Owing to my removal to central Nebraska the year following the storm, I was unable to make further observations to determine the rate at which the habitat was refilled.

SUMMARY

In western Iowa, the small town of Portsmouth was struck by a tornado at 3 A. M. on July 9, 1940. An estimated 1000 birds were killed in the town's area of 100 acres, and, following the storm, 87 were found alive. The storm apparently killed over 90 per cent of the birds in the path of its vortex.

Birds least affected by the wind and torrential rain were those roosting in buildings or nesting in tree hollows. Only seven species appeared to have survived.

In the following summer months, Mourning Doves, Robins, Redheaded Woodpeckers, House Wrens, and English Sparrows continued their nesting activities.

During the last week of August, the bird population in an undisturbed similar habitat at Lewis, Iowa, was compared with that of Portsmouth. Excluding English Sparrows, which were numerous in both areas, the bird population per acre averaged 12.7 at Lewis and 0.53 at Portsmouth; that at Portsmouth was still only four per cent of normal.

These observations revealed the remarkable stability of established breeding-bird populations. The void created by a tornado was not filled by an influx of birds from undisturbed areas a few miles away.

Ord, Nebraska

COMMUNITY SELECTION BY BIRDS ON THE HELDERBERG PLATEAU OF NEW YORK

BY S. CHARLES KENDEIGH

INTRODUCTION

A QUESTION that repeatedly arises in the ecological analysis of an avifauna is why various species are either restricted to, or are more common in, certain communities than in others. On a broad geographic scale, barring physical barriers of one sort or another, species are often limited by climatic conditions which they are unable to tolerate (Kendeigh, 1934). When the boundaries of a species' range agree with those of an ecological community, this may be due to coincidence in limits of tolerance to extremes in environmental conditions by species and community, or it may be due to some obligatory relation

of the species to that particular community (Trotter, 1912; Pitelka, 1941; Peterson, 1942; Brecher, 1943). Within any region of restricted size the macro-climate is relatively uniform, although differences in micro-climate may still occur between different parts of a single community or between different communities. Local segregation of species into different communities may, in some cases, be in response to these differences in micro-climate, although the significance of these small differences in climate is often difficult to evaluate (Moreau, 1934). Oftentimes the restriction of a species to a community appears to depend upon the occurrence of a particular niche within the community that the species requires.' As Lack and Venables (1939) explain, "A species may be limited in its habitat distribution by various factors: food (e. g. crossbill), feeding habit (flycatchers), song post (blackcap), nesting site (hole-nesters), nest material (nightingale), and roosting place (pheasant)." In many cases, on the other hand, there is no very obvious reason for the limitation of the species to a certain community.

The present study attempts to analyze the restriction of breeding birds, especially warblers, to various biotic communities in a sere that develops in abandoned fields on the Helderberg Plateau of New York. The work was centered at the Edmund Niles Huyck Preserve at Rensselaerville, about 30 miles southwest of Albany, during the summers of 1942, 1943, and 1944. This paper also includes some observations made by Dr. Eugene P. Odum for the two preceding years at the Preserve. Considerable literature was reviewed for compiling the information on nesting requirements of each species, but only those references actually cited are included in the bibliography.

Four distinct communities are recognized in this sere in abandoned fields: grassy fields, mixed shrubs and small trees, hemlock-beech, and beech-sugar maple-hemlock. Probably the last community is the ultimate climatic climax. This is a predominantly deciduous forest in which beech (Fagus grandifolia) and sugar maple (Acer saccharum) are particularly important and where there are only scattered hemlocks (Tsuga canadensis) present. The hemlock-beech community is predominantly evergreen in character, as the beech and yellow birch (Betula lutea) that occur along with hemlock are few and scattered. The composition of the avifauna was determined for each community and the size of the breeding bird population was measured for each of the last three communities. A similar study of grassland birds had previously been done in northwestern Iowa (Kendeigh, 1941).

The segregation of species into one or another community is not absolute as the communities are themselves not sharply delimited. Some birds follow isolated shrubby plants into otherwise grassy

fields, forest species penetrate into the older stages of the mixed shrub and small tree community, likewise shrub-inhabiting species regularly occur on the forest-edge, and finally the evergreen forest contains some deciduous trees and vice versa. When the same species occurs in two or more communities, it may not be equally abundant in each so that its more favored position is indicated. In analyzing the factors involved in community selection by birds, the difficulty is experienced that much of the evidence is intangible, obscure, inferential, and not subject to experimental proof at the present time. It is worth while, however, to marshall the evidence, such as it is, in hopes that the analysis may suggest a more objective approach in future studies.

GENERAL FEATURES

Grassland.—The characteristic species of the grassland community nest and feed on the ground: Vesper Sparrow (Pooecetes gramineus), Grasshopper Sparrow (Ammodramus savannarum), Bobolink (Dolichonyx oryzivorus), Meadowlark (Sturnella magna), Killdeer (Charadrius vociferus). Although most of these species may use elevated perches for singing, these perches are not required, as the birds commonly sing from the ground or from tall stalks of herbaceous plants. The Meadowlark, Bobolink, and Killdeer also have songs or calls that they give while in flight which are of aid to them in establishing territories or advertising for mates. When shrubs and trees invade the grassland, these species disappear.

Mixed Shrubs and Small Trees.—The bird's mores in the shrub and small tree community are as heterogeneous as is its species composition of plants and animals. The Yellow-throat is perhaps the least dependent on shrubs or trees as it feeds and nests in dense grass, herbs, or briers, and may sing from the ground or in flight. However, when shrubs are available it often makes use of them for these various purposes. The Towhee (*Pipilo erythrophthalmus*) also nests and feeds on the ground but requires shrubs or trees from which to sing and as a refuge from danger. The Chestnut-sided Warbler, Song Sparrow (*Melospiza melodia*), Field Sparrow (*Spizella pusilla*), and Catbird (*Dumetella carolinensis*) are outstanding in their dependence on shrubs, while most of the other species in this community use trees or tall shrubs indiscriminately.

Two things that birds in grassy fields, shrubs, and scattered trees have in common are large open spaces for flight and other activities and frequent exposure to the sun. Nests of all species, even those that occur on the ground, are ordinarily concealed in partial or complete shade, but other activities of the birds may be carried on under maximum light exposure. In this they differ from forest birds which spend more or less of their time under the canopy of trees, are more restricted in their flight, and are less exposed to the sun during the breeding season. Laboratory experimentation will be required to determine whether there is actually any difference in toleration to solar radiation and upon what physiological property it is based.

Forest.—The chief differences between the two types of forests above mentioned are at least four-fold. (1) The hemlock forest is everyreen, retaining its foliage and casting its deep shade throughout the year, in contrast with the deciduous forest where the light intensity within the forest changes drastically with the seasons. However, at the time that most of the forest inhabitants arrive in May, the deciduous forest is well on its way toward renewal of its foliage, so that the two forests become more nearly comparable in this respect. Furthermore, those species that nest earlier in the spring when the light differences are most pronounced, such as the Black-capped Chickadee (Parus atricapillus), White-breasted Nuthatch (Sitta carolinensis), Hairy Woodpecker (Dryobates villosus), Pileated Woodpecker (Ceophloeus pileatus), Blue Jay (Cyanocitta cristata), and Great Horned Owl (Bubo virginianus) are among those that occur with nearly equal abundance in the two forests.

(2) Another difference is the matter of food. Many forest birds are largely insectivorous during the breeding season. There are differences in species of insects found in deciduous and evergreen forests, although there is a decided ecological similarity between them and some of them belong to the same family (Blake, 1926). Modern concepts (McAtee, 1932) emphasize that birds mostly obtain their food from that which is most accessible to them, of the type that they require, without regard to species, so it is doubtful if limitation of birds to communities can be satisfactorily explained by the species of food organisms available. Seed-eating sparrows, however, are more often found in grassy and shrubby fields, where their type of food is abundant than in forests.

(3) There is a difference between deciduous and evergreen forests in the ground-covering that affects the food supply and location of nests of those birds that occur on the ground. The broad leaves of deciduous trees decompose relatively fast and form a rich, loose humus, often with an abundance of small animals. Needle leaves, when shed, turn brown and accumulate to form a thick compact layer on the ground that decomposes very slowly and contains fewer insects and other small animals useful for food (Blake, 1926).

(4) Finally, there is the difference in the size and arrangement of the leaves (Text-fig. 1). The hemlock leaves are short, needle-like,



TEXT-FIG. 1.—Difference in arrangement and size of leaves of hemlock and beech.

and arranged close together along the lateral sides of the small twigs. Deciduous trees have much larger leaves with broad surfaces from which food may be gleaned, and these leaves are suspended by means of petioles at greater intervals along the twigs.

Specific Nesting Requirements

THRUSHES.—Of the five thrushes found in the region, the Bluebird (Sialia sialis) and Robin (Turdus migratorius) are chiefly forest-edge species. The Veery (Hylocichla fuscescens) is also partial to the late shrub and early tree stage but penetrates the interior of both deciduous and mixed forests. One nest found of the Veery was on the ground well inside a beech-maple-yellow birch forest. The nest was made of broad leaves and rootlets. Another nest was in the fork of a small maple six inches above the ground, well within a maple-hemlock-beech wood. The nest was made of dried maple leaves. The Wood Thrush (Hylocichla mustelina) was found infrequently but in all instances was among deciduous trees, even in the hemlock-beech woods. However, this species will also nest in evergreen bogs (Root, 1942).

The Hermit Thrush (Hylocichla guttata) was recorded in equal abundance in the two types of forests, and this is reflected in its wide

[Auk July choice of situations for nesting. Peterson (1942) believes that it prefers mixed forests. Certainly the species is not averse to using deciduous as well as evergreen trees for song posts. One bird had a regular singing perch at the top of a dead tree projecting six feet above the canopy of a young maple forest and about 50 feet above the ground. Other males commonly sang, however, from much lower down, often in hemlocks only 15 feet from the ground. A nest described to me was on the ground in a patch of vew (*Taxus canadensis*) under hemlock. One nest found was in a clump of sedge under Labrador tea (Ledum groenlandicum) in a sphagnum bog. The nest was lined with pine needles. Another nest was in a partial opening surrounded by aspen, willow, and white pine (Pinus strobus). The nest was on the ground and made largely of moss with a lining of dried A fourth nest was placed on the ground near the center of the grass. hemlock-beech woods. It was placed in a depression under a spray of hemlock and made of dead hemlock twigs and plant stems. The most unique situation, however, was a nest placed three feet above the ground on a horizontal branch next to the main trunk of a small spruce which was eight feet tall and artificially planted in the forest edge. The nest was made of spruce needles and moss and was lined with pine needles, doubtlessly obtained from an artificial planting near by. This species appears to have a preference for evergreen nest-sites and nest materials when available.

VIREOS.—One of the most noticeable differences in the avifauna of deciduous and evergreen forests is the great number of Red-eyed Vireos (*Vireo olivaceus*) in the former and their virtual absence from the latter. Their activities were confined largely to the deciduous trees when in mixed forests. On the other hand, the single pair of Blueheaded Vireos (*Vireo solitarius*) recorded on the Preserve occurred among the hemlocks, although elsewhere they were also found in deciduous forest.

Four nests of the Red-eyed Vireo were located, three at a height of six feet and one at 12 feet above the ground in young trees of beech, basswood (*Tilia americana*), and sugar maple, all being fastened inside of slender horizontal forks as is usual for the species. The nests were made of dried grass, shreds of bark and weeds, and leaf stalks; two contained numerous small twigs of hemlock, and two contained broad pieces of white birch bark (*Betula papyrifera*). The Blue-headed Vireo built a nest seven feet up, suspended from a horizontal fork near the end of a hemlock branch. The nest was made of strips of white birch bark and plant stalks. The bird also nests in deciduous trees. There is no obvious reason why the Red-eyed Vireo should not also nest in hemlock, although it is not known to do so. One difference in the feeding habits of the two species was noticed. The Red-eyed Vireos commonly fed near the ends of the smaller twigs and from the broad leaf-surfaces themselves. They have difficulty in feeding on hemlock twigs because of the arrangement of the needle leaves, and likewise these needles furnish less surface from which food can be gleaned. Only once were two birds seen feeding in hemlock and they did so not by their usual movements outward to the tip of the twigs but by alighting from above onto sprays clumped together sufficiently to hold their weight. On the other hand, the Blue-headed Vireo, when feeding in hemlocks, seeks its food from near the base of side branches and from the numerous projecting dead stubs that occur in this forest.

WARBLERS.—The best represented family in the area is that of the wood warblers. Altogether, seventeen species were recorded during the three summers, but only with twelve species was sufficient information obtained to make worth while a consideration as to how these closely related species have become adjusted to a variety of communities and situations.

Black and White Warbler (Mniotilta varia).-The Black and White Warblers are more commonly found in or near the forest-edge and in abandoned fields as soon as a good stand of trees develops than in the forest-interior, but in the forest-interior they occur to about an equal extent in pure deciduous and in mixed forests. Most of their activities take place as they climb over the trunks of trees. However, when singing for territories or mates, they perch crosswise on dead branches near the tops of exposed trees. They nest on the ground. Two nests were found well inside beech-maple-hemlock forests. One was nestled under the buttresses at the base of a yellow birch. The outside of the nest was made of beech leaves, with the middle layer of shreds of bark including that of yellow birch, and the inside was lined with white rootlets. The other nest was on a low hillside, partially concealed under the spray of a hemlock branch caught to the ground by a mass of dead leaves. The nest consisted of dead beech leaves and hemlock twigs. Nests are invariably reported as sunken under the shelter of the base of a tree or a bush, stump, log, or rock. The nest is usually constructed of dead leaves, strips of bark, and grasses, and lined with rootlets or hair. The structure of the nest indicates a preference for materials from deciduous trees but not exclusively so.

Nashville Warbler (*Vermivora ruficapilla*).—The Nashville Warbler regularly sang and fed in both deciduous and evergreen trees on the forest margin and in shrubby fields at heights from 15 to 30 feet. No nests were found, but others report this species as breeding in both dry upland fields and occasionally in swamps as long as they have relatively open areas with scattered clumps of trees and shrubs. The nest is sunken in the ground, usually in a tuft of grass or moss under a tree or shrub, and is constructed of dead grass, bits of moss, leaves, strips of bark, and pine needles, and lined with grass, pine needles, rootlets, or hair.

Magnolia Warbler (*Dendroica magnolia*).—Although the Magnolia Warbler was observed a few times in the beech-maple-hemlock forest, it belonged almost exclusively to hemlock or evergreen communities. The species occurred equally well in the dense forest-interior and at the forest-edge, as well as in dense plantings of spruce (*Picea canadensis*, *P. abies*) and pine (*Pinus resinosa*). For song posts it commonly selected exposed dead branches of hemlock, but was also observed in birch, white ash (*Fraxinus americana*), and beech, usually between 10 and 45 feet above the ground. It fed in similar situations as it sang.

Of three nests found, one was made of dried leaf stalks with many spider nests on the outside, set simply on a horizontal limb of a small spruce with the short needles holding it in place. It was four feet from the ground and in a dense artificial planting. The birds divided their time between this spruce-pine planting and the near-by hemlock forest-edge. Another nest was placed 14 feet up in a medium-sized hemlock near the center of the hemlock-beech woods. It was placed precariously on top of a spray of needles six feet out from the trunk, depending again on the short needles projecting into the nest structure to hold it in place. The nest was flimsily made of hemlock twigs and dry grass and lined with brown tendrils of uncertain origin, probably the "moss-stems" of Nichols (1919). The third nest was also near the center of this same wood, six feet above the ground, and suspended in a dense spray of twigs, some of them dead, of a hemlock tree that had been blown over. The spray of twigs formed an intertwining meshwork that held up the nest. The nest was made of hemlock twigs and a small amount of dried grass.

From the literature, it seems that the Magnolia Warbler is very partial to spruce and hemlock forests with nests also found in fir, juniper, and rarely in deciduous shrubs and trees. Most observers have found the species more common in low second-growth trees in open situations than in dense forests. Most nests were placed within ten feet of the ground, although a few have been reported up to 35 feet. The nest may be constructed of twigs of spruce or hemlock, pine needles, or dried grass, and usually lined with black rootlets or horsehair. Mousley (1924) gives a photograph of a nest loosely placed in a fork of a spiraea bush. The occasional occurrence of the species in deciduous shrubs and forests (Brooks, 1940) must be distinctly a matter of second choice.

Black-throated Blue Warbler (*Dendroica caerulescens*).—The Blackthroated Blue Warbler occurred commonly in both types of forest but appeared to make more use of broad-leaved trees than of hemlock. They were commonly observed singing on exposed, often dead, branches, 18 to 36 feet above the ground, in either hemlock, beech, or maple trees. Likewise they fed in all situations. One nest was found only 60 feet from an open field in a young stand of secondgrowth deciduous trees. The nest was placed in a fork of a purpleflowered raspberry (*Rubus odoratus*) only a foot above the ground. Bark strips, including considerable white birch, entered into its outer construction, dried grass formed the middle portion, and the lining was of black rootlets and light-colored plant fibers.

In the experience of other observers the species is commonly found in deep forests with dense underbrush, the forests being either such hardwoods as oak, maple, beech, or chestnut, or pine-hemlock, or mixed evergreen-deciduous trees. They nest in the undergrowth from only a few inches above the ground in a clump of ferns to usually not over ten feet up in maple, beech, honeysuckle, balsam fir, rhododendron, laurel, speckled alder, and yew. The nest is generally described as bulky with an outer construction of small pieces of rotten wood and bark fibers or shreds held together with weed stalks, grasses, or spider webs and lined with black rootlets, black or white hairs, pine needles, or bits of moss. It appears that a dense undergrowth is a primary requirement while the species composition of the tree stratum is of secondary importance.

Black-throated Green Warbler (*Dendroica virens*).—All birds of this species on the Preserve and throughout the Helderbergs appeared confined to, or in the immediate vicinity of, hemlock trees and only infrequently did they visit deciduous trees. Their song posts and feeding areas were commonly from 20 to 60 feet above the ground. Two nests discovered, one by Odum, were 18 and 20 feet up in hemlocks although others have reported them from close to the ground in scraggly forests to as high as 70 feet in tall trees. One of the two nests was placed in the angle formed by two small side branches with the main trunk. Although nests are probably placed more commonly, when in hemlock, well out on sprays of horizontal branches, Burleigh (1927) and Saunders (1938) report nests in birch and beech placed next to the trunk and similarly supported by one or more side branches. The nest may be composed of grasses, weed stems, spruce twigs, birch bark, rootlets, pine twigs, or shredded bark, and lined with hair, plant fibers, or fern leaves; the variety of material suggests that the species uses what is available in the vicinity.

An interesting variation in ecological position occurs with this Brooks (1940) has reported that, in the Central Allegheny species. Mountains, Black-throated Green Warblers are commonly found in northern hardwoods and in oak-hickory forests and are not dependent on hemlocks or other conifers for nest-sites. Odum remarks in a letter that a subspecies (D. v. waynei) consistently nests in trees other than conifers in the coastal region of South Carolina. At elevations over 2000 feet in the Catskill Mountains, this Warbler was found to be very abundant in extensive forests of nearly pure beech and sugar The fact that on occasions, at least, the bird builds its nest in maple. a crotch between the main trunk and side branches in hemlock would permit their choosing similar positions in deciduous trees. There is evidence from rotting stumps and logs scattered through this deciduous forest in the mountains that conifers were once more abundant than at present. Perhaps this species is more plastic in choice of nestsites than its nearest competitors, and when the conifers became eliminated the species quickly became adjusted to its new environment and even increased in number.

Blackburnian Warbler (*Dendroica fusca*),—This species is the most strictly confined to hemlock trees of any warbler in this region. It belongs to the tree-tops, singing and feeding at heights of 35 to 75 feet from the ground. Rarely was the bird seen in deciduous trees, and even in woods where the hemlock occurred singly or in small groups the bird was almost invariably associated with these isolated trees.

One nest found near the center of the hemlock-beech forest was 35 feet up in a hemlock, six feet out on a horizonal branch, and about ten feet from the top of the tree. The nest was well supported on three horizontal branches. Other nests reported in the literature range from 18 to over 80 feet above the ground in hemlock, white pine, spruce, cedar, and rarely in sugar maple and chestnut. The nest is commonly made of hemlock twigs, rootlets, or pine needles, sometimes with interwoven *Usnea* lichen, and lined with horsehair or fine lichens.

Chestnut-sided Warbler (*Dendroica pensylvanica*).—One of the most characteristic and well adjusted species in shrubby fields is the Chestnut-sided Warbler. It regularly does all its feeding in bushes and young trees, usually within ten feet of the ground. It may sing from a low bush but more commonly assumes a higher perch, often an exposed dead branch, and occasionally goes as high as 30 feet. It may do some feeding at this height, but its obvious purpose there is

singing. Four nests found by Odum and myself were in bracken fern (*Pteris aquilina*), in briers, and in a cultivated shrub, at heights of 1, $2\frac{1}{2}$, $3\frac{1}{2}$, and 6 feet from the ground, fastened between vertical stalks, and made of dry grass, stems, and rootlets.

All observers agree that the species avoids the dense forest and is found only in open situations. Chapman (1907) and Forbush (1929) mention that they also avoid evergreen trees. There is no known record of a nest over six feet from the ground and the common height is only two feet. Grasses, plant fibers of various sorts, and bark shreds are commonly used in the construction of the nest. The outside is usually covered with spider webs and plant-down and the lining may be grass, rootlets, or hair.

Oven-bird (Seiurus aurocapillus).—One of the most abundant warblers, equally numerous in the hemlock-beech and in the beechmaple-hemlock forests, is the Oven-bird. Although generally considered a characteristic bird of deciduous forests, various observers have reported it also in forests of white pine, spruce, and balsam fir Brooks (1940) reports that it is absent in older, more mature stands of spruce. Eaton (1914) probably states the true situation in that the species "prefers a rich deciduous woodland—but is equally common in mixed woodlands, and in the North Woods I have found it where the growth was predominantly spruces and pines with only a few deciduous trees intermingled."

The Oven-bird uses the trees for overhead protection and sings from their lower, often dead, branches as well as from the ground. The species also has a flight song as do many ground birds, although here it would seem unnecessary and actually it is not frequently given. Most of the feeding is done from the ground, although some food may be obtained from the lower branches of trees. All nests are on the ground.

One of the four nests found was in a patch of yew, the other three on hillsides covered with dead leaves. The nests were, in all cases, made of the dead leaves of maple and beech, dried grass, leaf stalks, and black rootlets. In no case did hemlock material enter the construction. Chapman (1907) describes their nests as composed largely of dried leaves and leaf skeletons, with occasional bits of moss, and as rather coarsely lined with grasses, blossom stalks, etc. In the nests were "dead and decayed leaf stems and leaves of the chestnut, oak, beech, maple, cherry, dogwood and hickory, principally the first two." Forbush (1929) and Nice (1931) record nests lined with white pine needles.

It may well be that the occurrence of dead leaves from broad-leaved

14

trees is prerequisite before nests can be built, and the occurrence of the species in needle-leaved evergreen forests is conditioned on the occurrence of at least scattered broad-leaved trees to furnish nest material. Certainly in the hemlock-beech community studied, Ovenbirds tended to avoid the purest stands of hemlock, and the territories of occasional birds that did occur in such situations extended well out into the forest-edge where there were many deciduous shrubs and trees. Through most of the forest there were sufficient yellow birch and beech to furnish nest material.

There is no obvious explanation of why this ground-adjusted species should not also occur in the early stages of the mixed shrub community or even in grassland. Peterson's (1942) statement that they require a "closed crown" appears to be true, and there may be some physiological or climatic factor involved that makes a closed canopy desirable. Hann (1937) states that no nests that he found were placed within 60 feet of the forest-edge, but he made the observation that "all nests seemed to get a little sunshine each day, but in most cases the amount was small."

Louisiana Water-Thrush (Seiurus motacilla).—The Louisiana Water-Thrush is fairly common along streams in the vicinity. None was listed for the particular areas intensively studied, probably because the streams that traverse them are temporary, drying up in late spring. One nest was placed elsewhere in a situation quite typical of the species—depressed into the somewhat mossy ground under the projecting roots and base of a small tree. The nest was half-way up a ten-foot bank at the edge of a permanent pool of a stream inside a deciduous forest. It was constructed of dead leaves and leaf-stalks of maple and beech. The chief requirement of this species appears to be nearness to small streams along the edges of which it gets all its food. The Northern Water-Thrush (Seiurus noveboracensis) was recorded once in 1943 at the 'vly,' a sphagnum bog surrounded by hemlock, white pine, and black spruce (Picea mariana); and Odum found a nest with young birds in a hemlock-yellow birch bog.

Yellow-throat (*Geothlypis trichas*).—Although very common in fields containing grasses, herbs, and shrubs, the Yellow-throat appears partial to patches of tall herbs and succulent plants other than grasses, especially such as grow in damp habitats. One nest was found at the edge of a pond in a clump of lilies, raised one-and-a-half feet above the ground, and loosely held in a fork made by adjacent leaves. It was composed largely of dry grasses. Another nest was in a small opening at the edge of the hemlock-beech forest. It was placed in a patch of fern (*Onoclea sensibilis*) about eight inches above the ground. The nest was composed of dried grass with beech leaves on the outside.

Authorities agree that the species is common where rank growths of grasses, herbs, briers, bushes, and trees grow in damp situations. However, they also occur in drier habitats and their requirement is probably more for the dense growth of low vegetation, such as is more prevalent in wet habitats, than because of any direct relation to the water itself. Nests are reported usually on or near the ground in clumps of grasses, weeds, or briers, but there are records of nests four and five feet up in bushes (Chapman, 1907; Todd, 1940). Nests are usually made of coarse grass, leaves, weed stalks, and strips of bark, and lined with fine grass or horsehair.

The Yellow-throat feeds on or near the ground and occasionally up to five feet in shrubs. It commonly sings from the midst of ground vegetation, from shrubs, or occasionally from tops of trees 40 feet high. It is not dependent upon elevated song posts, however, as it has a flight song. Although well adjusted to the ground stratum, it is not extensively found in the grassy field community.

Canada Warbler (*Wilsonia canadensis*).—The Canada Warbler was more numerous in the hemlock-beech forest than elsewhere but was not confined to it and showed some partiality for the forest-edge over the forest-interior. Males sang all the way from two to 32 feet above the ground, mostly in hemlock. At the greater heights the birds did nothing but sing, usually from exposed perches; at intermediate heights they both sang and fed, while near or on the ground they spent most of their time feeding.

One nest found was in a hummock of moss at the edge of a small wooded bog under a limb of a fallen tree covered with *Cladonia* lichen. The nest was only a foot above water and was surrounded by cinnamon fern (*Osmunda cinnamomea*) and young hemlock. Another old nest was on the side of a deep wooded ravine, sunken in a thick bank of moss and surrounded by yew. It was under hemlock, yellow birch, and striped maple (*Acer pennsylvanicum*). A third nest, containing young birds, was in a bank at the side of a small stream that contained water only in the spring. The nest was well sheltered under roots in the middle of the deciduous forest with only scattered hemlock about. Moss was almost lacking in the vicinity.

The first nest was made of fern leaves, other leaves that were probably beech, grass stems and shreds, and lined with both black and white rootlets. The second nest was made almost entirely of rootlets with the lining all black. The third nest was constructed of dry deciduous leaves and stems, grass, bark shreds, and black rootlets.

Other observers record the Canada Warbler as a bird of dense deciduous undergrowth in damp woods or forest-edges and occurring Vol. 62 1945

in deciduous or mixed forests. The undergrowth may be rhododendron, laurel, azalea, blueberry, blackberry, or ferns. The nest is usually sunken in a moist, mossy bank, in ferns, under rotting logs, or in other similar situations. It may be composed of dry leaves, grass, weed stalks, moss, or bark-strips, and lined with grass or rootlets.

It appears that this species prefers a forest canopy, although not necessarily a dense one, since the forest-edge is commonly used, as long as there are shrubs or low vegetation present and a moist bank or other shelter in which to place its nest. The nest-site may be concerned in its community selection. Although it uses a variety of materials from which to build its nest, it appears not commonly to use any parts of evergreen trees. The fact that locally the species was more common in the hemlock-beech forest than elsewhere was probably due not to affinity for hemlock but rather to the occurrence there of the damp, shrubby areas with mosses and ferns that it prefers.

Redstart (*Setophaga ruticilla*).—On the Preserve, Redstarts were found chiefly in tall shrubs and open woods and had not penetrated the forests proper. Males were occasionally observed giving their territory songs 40 feet above the ground, but the usual height was half of this. Food was secured from trees, shrubs, and the ground. Most authorities state that the species prefers second growth and usually places its nests in saplings of various broad-leaved trees. However, in one locality on the Helderberg plateau a dense colony was found in a sugar maple grove where the trees formed a canopy 60 feet high. The birds kept mostly at the lower levels.

Three nests were found, one eight feet above the ground in a vertical fork of a hawthorn (*Crataegus*), the other two, each six feet up in a vertical fork of a viburnum. The first nest was insecurely fastened and in an exposed situation alongside a road, so its later destruction was probably due to a heavy wind. Nests are almost invariably in vertical forks at heights of six to 12 feet above the ground, but occasionally as low as two feet and as high as 35 feet. Nests are made of shreds from plant stalks, plant down, bark strips, grasses, and spider webs, and are lined with fine grasses, rootlets, or hair.

DISCUSSION

Each species must be considered independently when analyzing its dependency on the environment, as different species exhibit various degrees of segregation to particular communities and each species may have a different set of limiting factors. Morphological adaptations of animals to special environmental situations have been much emphasized and are necessarily fundamental. The color or color

431

pattern may conceal a species from its predators in one community better than in another and afford it a greater chance of producing abundant offspring. However, structural and color adaptations do not explain the segregation of the species here under consideration.

Closely joined with structural modifications are functional adjustments. Palmgren (1932) has explained the avoidance of birch trees with their drooping branches by *Regulus r. regulus* as due to the weak functional development of a particular muscle in the legs. It is quite possible that separation of forest and non-forest inhabiting species may depend on the functional units of the retina and on the adaptation of the eyes to light intensity (Walls, 1942). Different degrees of tolerance to climatic factors other than light intensity appear to be important in explaining geographic dispersal, but the small differences in micro-climate between various local communities do not seem sufficient to account for the pronounced local segregation of species. Much more detailed experimentation in the physiology of birds must be conducted, however, before the full significance of these factors can be ascertained.

In addition to its morphological and physiological adjustments to the environment, each species also has a psychological adjustment for the utilization of its particular niche in the community that takes the form of a definite behavior pattern (Lack, 1933, 1937; Moreau, 1935; Mayr, 1942; Miller, 1942). Such a behavior pattern, for example, is that of the Oven-bird that builds an overarching nest of broad leaves in contrast to the Canada Warbler that gets essentially the same overhead protection by placing the nest under some overhanging root, log, or clump of moss. A stereotyped behavior pattern appears to limit the Magnolia Warbler to building a nest that requires the interlocking leaves or twigs of a conifer to hold it in place and only rarely permits it to anchor the nest in the vertical fork of a deciduous tree or shrub as the Redstart regularly does.

Behavior patterns may possibly be acquired in each generation by imitation and learning in a manner similar to that described by Cushing (1941, 1944) for mate preference and food habits. On the other hand, the behavior may involve definite patterns of nerve cells and connections that are as subject to modification, inheritance, and evolution as are any morphological features of the organism. The Black-throated Green Warbler appears locally to be breaking away from a nest-building behavior pattern similar to that of the Magnolia Warbler and to be acquiring the ability to build in semi-vertical forks that permits it to inhabit deciduous forests. It is impossible to be certain at the present time whether such a modification in behavior represents a definite mutation or whether it is a change in 'tradition' that is passed on to each succeeding generation through conditioning the young in favor of a particular set of environments! factors. Similarly it is uncertain whether a difference in tolerance to light or a difference in behavior patterns evolved in the past for some other reasons explains the occurrence of Chestnut-sided Warblers only in open situations and the Black-throated Blue Warblers only within the forest, although both species build nests in forks of bushes or plants close to the ground.

It is possible that some behavior patterns have arisen merely through chance performing of an act over several generations in a particular way without any special benefit being thereby derived (Lack, 1940), but to have a behavior pattern become stereotyped so that succeeding generations perform in the same way with little modification would seem to require some advantage to the species and to be subject to the regular processes of evolution. These advantages may include the avoidance of unfavorable physical factors, such as extremes of climate, or the establishment of better biotic inter-relations.

The avoidance of excessive and continuous strife with competitors requiring similar feeding areas, nesting material, nest-sites, and song posts, must be a potent factor in successful reproduction and in evolution. Occupancy of a new unfilled niche within the same community or in another community may well proceed along with the differentiation of the race or species itself. As is well known, diversification in niche requirements reduces interspecific competition and permits a greater and more varied population to inhabit an area. The warblers are so prominent in the mixed evergreen-deciduous forest because they fill so many of these diverse niches: top level of evergreen trees (Blackburnian), middle level of usually evergreen trees (Black-throated Green), low level of evergreen trees (Magnolia), secondary deciduous growth (Redstart), tree trunks (Black and White), shaded shrubs (Black-throated Blue), sunlit shrubs (Chestnut-sided), wet shaded ground (Canada), wet sunlit ground (Yellow-throat), dry shaded ground (Oven-bird), dry sunlit ground (Nashville). Establishment of behavior patterns that are passed on by inheritance or by tradition insures that the offspring of each generation will automatically utilize the niche to which it belongs and thereby avoid the conflict and wastage of energy and time that would be necessitated were the assignment to niches within the community independently worked out by each generation. Behavior patterns once established are slow to change, as are anatomical or functional features, but they do change, for witness the Black-throated Green Warbler invading the deciduous

forest in the mountains. Behavior patterns have seemingly evolved to stabilize these adjustments and maintain the species' position within the community from generation to generation with the greatest economy and efficiency of effort.

SUMMARY AND CONCLUSIONS

1. Community selection by birds of shrubby fields or forests rather than grassland is correlated with the use of elevated positions for songposts, nest-sites, or feeding areas.

2. Selection of forests rather than shrubby fields or grassland is correlated with the avoidance of high light intensity and with a greater restriction of free movement.

3. Preference for either evergreen or deciduous forest is correlated primarily with the size and shape of the leaves and with their arrangement on the twig rather than with differences in persistence of the foliage, in food supply, or in micro-climate. This preference is effected in different species through choice of material used in nest construction, in choice of nest-site, or in manner of feeding.

4. The avoidance or reduction of interspecific competition is an important factor in the evolutionary development of a preference for a particular niche.

5. Behavior patterns stabilize through succeeding generations the local segregation of species into different communities and their positions within these communities.

LITERATURE CITED

BLAKE, IRVING HILL

1926. A comparison of the animal communities of coniferous and deciduous forests. Ill. Biol. Mono., 10: 1-148.

- BRECHER, LEONARD C.
 - 1943. The relation of vegetational life forms to the distribution of breeding birds. Kentucky Warbler, 19: 41-49.

BROOKS, MAURICE

1940. The breeding warblers of the central Allegheny Mountain region. Wilson Bull., 52: 249-266.

BURLEIGH, THOS. D.

1927. Further notes on the breeding birds of northeastern Georgia. Auk, 44: 229-234.

CHAPMAN, FRANK M.

1907. The warblers of North America. Pp. i-ix, 1-306 (N. Y.).

CUSHING, JOHN E., JR.

- 1941. Non-genetic mating preference as a factor in evolution. Condor, 43: 233-236.
- 1944. The relation of non-heritable food habits to evolution. Condor, 46: 265-271.

Vol. 62

EATON, ELON HOWARD

1914. Birds of New York. Pt. 2, Land Birds, N. Y. St. Mus., Mem. 12: 1-719. FORBUSH, EDWARD HOWE

1929. Birds of Massachusetts and other New England states. Pt. 3, pp. i-xlviii, 1-466. (Boston).

HANN, HARRY W.

1937. Life history of the Oven-bird in southern Michigan. Wilson Bull., 49: 145-237.

KENDEIGH, S. CHARLES

1934. The role of environment in the life of birds. Ecol. Mono., 4: 299-417.

1941. Birds of a prairie community. Condor, 43: 165-174.

LACK, DAVID

1933. Habitat selection in birds. Jour. Animal Ecol., 2: 239-262.

1937. The psychological factor in bird distribution. British Birds, 31: 130-136.

1940. Habitat selection and speciation in birds. British Birds, 34: 80-84.

LACK, DAVID AND VENABLES, L. S. V.

1939. The habitat distribution of British woodland birds. Jour. Animal Ecol., 8: 39-70.

MAYR, ERNST

1942. Systematics and the origin of species. Pp. i-xiv, 1-334. (Columbia Univ. Press.)

McAtes, W. L.

1932. Effectiveness in nature of the so-called protective adaptation in the animal kingdom, chiefly as illustrated by the food habits of nearctic birds. Smith. Misc. Coll., 85: 1-201.

MILLER, ALDEN H.

1942. Habitat selection among higher vertebrates and its relation to intraspecific variation. Amer. Nat., 76: 25-35.

MOREAU, R. E.

- 1934. A contribution to tropical African bird-ecology. Jour. Animal Ecol., 3: 41-69.
- 1935. A critical analysis of the distribution of birds in a tropical African area. Jour. Animal Ecol., 4: 167-191.

MOUSLEY, HENRY

1924. A study of the home life of the Northern Parula and other warblers at Hatley, Stanstead County, Quebec, 1921–1922. Auk, 41: 263–288.

NICE, MARGARET MORSE

1931. A study of two nests of the Ovenbird. Auk, 48: 215-228.

NICHOLS, JOHN TREADWELL

1919. Problems suggested by nests of warblers of the genus *Dendroica*. Auk, 36: 225-228.

PALMGREN, PONTUS

1932. Zur Biologie von Regulus r. regulus (L.) und Parus atricapillus borealis Selys. Acta Zool. Fennica, 14: 1-113.

PETERSON, ROGER T.

1942. Life zones, biomes, or life forms? Audubon Mag., 44: 21-30.

PITELKA, FRANK A.

1941. Distribution of birds in relation to major biotic communities. Amer. Midl. Nat., 25: 113-137. ROOT, OSCAR M.

1942. Wood Thrush nesting in the coniferous bogs of Canadian Zone. Auk, 59: 113-114.

SAUNDERS, ARETAS A.

1938. Studies of breeding birds in the Allegany State Park. N. Y. St. Mus. Bull., 318: 1-160.

TODD, W. E. CLYDE

1940. Birds of western Pennsylvania. Pp. i-xv, 1-710. (Univ. Pittsburgh Press.)

TROTTER, SPENCER

1912. The faunal divisions of eastern North America in relation to vegetation. Jour. Acad. Nat. Sci. Phil. (2nd. Ser.), 15: 207-218.

WALLS, GORDON LYNN

1942. The vertebrate eye and its adaptive radiation. Cranbrook Inst. Sci., Bull. 19: i-xiv, 1-785.

Department of Zoology University of Illinois

Champaign, Illinois

TWENTIETH SUPPLEMENT TO THE AMERICAN ORNITHOLOGISTS' UNION CHECK-LIST OF NORTH AMERICAN BIRDS¹

In view of the existing commercial situation relating to the production of books, in which good grade paper is difficult to obtain and costs are high, it is still not practicable to issue a complete revision of the A. O. U. Check-List, though need for such a volume is fully recognized. The Council of the Union at the meeting held in New York City in October, 1944, instructed the Committee on Classification and Nomenclature to prepare a further supplement for publication in The Auk summarizing action of the Committee during the past year.

The report herewith includes cases that have been brought to attention to the close of the year 1944, and covers most of the changes in names, status, and new forms proposed to that time. A number are still under consideration for final decision.

In addition to the matters listed beyond, the Committee has given attention to various questions of procedure for the final manuscript, among which may be mentioned one important change under which geographic names, particularly in Latin America, will follow the official spelling in the country concerned since this is the generally accepted modern practice. Under this, for example, Lower California of earlier editions will become Baja California, and names like Belém and Perú will include an accent.

¹ The Nineteenth Supplement was published in The Auk, vol. 61, July, 1944, pp. 441-464.