* Lichtenstein
Eastern Goldfinch ..... *Spinus tristis tristis* (Linnaeus)
Slate-colored Junco ..... *Junco hyemalis hyemalis* (Linnaeus)
Eastern Tree Sparrow ..... *Spizella arborea arborea* (Wilson)
Eastern Song Sparrow ..... *Melospiza melodia melodia* (Wilson)

Seasonal Migrants

Sharp-shinned Hawk ..... *Accipiter velox velox* (Wilson)
Broad-winged Hawk ..... *Buteo platypterus platypterus* (Vieillot)
Eastern Pigeon Hawk ..... *Falco columbarius columbarius* Linnaeus
Eastern Sparrow Hawk .... *Falco sparverius sparverius* Linnaeus
Yellow-bellied Sapsucker ... *Sphyrapicus varius varius* (Linnaeus)
Yellow-bellied Flycatcher .. *Empidonax flaviventris* (Baird and Baird)
Eastern Hermit Thrush .... *Hylocichla guttata faxoni* Bangs and Penard
Olive-backed Thrush ..... *Hylocichla ustulata swainsoni* (Tschudi)
Gray-cheeked Thrush ..... *Hylocichla minima aliciae* (Baird)
Veery ..... *Hylocichla fuscescens fuscescens* (Stephens)
Eastern Ruby-crowned Kinglet ..... *Corthylio calendula calendula* (Linnaeus)
Yellow-throated Vireo ..... *Vireo flavifrons* Vieillot
Blue-headed Vireo ..... *Vireo solitatius solitarius* (Wilson)
Eastern Warbling Vireo .... *Vireo gilvus gilvus* (Vieillot)
Black and White Warbler .. *Mniotilta varia* (Linnaeus)
Prothonotary Warbler ..... *Protonotaria citrea* (Boddaert)
Golden-winged Warbler .... *Vermivora chrysoptera* (Linnaeus)
Orange-crowned Warbler ... *Vermivora celata celata* (Say)
Nashville Warbler ..... *Vermivora ruficapilla ruficapilla* (Wilson)
Eastern Yellow Warbler ... *Dendroica aestiva aestiva* (Gmelin)
Magnolia Warbler ..... *Dendroica magnolia* (Wilson)
Cape May Warbler ..... *Dendroica tigrina* (Gmelin)
Black-throated Blue Warbler ..... *Dendroica caerulescens caerulescens* (Gmelin)
Myrtle Warbler ..... *Dendroica coronata* (Linnaeus)
Black-throated Green Warbler ..... *Dendroica virens virens* (Gmelin)
Cerulean Warbler ..... *Dendroica cerulea* (Wilson)
Blackburnian Warbler ..... *Dendroica fusca* (Müller)
Chestnut-sided Warbler .... *Dendroica pensylvanica* (Linnaeus)
Bay-breasted Warbler ..... *Dendroica castanea* (Wilson)
Black-poll Warbler ..... *Dendroica striata* (Forster)
Oven-bird ..... *Seiurus aurocapillus* (Linnaeus)
Northern Water-Thrush ... *Seiurus noveboracensis noveboracensis* (Gmelin)
Louisiana Water-Thrush ... *Seiurus motacilla* (Vieillot)
Connecticut Warbler ..... *Oporornis agilis* (Wilson)
Northern Yellow-throat .... *Geothlypis trichas brachidactyla* (Swainson)
Wilson's Warbler ..... *Wilsonia pusilla pusilla* (Wilson)
Canada Warbler ..... *Wilsonia canadensis* (Linnaeus)
American Redstart ..... *Setophaga ruticilla* (Linnaeus)
Eastern Red-wing ..... *Agelaius phoeniceus phoeniceus* (Linnaeus)
Baltimore Oriole ..... *Icterus galbula* (Linnaeus)
Rusty Blackbird ..... *Euphagus carolinus* (Müller)
Scarlet Tanager ..... *Piranga erythromelas* Vieillot
Rose-breasted Grosbeak .... *Hedymeles ludovicianus* (Linnaeus)
Eastern Purple Finch ..... *Carpodacus purpureus purpureus* (Gmelin)
Eastern Chipping Sparrow . *Spizella passerina passerina* (Bechstein)
White-crowned Sparrow ... *Zonotrichia leucophrys leucophrys* (Forster)
Gambel's Sparrow ..... *Zonotrichia leucophrys gambeli* (Nuttall)
White-throated Sparrow ... *Zonotrichia albicollis* (Gmelin)
Eastern Fox Sparrow ..... *Passerella iliaca iliaca* (Merrem)
Swamp Sparrow ..... *Melospiza georgiana* (Latham)

Aestival Residents

Eastern Mourning Dove ... *Zenaidura macroura carolinensis* (Linnaeus)
Yellow-billed Cuckoo ..... *Coccyzus americanus americanus* (Linnaeus)
Black-billed Cuckoo ..... *Coccyzus erythropthalmus* (Wilson)
Ruby-throated Hummingbird ..... *Archilochus colubris* (Linnaeus)
Northern Crested Flycatcher ..... *Myiarchus crinitus boreus* Bangs
Eastern Wood Pewee ..... *Myiochanes virens* (Linnaeus)
Wood Thrush ..... *Hylocichla mustelina* (Gmelin)
Red-eyed Vireo ..... *Vireo olivaceus* (Linnaeus)
Maryland Yellow-throat ... *Geothlypis trichas trichas* (Linnaeus)
Bronzed Grackle ..... *Quiscalus quiscula aeneus* Ridgway
Eastern Cowbird ..... *Molothrus ater ater* (Boddaert)
Indigo Bunting ..... *Passerina cyanea* (Linnaeus)
Dickcissel ..... *Spiza americana* (Gmelin)

Incidental Visitors

Great Blue Heron ..... *Ardea herodias herodias* Linnaeus
Eastern Green Heron ..... *Butorides virescens virescens* (Linnaeus)
Black-crowned Night Heron ..... *Nycticorax nycticorax hoactli* (Gmelin)
Cooper's Hawk ..... *Acanthis linaria linaria* (Linnaeus)
King Rail ..... *Rallus elegans elegans* Audubon
Virginia Rail ..... *Rallus limicola limicola* Vieillot
Sora ..... *Porzana carolina* (Linnaeus)
American Woodcock ..... *Philohela minor* (Gmelin)
Eastern Whip-poor-will .... *Antrostomus vociferus vociferus* Wilson
Eastern Nighthawk ..... *Chordeiles minor minor* (Forster)
Chimney Swift ..... *Chaetura pelagica* (Linnaeus)
Purple Martin ..... *Progne subis subis* (Linnaeus)
Carolina Chickadee ..... *Penthestes carolinensis carolinensis* (Audubon)
Common Redpoll ..... *Acanthis linaria linaria* (Linnaeus)

SUMMARY AND CONCLUSIONS

1. The birds of the elm-maple associes were characterized by continuous fluctuations in numbers throughout the various aspects of the community.

2. The vernal and autumnal peaks corresponded with the two main insect peaks. These maximum levels were reached during 1934 and 1935 when the average mean daily temperature registered 59 to 61° F.

3. The local movements of the birds in the community from forest to forest edge were in part caused by changes in weather factors, such as prevailing winds and temperature. These local movements were most pronounced during the hiemal period, when cold west or southwest winds drove the birds to the east forest edge for protection. On the other hand, the appearance of insects that had been hibernating on the surface of the ground layer during warm periods stimulated variable movements in the bird populations.

4. The aestival aspect was one of comparative stability of the nesting population. It was marked by territorial coactions—competition for suitable mates, nest building and territorial space within the community for the care and feeding of the young as well as for the adults.

5. The methods of censusing (cruising and sampling) were on a quantitative basis, and the results, other than for the breeding season, are relative in

character. There was considerable movement from place to place and some birds were doubtless counted more than once during a particular censusing operation.

6. There were vertical limitations of territories to layer societies of shrubs, trees, etc., as well as horizontal limitations within a layer society.

7. There is a limitation as to available sites within a layer society depending upon the structural adaptations of the species and the physical habitat.

8. The climax association had few nesting species. The major nesting population was confined to the developmental communities.

9. The population density for the nesting species was 0.3 hectares (0.74 acres) per pair in 1934 and 0.32 hectares (0.79 acres) per pair in 1935.

10. The coactive activity of the birds within the community was found to change with the seasonal aspects. The most abundant insect and plant foods of each aspect were selected by the birds (Table 8).

11. There was a reversal of the food nexes of the aestival and hiemal periods (Fig. 12).

12. The avian population is an important influent element which varies its effects on the community in accord with the seasonal phenomena.

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