

THE CONDOR

VOLUME 49

MARCH-APRIL, 1947

NUMBER 2

BREEDING BIRDS OF THE FOREST EDGE IN ILLINOIS

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The forest edge is a meeting place of two distinct communities, forest and grassland, and combines many characteristics of each. This study was made to determine if the avifauna of the forest edge was sufficiently different to constitute a community unit distinct from either the forest interior or open country and to analyze avian responses to the "edge" habitat. Lay (1938) and Beecher (1942) have shown the relation between edge and increased population densities of birds in any area. Shelford (1927:262) presents a good description of the original extent of forest edge in Illinois: "The forest margin or edge is a familiar natural situation. About Chicago there are groves of trees which are probably exactly as they were before settlement. The forest ends: the prairie begins. The line between the two is markedly a narrow border of shrubs and rank weeds, usually only a few feet wide. In other places the forest ends at a marsh side, lake side, or stream side, but almost always with the thicket of shrubs and rank weeds. A remarkably large number of animals belong to this forest margin."

As these forests are cut up into fragments and the prairies plowed right to the edge of the forest, the natural forest edge disappears. If undisturbed, however, in a short time shrubs, seedlings, and vines sprout along the outer border of the remaining forests. There are now many small, scattered islands of forest, exposed to open fields on all sides, with a very narrow border of small trees and shrubs and weeds. Young trees and shrubs are prevented from broadening the forest border by cultivation. But essentially the same type of habitat occurs "along the wooded streams into the great plains and toward the east through the forest area, as the shrubby bluff, the creek and river margin, the fired area, and the marsh margin" (Shelford, 1927:275). It is found along roadsides, fence-rows, and in pastures and open woods. In all these places, a forest-edge habitat which comes into existence through man's activities appears as much like the natural forest edge as can be formed under modified conditions. Among themselves, these forest edges vary in character according to the extent to which they are burned, cut, grazed, fenced in, and disturbed in general, and according to their relation to neighboring habitats such as forest, water, or fields. Together or individually, these factors will influence the character of the habitat and the composition of the avifauna.

This study of the forest edge was made during the summer of 1943 in two oak-maple forests at Urbana, Champaign County, Illinois. The two tracts, Trelease Woods and Brownfield Woods, total 56 acres and 64 acres, respectively. They are marked out into squares by permanent stakes set 50 meters (162 feet) apart. On each field trip the observer went around the area looking into the forest and counting the birds in the forest edge, then walked back and forth through the interior of the forest following the stakes and mapping the location of all species seen. All surveys were made in the morning and total 53 hours at Trelease Woods between April 18 and August 12, and

38 hours at Brownfield Woods between June 17 and August 11. Surveys totaling about half of the hours at Trelease Woods were conducted by S. C. Kendeigh and H. C. Siebert, University of Illinois, whose assistance is gratefully acknowledged. Suggestions and helpful criticisms were made by S. C. Kendeigh throughout this study.

Description of study areas.—Trelease Woods and Brownfield Woods are mesophytic forests, flat, rectangular tracts, relatively undisturbed, with tall mature trees, good undergrowth, and poor drainage. Both are bordered on all sides by farmland or country roads and their vegetation is practically identical. Red oak (*Quercus borealis*) and sugar maple (*Acer saccharum*) are the dominant trees, with numbers of burr oak (*Quercus macrocarpa*), slippery elm (*Ulmus fulva*), hackberry (*Celtis occidentalis*), American elm (*Ulmus americana*), linden (*Tilia americana*), hickory (*Carya* sp.), red haw (*Crataegus* sp.), and black cherry (*Prunus serotina*) present. Seedlings of these trees, along with spice bush (*Benzoïn aestivale*) and pawpaw (*Asimina triloba*) constitute the shrub stratum.

The forest edge is a narrow strip extending around the area, 1.25 miles long in Trelease and 1.4 miles long in Brownfield Woods. It is moderately well developed in the northeast corner of Trelease Woods, where haws, blackberries (*Rubus* sp.), sumac (*Rhus glabra*), and seedlings have formed a natural shrubby growth; but elsewhere in both woods the edge varies from a thin, closed canopy to a wide opening exposing the interior. Around the entire border of Trelease and on two sides of Brownfield Woods occurs a narrow grass-weed strip which is cut annually and meets the forest trees abruptly. In the northwest corner of Brownfield Woods is a rectangular area of this same grass-weed vegetation; the edge is closed chiefly by seedlings and hanging limbs of trees. The edge really extends inward a short distance at a decreasing height as well as outward because the forest meets the open country so abruptly.

For comparative purposes another form of forest edge was censused. This was a narrow isolated strip of trees and shrubs along a creek near Trelease Woods. Here there was no forest interior. The area was pastured and the vegetation consisted of scattered willows (*Salix* sp.), sycamores (*Platanus occidentalis*), honey locust (*Gleditsia triacanthos*), elm, hawthorns, rose bushes (*Rosa* sp.), poison ivy (*Rhus toxicodendron*), smilax (*Smilax* sp.), grapevines (*Vitis* sp.), and an abundance of weeds.

In order to compare the birds of the forest interior in Trelease and Brownfield woods with those of a more extensive tract, the unbroken forest at Turkey Run State Park, Indiana, was used. In the section of the forest studied there is no man-made forest edge, although the forest ends abruptly along streams, cliffs, and deep gorges. The forest consists of beech (*Fagus grandifolia*), sugar maple, black cherry, dogwood (*Cornus florida*) and tulip trees (*Liriodendron tulipifera*).

FOREST-EDGE SPECIES

In the present study forest-edge birds are considered to be those species which are confined to the border of the forest or which use both the forest and the surrounding field in their activities. Some species penetrated only a short distance into the woods and seldom far into the fields, while others ranged widely into the surrounding country and nested either deep in the forest or near its border.

Figure 7 illustrates the territories of representative species that are confined to the forest edge in all their activities. The census maps show how points where birds were observed on successive dates aggregate into distinct groups, indicating the identity of particular adults on their territories. Other species use the forest interior and forest edge indiscriminately (figs. 8 and 9); still others occur principally in the forest interior

(fig. 9). Such species as the crow and starling nest in the woods but forage often at considerable distances in the surrounding open country.

Densities of the breeding populations on the two study areas are given in table 1. The density of the total population of each forest is not given. Kendeigh (1944:94) has

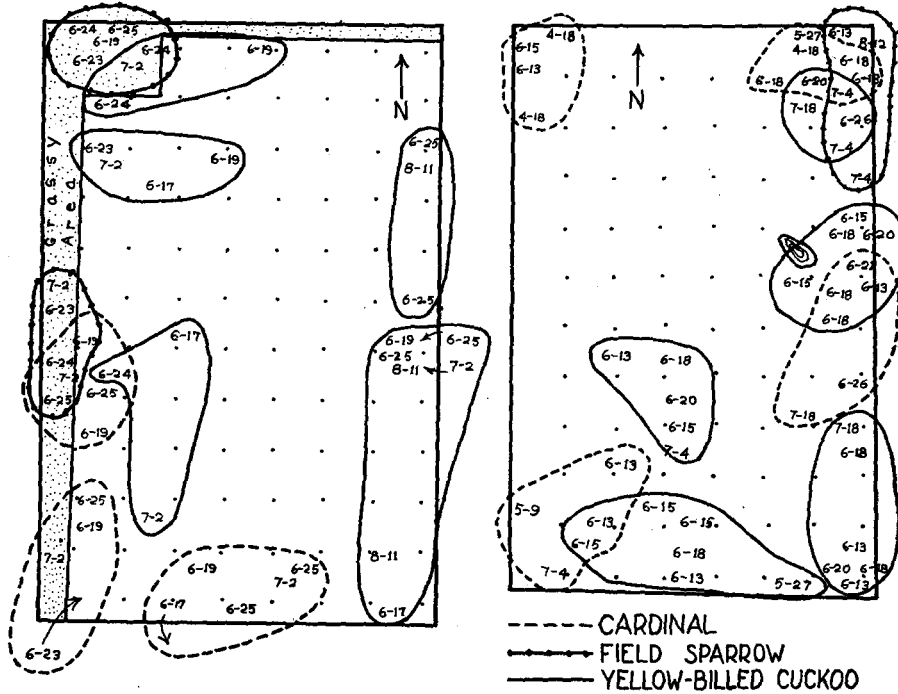


Fig. 7. Composite census maps for Cardinal, Field Sparrow, and Yellow-billed Cuckoo, forest-edge species; figures indicate dates when observed. Left, Brownfield Woods; right, Trelease Woods. Both areas are staked off at 50-meter intervals, as shown.

pointed out that when one analyzes the population by species, such an expression of density is not justified. The density of species whose activities are confined to the forest should be separated from the density of the forest-edge species. According to Kendeigh, density of the forest population is best expressed as pairs per 100 acres, and the forest-edge population in pairs per mile, since the narrow forest edge is usually without significant breadth. Species which occurred in both the forest interior and the forest edge were placed according to the location of the territories of pairs into whichever group they fit. Thus, in the case of the Crested Flycatcher at Trelease Woods, four pairs were considered interior birds and three pairs forest-edge species (see fig. 9).

It will be noted in table 1 that on the basis of total numbers of pairs, the forest edge in both woods has a greater total than the forest interior. Lay (1938:256) found this true in a Texas woodland, and it is a generally known fact that numbers of birds are greater in forest-edge habitats than in dense woods. Kendeigh (1944:97), after a study of the relative densities of forest-edge and forest-interior birds in fifteen widely scattered areas, concluded that "a census is very likely not to show the true density of forest-interior birds if forest-edge birds constitute more than one-third of the total population." In this study of Trelease and Brownfield woods, forest-edge species made up 63 per cent of the total population. Doubtless the amount of exposure to open country around the edge of these two areas is important and may account for the infiltration

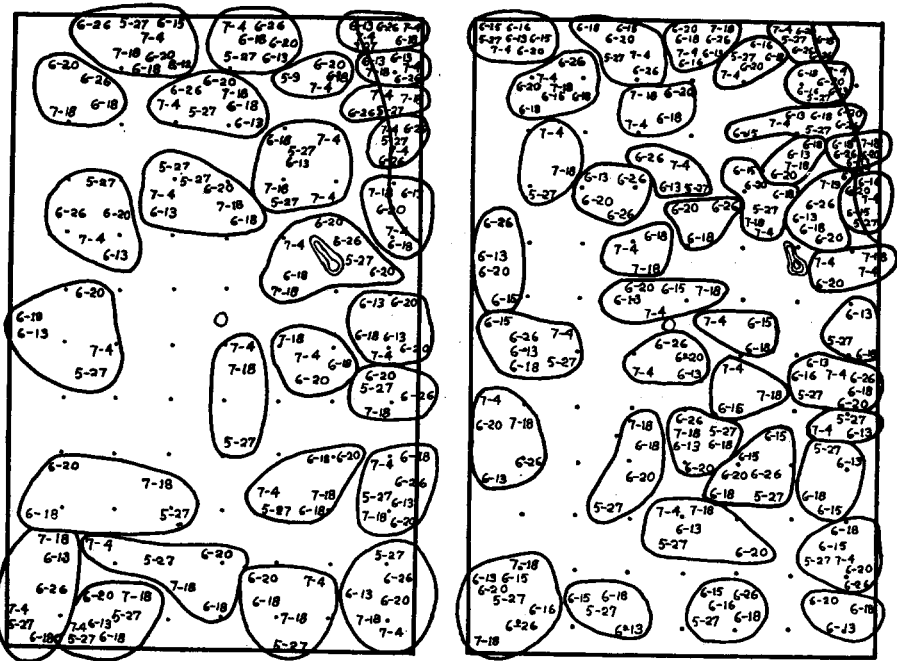


Fig. 8. Census maps for Trelease Woods. Left, Indigo Bunting; right, House Wren. Note occurrence both in the interior and at the edge.

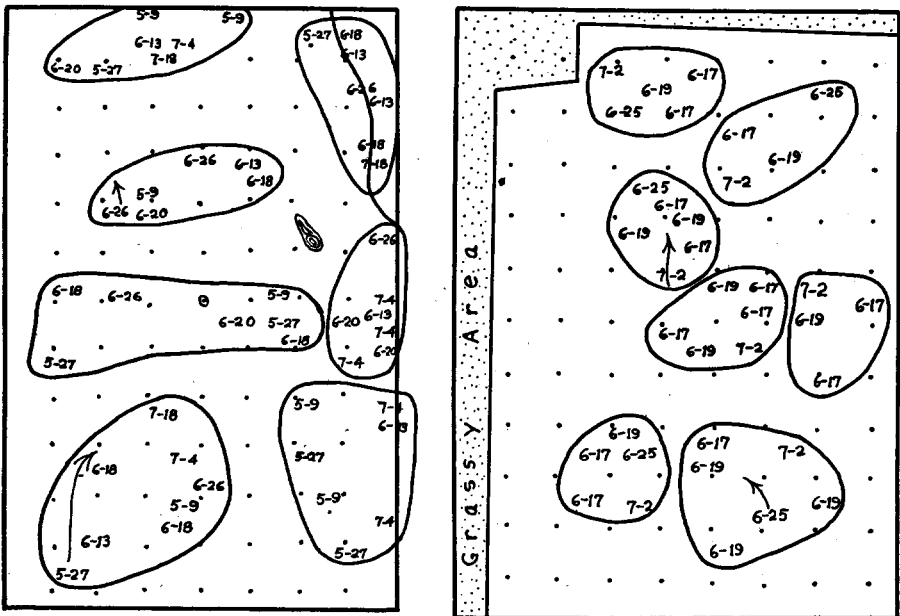


Fig. 9. Left, map for Crested Flycatcher in Trelease Woods, showing occurrence of 3 pairs at edge and 4 in the interior. Right, map for Red-eyed Vireo at Brownfield Woods, showing occurrence in interior only.

of the forest-edge species like the House Wren and Indigo Bunting. "Or the larger percentage of forest-edge species may simply indicate that the community or habitat is no longer a true forest one and is changed in various ways that are less favorable for forest birds" (Kendeigh, 1944:97) or, at least, more favorable for forest-edge species.

In the pastured creek margin near Trelease Woods which was censused for comparative purposes, ten species were regularly recorded, nine of which were also edge inhabitants of Brownfield and Trelease woods, namely, Mourning Dove, Field Sparrow, Cardinal, Goldfinch, Blue Jay, Robin, Yellow-billed Cuckoo, Crested Flycatcher and Indigo Bunting. The Brown Thrasher (*Toxostoma rufum*) is the only species recorded in the

Table 1

Number of Pairs of Breeding Birds of the Forest Edge (FE) and Forest Interior (FI) in 1943

Species	Trelease Woods			Brownfield Woods		
	FE	FI	Total	FE	FI	Total
Cooper Hawk, <i>Accipiter cooperii</i>	1	0	1	0	0	0
Mourning Dove, <i>Zenaidura macroura</i>	0	0	0	1	0	1
Yellow-billed Cuckoo, <i>Coccyzus americanus</i>	4	1	5	5	0	5
Ruby-throated Hummingbird, <i>Archilochus colubris</i>	♂	♀	1	♂	♀	1
Yellow-shafted Flicker, <i>Colaptes auratus</i>	1	0	1	1	0	1
Red-bellied Woodpecker, <i>Centurus carolinus</i>	0	1	1	0	2	2
Red-headed Woodpecker, <i>Melanerpes erythrocephalus</i>	1	0	1	1	0	1
Hairy Woodpecker, <i>Dryobates villosus</i>	0	1	1	0	3	3
Downy Woodpecker, <i>Dryobates pubescens</i>	0	6	6	0	5	5
Crested Flycatcher, <i>Myiarchus crinitus</i>	3	4	7	4	2	6
Wood Pewee, <i>Myiochanes virens</i>	3	5	8	5	0	5
Blue Jay, <i>Cyanocitta cristata</i>	1	0	1	1	0	1
Crow, <i>Corvus brachyrhynchos</i>	9	0	9	9	0	9
Tufted Titmouse, <i>Parus bicolor</i>	0	3	3	0	4	4
House Wren, <i>Troglodytes aedon</i>	25	15	40	23	14	37
Carolina Wren, <i>Thryothorus ludovicianus</i>	0	1	1	0	1	1
Robin, <i>Turdus migratorius</i>	0	0	0	4	0	4
Wood Thrush, <i>Hylocichla mustelina</i>	0	2	2	0	4	4
Starling, <i>Sturnus vulgaris</i>	15	0	15	15	0	15
Red-eyed Vireo, <i>Vireo olivaceus</i>	0	10	10	0	7	7
Ovenbird, <i>Seiurus aurocapillus</i>	0	1	1	0	0	0
Kentucky Warbler, <i>Oporornis formosus</i>	0	0	0	0	2	2
Yellow-throat, <i>Geothlypis trichas</i>	3	0	3	2	0	2
Cardinal, <i>Richmondia cardinalis</i>	3	0	3	3	0	3
Indigo Bunting, <i>Passerina cyanea</i>	18	9	27	9	3	12
Goldfinch, <i>Spinus tristis</i>	3	0	3	2	0	2
Field Sparrow, <i>Spizella pusilla</i>	1	0	1	2	0	2
Total pairs	91.5	59.5	151	87.5	47.5	135
Total species	16	14	24	17	12	25
Density per 100 acres		106			74	
Density per mile	73			62.5		

pasture and not in the woods, and it nested in a roadside stand of thick shrubs near Brownfield Woods. Thus, nine species were found in both areas of forest edge; an additional one was present in shrubby pasture; four additional species were present in the forest border of Brownfield and Trelease woods. This situation is to be expected when the faunas of two forest edges are compared: most common species will occur in both habitats, but, because of some environmental differences, each area will have some additional species conspicuously present or absent. If the census areas were of larger size and had the same facilities, perhaps there would be complete correspondence.

In an analysis of forest-interior species, it was found that all species which occurred exclusively in the forest interior of Trelease and Brownfield woods, with the exception

of the Hairy Woodpecker, occurred in the forest interior of the larger unbroken tract at Turkey Run. In addition, the Turkey Run forest included the Crested Flycatcher and Wood Pewee which are found in both the interior and edge at Trelease and Brownfield woods and the Flicker, Robin, and Cardinal.

BEHAVIOR ADJUSTMENTS

Why some species are restricted to, or are common in, one community and absent or uncommon in another is a question which arises often in ornithological studies. Various answers have been offered to this question of community selection. First, there may be coincidental agreement in environmental relations between a species and the community in which it occurs; "this may be due to coincidence in limits of tolerance to extremes in environmental conditions by species and community" (Kendeigh, 1945:418). Second, differences in micro-climate may occur between different parts of a community or between different communities to which the species responds (Kendeigh, 1945). And third, there may be some obligatory relation of the species to a particular community (Trotter, 1912; Pitelka, 1941; Kendeigh, 1945); this obligatory relation may involve the occurrence within the community of a particular niche that the species requires, such as will be shown here for the Field Sparrow.

In this study, species were classified according to three main types of community selection: those confined in their activities entirely to the forest edge, those inhabiting both edge and interior, and those confined to the forest interior. All evident reasons for community selection were analyzed carefully through observation of responses and behavior of each species to the forest edge or the forest interior. Factors influencing habitat restriction, such as food, feeding habit, singing post, nesting site, nest materials, and roosting place, were noted for each species insofar as possible. A species may be limited in its habitat distribution by any one or more of these factors (Lack and Venables, 1939). The behavior adjustments of six species proved particularly interesting.

Field Sparrow.—In this study and in previous studies of four Field Sparrow nests, it seemed apparent that the exact site of the nest itself is exceedingly variable. Walkinshaw (1936) found nests placed in grass, sorrel, or clover just above the ground, in blackberry bushes, and in young oak trees—"in fact any type of dense, short vegetation in any open field or on a dry side-hill might be a nesting site of the field sparrow." The important factor appears to be the availability of shrubs, trees, fences, or other objects which stand higher than the surrounding vegetation. From these posts the male can sing, keep watch on the nest, and chip when intruders approach. To these perches the female flies when flushed, and from them she flies to the nest with food for the young. The exact height and form (tree, shrub, post, or wire) apparently is insignificant, as long as the post provides a view of the nest and is near enough for the bird to chip at invaders. The low outer branches of tall mature trees, 15-20 feet away, served the purpose nicely for three nests observed near Cerro Gordo, Illinois, in 1940-41; tall trees approximately this same distance from the nest were used in a similar manner by a pair of Field Sparrows breeding on the border of a wood near Dune Park, Indiana, in 1943; a barbed wire fence around Brownfield and branches of the trees along the edge were utilized by the pair observed in this study. The grasses used as nesting material are widely available, and food is not a limiting factor. Hence, the singing and lookout posts in or near a relatively open situation providing some ground cover appear to be the only limiting habitat requirements of this species. These are obviously not too restricting, and shrubby fields, open woods, borders of forests, and roadsides all furnish just such conditions.

The three pairs of Field Sparrows studied in Brownfield and Trelease woods confined themselves quite closely to the actual forest border. I recorded none farther in the

forest than on the branches of the outermost trees nor farther into the fields beyond the fence than 40-50 feet. This species can thus be classified as a typical forest-edge bird.

Ruby-throated Hummingbird.—This species was observed in each woods studied, and its distribution, according to sex, was quite distinctive. In each area, a male was always observed along the forest border, and a female, with the exception of one occasion, in the forest interior. The sexes maintained separate territories and were not seen together until August 12, when three birds, a male, a female, and a third presumably a juvenile, were recorded on the forest border of Trelease Woods. Pitelka (1942:201) indicated the conspicuous independence of individual hummingbirds, the lack of relationship between the sexes, and the separate feeding territories which both sexes may maintain. In these Illinois woods the two sexes lived so definitely in different ecological communities that the male is considered as belonging to the forest edge and the female to the forest interior. In table 1, where birds are classified according to pairs that inhabit the forest edge or forest interior, the unusual sexual distribution of hummingbirds causes some totals to work out in fractions.

Crested Flycatcher and Wood Pewee.—These species are usually forest birds, although they are often found in open groves and not infrequently in towns. In these two woods they nested both in the interior and near the edge; the edges here are extremely narrow and in many places just twenty feet inside the border, forest conditions are, to all appearances, identical with those in the center of the woods. If no significant differences in environmental factors occur within the border, it would follow that the territories of interior species would often extend close to the edge. Although nests were not found, general observations led to the belief that both species nested at least 100 feet from the forest edge.

Both species, however, often used the edge for feeding. The Crested Flycatcher was found to be the most common bird on the border fences during the period of this study. Time after time it perched on a barbed wire, swooped over a daisy patch after insects, returned to the fence to eat them, and then repeated the performance. On one occasion a Crested Flycatcher was observed to feed, fly into the woods with insects in its mouth, reappear on the fence a short time later, and resume feeding. The Wood Pewee behaved similarly on numerous occasions.

It is logical that the birds feeding on the edge of the forest would seek food where it is most abundant. In these two woods the largest hordes of insects observed along the edge were clustered on or around the patches of daisies, asters, and wild carrots that stood between the fence and the forest trees. The nearest perch was the fence, and from it the Crested Flycatcher and Wood Pewee launched swooping flights at insects throughout the month of June. It is interesting to note that when later observations were made in August, the daisies, asters, and wild carrots had been succeeded by tall stands of giant ragweed and goldenrod, in some places taller than the fence. There was no fence-feeding at this date. The change in plant height, the passing of the nesting season, and the abundance of insects in higher strata may all have influenced the changed habit.

House Wren and Indigo Bunting.—Both of these species are usually considered forest-edge birds, but in this study they were found to occur uniformly (or almost so) throughout Brownfield and Trelease woods, as well as along the edge. Beginning with one pair at Trelease Woods in 1927, the House Wren has gradually invaded the area and has become more and more abundant until in 1942, 31 pairs were present, and in 1943, 40 pairs. The Indigo Bunting has been abundant in Trelease each year since 1927, but has occurred chiefly along the forest edge until the past few years, when it apparently invaded the interior in increasing numbers (Twomey, 1945; Kendeigh, 1944).

It seems probable that the habitat requirements of these two species could be met equally well inside a woods like Trelease Woods and around its border. Nesting sites, nesting material, singing posts, cover, and food are all available abundantly in both places. Yet similar conditions occur in many other forests, and such large numbers of House Wrens and Indigo Buntings do not occur there. The other species which occur in the interior of Trelease and Brownfield woods are true forest birds, by comparison with Turkey Run's large forested areas at least, belying the possibility of forest-edge conditions prevailing throughout the woods. Two considerations are advanced regarding this unusual habitat occurrence: (1) The occurrence in the forest interior of House Wrens and Indigo Buntings may be an example of Lack's (1933) "modification of a habitat preference": when more birds are present than their typical locally available habitat can accommodate they may become less restricted in the type of breeding ground which they select. (2) Kendeigh (1945) describes a similar changing behavior pattern in the process of evolution but not for reasons of lack of space. He indicates that every species has a definite behavior pattern which limits it to a particular niche in the community. He calls attention to the stereotyped behavior of the Magnolia Warbler (*Dendroica magnolia*) in building a nest which requires the interlocking leaves or twigs of a conifer to hold it in place; this behavior pattern appears to limit the species almost entirely to coniferous forests. In contrast, the Black-throated Green Warbler (*Dendroica virens*) 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, permitting it to inhabit deciduous forests. Perhaps a similar change, at present unknown, is taking place in the behavior patterns of the House Wren and Indigo Bunting, allowing them to invade a habitat formerly unoccupied by them.

DISCUSSION

A thorough survey of many types of edge is needed before the validity of forest edge as a community is established, but on the basis of this study and the related literature, I feel that the forest edge merits consideration as a distinct community. It has been shown that the forest edge is inhabited by a set of species different from that of the forest interior and that of the open field. As pointed out, there is some overlap, but among the three samples of edge compared in this study, two along a forest margin and one along a pastured creek, most of the species occurred in all three. Species which may be considered primarily forest-edge birds are the Field Sparrow, Mourning Dove, Cardinal, Goldfinch, Blue Jay, Robin, Yellow-billed Cuckoo, Indigo Bunting, Yellow-throat, Yellow-shafted Flicker, Red-headed Woodpecker, Crow, House Wren, Wood Pewee and Starling.

That certain species have made psychological adjustments to particular niches in the forest edge is further justification for the view proposed above. These adjustments take the form of specific behavior patterns (Lack, 1933, 1937; Moreau, 1935; Mayr, 1942; Miller, 1942; Kendeigh, 1945). One example, that of the Field Sparrow, has been discussed. Among others, the Yellow-throat uses the lower, outer part of the forest edge which borders and extends into the fields, whereas the Yellow-billed Cuckoo prefers that part which is the actual tree border and sometimes moves a short distance into the forest.

Finally, it may be observed that forest-edge communities provide light conditions somewhat intermediate between those of forest and field. There is greater freedom of movement along the edge than within the forest interior, but less freedom of movement than in the open field; physically, the edge habitat of grasses, shrubs and tree seedlings

is a step between forest and field. Walls (1942) was able to separate nocturnal and diurnal species according to the relative representation of rods and cones in the retina and thus to reveal an adaptation of the eye to light intensity. Perhaps a similar difference exists between forest and non-forest species. It is suggested that environmental relations such as these pertaining to light may be important factors in the relation which forest-edge species bear to neighboring, physically differing habitats.

SUMMARY

In a study of two central Illinois forests in the summer of 1943, fourteen species of birds were found to occur primarily along the forest edge and ten species in the forest interior. The Crested Flycatcher, Wood Pewee, Indigo Bunting, and House Wren were found in both habitats. Males of the Ruby-throated Hummingbird were forest-edge birds, the females forest-interior birds. The densities of the two forest-edge populations studied were 73 and 62.5 birds per mile, respectively; the densities of the forest-interior populations were 106 and 74 birds per 100 acres, respectively. The forest edge is considered to be a distinct community because it is inhabited by a characteristic set of species and because some, at least, of the birds which inhabit it display psychological adjustments to particular niches available only in the forest edge.

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