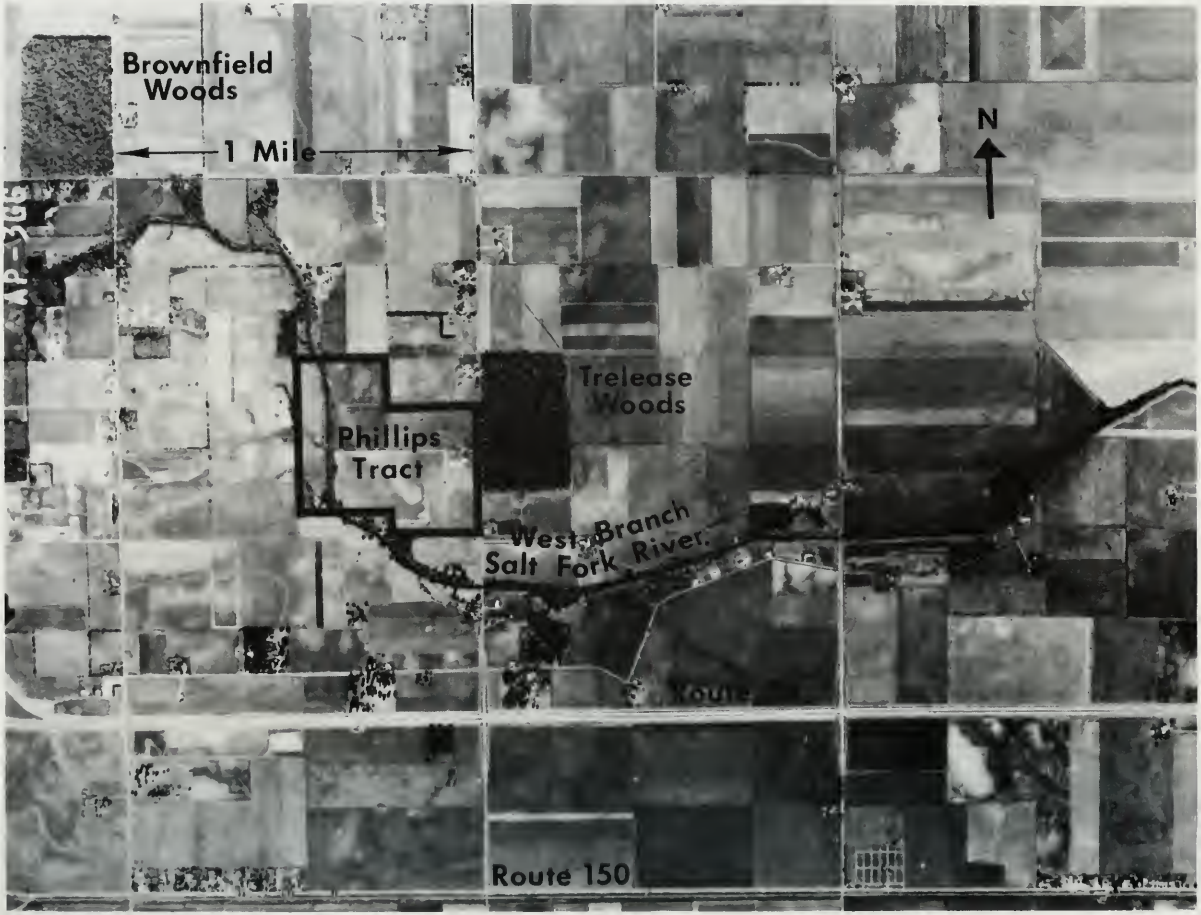
Bird Populations in East Central Illinois: Fluctuations, Variations, and Development over a Half-Century

S. CHARLES KENDEIGH

ILLINOIS BIOLOGICAL MONOGRAPHS 52

UNIVERSITY OF ILLINOIS PRESS

Bird Po
Fluctua
over a I


Brownfield
Woods
1 Mile
N
AP-3G5
Trelease
Woods
Phillips
Tract
West Branch
Salt Fork River
Route 150

Bird Populations in East Central Illinois: Fluctuations, Variations, and Development over a Half-Century

S. CHARLES KENDEIGH

ILLINOIS BIOLOGICAL MONOGRAPHS **52**

UNIVERSITY OF ILLINOIS PRESS

ILLINOIS BIOLOGICAL MONOGRAPHS

Volumes 1 through 24 contained four issues each. Beginning with number 25 (issued in 1957), each publication is numbered consecutively. Standing orders are accepted for forthcoming numbers. The titles listed below are still in print. They may be purchased from the University of Illinois Press, 54 East Gregory Drive, Box 5081, Station, A, Champaign, Illinois 61820. Out-of-print titles in the Illinois Biological Monographs are available from University Microfilms, Inc., 300 North Zeeb Road, Ann Arbor, Michigan 48106.

KOCH, STEPHEN D. (1974): The *Eragrostis-pectinacea-pilosa* Complex in North and Central America (Gramineae: Eragrostoideae). 86 pp. 14 figs. 8 plates. No. 48. $7.95.

KENDEIGH, S. CHARLES (1979): Invertebrate Populations of the Deciduous Forest: Fluctuations and Relations to Weather. 153 pp. Illus. Tables. No. 50. $12.50.

LEVINE, NORMAN D., And VIRGINIA IVENS (1981): The Coccidian Parasites (Protozoa, Apicomplexa) of Carnivores. 205 pp. Illus. Glossary. Index. No. 51. $15.95.

Library of Congress Cataloging in Publication Data

Kendeigh, S. Charles (Samuel Charles), 1904-
Bird populations in east central Illinois.

(Illinois biological monographs ; 52)
Bibliography: p.
Includes index.
1. Bird populations—Illinois. I. Title.
II. Series.
QL684.13K46 598.29773 81-16073
ISBN 0-252-00955-X AACR2

Frontispiece: Aerial photograph (September 1966) of William Trelease Woods and surrounding area (1 mile = 1.6 km). Courtesy U.S. Department of Agriculture.

Acknowledgments

I wish to acknowledge the comments and suggestions of James R. Karr, Mercedes S. Foster, A. J. Erskine, John T. Emlen, and Chandler S. Robbins who read early drafts of the entire manuscript and of Roland R. Roth who read the section dealing with succession on abandoned farmland. Hurst H. Shoemaker helped with the bird censuses at William Trelease Woods in 1941, 1944, and 1945 and John M. Edgington from 1973 through 1976. Without the participation of many graduate students this study could not have been carried out.

Students concerned with the bird counts at William Trelease Woods with the years in which they participated are: I. H. Blake, 1924–25 (publ. 1926); A. S. Hyde, 1926–29; A. C. Twomey, 1933–35 (publ. 1945); R. G. Lindeborg, 1935–37; C. T. Black, 1936–38; S. E. Jones, 1937; J. M. and D. Speirs, 1938–41, 1945–46; E. J. Koestner, 1939–41; H. C. Seibert, 1941–43, 1945–47; T. W. Roberts, 1942; V. R. Johnston, 1943 (publ. 1947); B. J. Fawver, 1946–47, 1949; M. M. Hensley, 1947–48; M. B. Eyster, 1948–50; G. R. Webb, 1948; D. A. James, 1949–53; R. K. Stubbs, 1950–51; C. M. Weise, 1952–53; G. C. West, 1953–58; W. L. Gillespie, 1954–58; R. D. Brewer, 1955–56; R. V. Kennedy, 1956–57; G. W. Cox, 1957; R. M. Eiseman, 1958; N. Forsythe, 1959; W. S. Brooks, 1960–65; L. B. Barnett, 1966–68; R. P. Balda, 1966; R. R. Roth, 1967–68, 1971; R. J. Clemans, 1968–72; B. W. Cain, 1971; E. D. Pentecost, 1971; D. J. Moriarty, 1972.

Students participating in the bird counts on abandoned farmland and in the forest at Robert Allerton Park with, for many, the dates of their Master of Science theses in parentheses are: D. G. Allison, 1946 (1947); M. M. Hensley, 1947 (1948); R. W. Reese,

1948 (1949); E. B. Holmes, 1949 (1950); C. M. Weise, 1950 (1951); D. H. Van Horn, 1951 (1952); R. W. Pearson, 1951 (1962); M. J. Robertson, 1953, 1955 (1959); J. Bursewicz, 1959 (1961); G. M. Schwager, 1960 (1961); R. P. Balda, 1962 (1963); R. M. Case, 1963 (1964); R. E. Pointer, 1964 (unpublished data); S. S. Borst, 1965 (1967); R. R. Roth, 1966 (1967), 1971; J. E. Hudson, 1967 (1968); C. W. Zellmer, 1968 (1969); W. H. L. Collier, 1969 (1971).

Contents

1. Introduction

Quantitative studies of bird populations have been carried on in east central Illinois since the beginning of the twentieth century. These permitted detailed analyses of the changes that have occurred and their probable causes. Similar changes have doubtless occurred in other parts of the country and hence are of general interest. Walcott (1974) summarized observations by bird students at Cambridge, Massachusetts, at intervals over a period of 105 years (1860 to 1964), and Lack (1969) reported annual censuses from 1928 to 1967, interrupted only during the war years, of land birds on a small island off southeast Wales. The National Audubon Society has long been concerned with obtaining quantitative data on fluctuations of bird populations in North America, beginning with the Christmas bird counts in 1900, breeding bird censuses in 1937, and winter bird population studies in 1947–48. Summaries of the data occur regularly in the Society's *American Birds*. Coordinated studies of this sort are being undertaken in other parts of the world (Pinowski and Williamson, 1974).

I am here concerned with analyzing variations in species composition and population sizes of the avifauna in east central Illinois over the half century from 1924 through 1976. East central Illinois includes Vermilion, Champaign, and Piatt counties with an extension into McLean County to include Funk Forest (Fig. 1). The region was originally covered by tallgrass prairie with forest largely limited to the floodplains and adjacent uplands along the rivers. Topographic relief is low, with elevaton of the upland varying only between about 200 and 225 m above sea level.

Graber and Graber (1963) provided a background for the present study in their comparison of population changes over the entire state of Illinois for the 50-year interval, 1906–9 to 1956–58.

Intensive observations, chiefly in Champaign County, by Smith (1930) and his classes in ornithology at the University of Illinois between 1903 and 1922, were summarized in a table of spring migration dates. Kendeigh et al. (1976) compiled a checklist for Piatt, Champaign, and Vermilion Counties that included 292 species of which 38 were permanent residents, 114 were transients, 75 were summer residents, 20 were winter visitors, 37 were accidental or very rare, and 8 are no longer present.

The present study is concerned with breeding bird populations in six upland and four bottomland or floodplain forests along the Sangamon River on the west and the Vermilion–Salt Fork River System on the east and how succession of bird populations on abandoned farmlands and on areas that have been stripped for coal lead to the climax community found in the forest. Unfortunately there was no large area of original prairie available for comparative study. Comparison of populations in the forested areas show the effects on species composition and community structure of tract size, habitat, and location in different river systems. The size of the tract, especially when surrounded by a different kind of vegetation, is of considerable importance in evaluating areas for preservation.

The longest and most concentrated monitoring of bird populations was undertaken at William Trelease Woods (Frontispiece). Succession of bird populations on abandoned farmland was studied from 1946 to 1971 at Robert Allerton Park. Christmas bird counts were taken over the region from 1941 to the termination of field observations in 1976. They are included to show whether fluctuations in bird populations at William Trelease Woods, especially permanent resident species, are representative for the region.

Fluctuations in population size have been shown in graphical form, and statistical analyses have been kept to a minimum. The population data, however, are presented in table form through the text and in appendices for whatever use other investigators may wish to make of them.

2. Location of Raw Data

Field data and notes on breeding and wintering bird populations and summary maps showing territories of individual species are filed in the archives of the University of Illinois Main Library at Urbana, Illinois. Unpublished Master of Science theses are in the stacks of the Main Library. These records and reports are available for use by other investigators.

3. Description of Forest Census Areas

The following accounts are derived in part from forestry publications. Analysis of the vegetation as it exists at the present time (1979–81) has been undertaken by J. R. Karr and J. G. Blake under a U.S. Fish and Wildlife Service contract (14-16-009-79-023) using modern procedures such as described by James and Shugart (1970) and others. Their report will be available after completion. It must be kept in mind, however, that the forest vegetation in some of my own census areas has changed considerably during the past half-century.

William Trelease Woods

William Trelease Woods, an isolated tract of approximately 24 ha (not 22.3 ha, as was incorrectly reported in the Breeding Bird Census and Winter Bird-Population Studies in *American Birds*) is located about 6.5 km northeast of Urbana in Champaign County

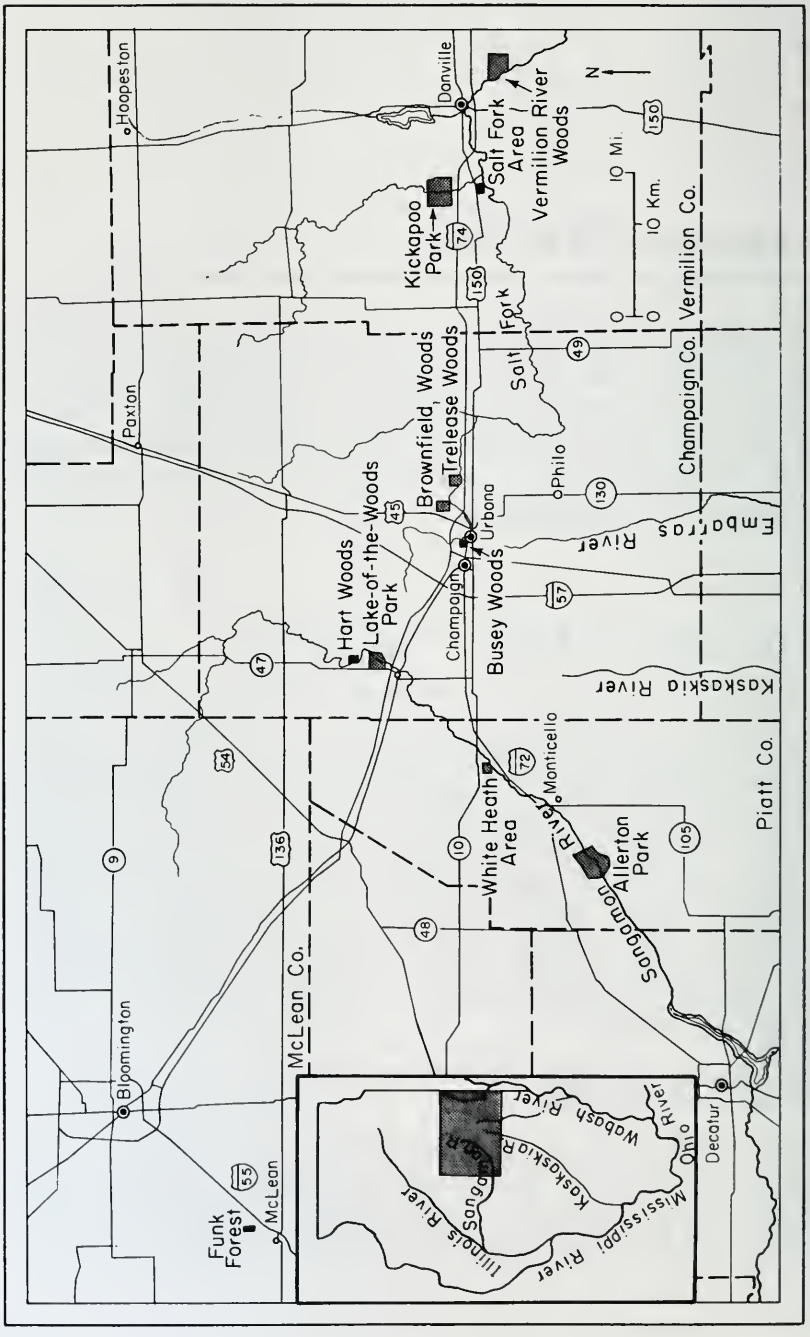


Fig. 1. East central Illinois with location of study areas.

(40°08′ N, 88°18′ W) (Fig. 1). Before settlement by white men, it was part of the so-called Big Grove, which covered about 26 km^2. The Big Grove was originally surrounded by prairie except for a corridor of trees along the West Branch of the Salt Fork River that connected with more extensive forest along the Vermilion River near the Illinois-Indiana state boundary. Most of the timber of the Big Grove was logged during the nineteenth century, except for this woods and Brownfield Woods (Fig. 1). William Trelease Woods was never clear cut, but the southern half served as a woodlot at one time, and some grazing was permitted. The tract was acquired by the University of Illinois in 1917–18 and has been protected from human disturbance since then, except for creation of a small pond along the east border in 1936.

The principal trees in the woods at the present time, in descending order of importance (sum of percent relative density and relative basal area) are sugar maple (*Acer saccharum* L.), hackberry (*Celtis occidentalis* L.), white ash (*Fraxinus americana* L.), slippery elm (*Ulmus rubra* Mühl.), basswood (*Tilia americana* L.), red oak (*Quercus rubra* L.), and Ohio buckeye (*Aesculus glabra* Willd.). Prior to the early 1950s, American elm (*Ulmus americana* L.) was a prominent species, but diseases later reduced it to minor importance. Sugar maple formerly covered about 30% of the area, mixed hardwoods 45%, and American elm 25% (Boggess, 1964). There was a total of 368 trees ha^{-1}, 7.6 cm and over in diameter breast height (DBH), with a basal area of 21 $m^2 ha^{-1}$. With disappearance of American elm in the 1950s, slippery elm and hackberry have increased. A relatively dense shrub stratum occurs irregularly and consists predominantly of pawpaw (*Asimina triloba* (L.) Dunal) and spicebush (*Lindera benzoin* (L.) Blume). A diversity of flowering herbs is conspicuous in spring, while in the summer wood nettle (*Laportea canadensis* (L.) Gaudichaud-Beaupré) is ubiquitous.

The woods has 2.0 km of edge, and in the early years farm crops of corn, soybeans, wheat, and oats came close to the forest along the south, east, and north borders so that the forest edge was quite narrow. In 1943 an eight-hectare field adjacent to the south border was planted with prairie grasses, and a good stand of tallgrass prairie was developed during the next few years. Shrubs

and trees slowly spread into the grassland. Likewise, a narrow strip was added along part of the east border and all of the north border, and a cinder road was built in this strip. A country road with two farm homes extends along the west side.

Funk Forest

Funk Forest is in McLean County (Fig. 1) about 24 km southwest of Bloomington between the towns of Funks Grove and McLean (40°21′ N, 89°09′ W). It is a rectangular 24-ha area at the south end of an extensive, nearly virgin, forest tract and was acquired by the University of Illinois in 1950. There is contact with open fields along the entire east and most of the south sides. Timber Creek, part of the Sangamon River System, crosses the area about a quarter of the distance from the south border. The south bank rises sharply and forms a bluff up to 12 m high.

Sugar maple is the leading dominant followed by white oak (*Quercus alba* L.), slippery elm, and American elm. There are 333 trees ha^{-1} with a basal area of 27 $m^2 ha^{-1}$. Some maples and oaks reach diameters of 76 cm (Boggess and Geis, 1966). The American elm was still present at the time the bird censuses were taken by Calef (1953) in 1950 and 1951.

Robert Allerton Park

There are some 180 ha of upland forest in the 600-ha Robert Allerton Park (Fig. 1), located along the Sangamon River (39°59′ N, 88°39′ W). The park was acquired by the University of Illinois in 1946. White oak ranks first in importance in the composition of the tree flora, based on percentage of total basal area (22 $m^2 ha^{-1}$), followed by black oak (*Quercus velutina* Lam.), red oak, white ash, sugar maple, and some 14 other species (Batzli, 1977). Sugar maple represents an invading species (Boggess and Geis, 1967) which apparently first appeared around 1900 (F. L. Johnson, personal communication). Selective cutting for oak is believed to have occurred in the Park between 1847 and 1965 (Johnson and Bell, 1975), and some logging may have occurred again in the mid 1890s (Sipp and Bell, 1973). Narrow roads, graded to permit access by automobiles, circle through the forest.

An area of about 7.3 ha (Fig. 26, 27:1) was censused by Allison (1947) in 1946. An adjacent area of 12.6 ha (Fig. 27:2) was censused over six years (Appendix 3): 1949 (Holmes, 1950), 1950 (Weise, 1951), 1951 (Van Horn, 1952), 1962 (Balda, 1963), 1964 (Pointer, unpubl. data), and 1966 (Roth, 1967). The first three censuses were taken before death of the American elm from disease, the last three censuses after the tree's disappearance but before the complete recovery of the forest.

Of the extensive floodplain forest along the Sangamon River at Robert Allerton Park (Bell, 1974), the portion censused was roughly triangular and contained 10.0 ha (Fig. 26, 27:3). It was bordered on the west and north by the river and similar floodplain forests and on the southeast by a bluff adjacent to the upland forest above described. In terms of percentage of total basal area of trees (21 $m^2 ha^{-1}$) measured between 1972 and 1974, silver maple (*Acer saccharinum* L.) was the most important dominant, followed by green ash (*Fraxinus pennsylvanica* Marsh.), bur oak (*Quercus macrocarpa* Michx.), sycamore (*Platanus occidentalis* L.), big shagbark hickory (*Carya laciniosa* (Michx. f.) Loud.), hackberry, and ten other species (Batzli, 1977). The forest was essentially virgin. Numerous vines hung from the trees, patches of common elder (*Sambucus canadensis* L.) and buttonbush (*Cephalanthus occidentalis* L.) were present, and during the summer the ground was densely covered with wood nettle and poison ivy (*Rhus radicans* L.), which reached heights of 1–1.5 m. Death of elm trees in the 1950s disrupted the canopy considerably in the north central part of the area, which came to simulate a broad forest edge.

Bird censuses (Appendix 3) were taken in 1949 (Homes, 1950), 1950 (Weise, 1951), 1951 (Van Horn, 1952), 1963 (Case, 1964), and 1967 (Hudson, 1968).

White Heath Area

This 20-ha study area lies a short distance upstream from Robert Allerton Park (Fig. 1) in Piatt County. It is about 1.6 km north of White Heath village, on the north side of the Sangamon River, and immediately east of a secondary highway. Farmland occurs

above the bluff on the north. There has been no recent logging or grazing in the area but the forest is relatively young second growth. Similar forest extends along both sides of the river in both directions.

The principal dominants in order of decreasing importance are slippery elm, silver maple, hackberry, green ash, and hawthorn (*Crataegus* sp.). The number of trees over 6.2 cm (DBH) is 583 ha^{-1}. Climbing grape (*Vitis* sp.) and poison ivy make dense tangles in trees, shrubs, and over fallen logs and the ground is covered with giant ragweed (*Ambrosia trifida* L.) and wood nettle in the summer. The area was censused by Fawver (1947) in 1946.

Hart Memorial Woods

Hart Memorial Woods lies about 4.8 km northeast of Mahomet in Champaign County (Fig. 1) on the east side of the Sangamon River (40°14′ N, 88°21′ W). It contains 14.2 ha of which about 9.1 ha are upland. The upland forest is continuous for several kilometers to the south, but on the north and east the forest is bounded by farmland, a road, and dwellings. The University of Illinois acquired the area in 1965.

White oak is most important in the upland, then black oak, slippery elm, and red oak. American elm occurred before the epidemic. Sugar maple is absent. There are 310 trees ha^{-1} 7.6 cm or over (DBH), with a basal area of 278 $m^2\,ha^{-1}$ (Root et al., 1971). Logging occurred here about 125 years ago (Johnson and Bell, 1975). The breeding birds were censused by Blem and Blem (1975) in 1966 and 1967 and by Willson (1974) in 1969 and 1970. The populations for the first two years, as originally reported, have been revised for some species, and averages have been made for the four years.

A wooded bluff divides the upland forest from the 5-ha floodplain forest, which is part of a continuous forest along the river. Open fields occur across the river. American elm formed nearly a pure cover before the advent of the elm diseases, but at the time of the censuses, silver maple, green ash, and small young American elm were most important, followed by seven other species (Root et al., 1971). Total trees number 154 ha^{-1} and basal area is 132 $m^2\,ha^{-1}$. It is a young forest.

Salt Fork Area

This area of 6.2 ha is on the north side of the Salt Fork River above its entry into the Vermilion River, southwest of Danville, Illinois (Fig. 1). The area was strip-mined for coal between 1900 and 1910 and at the time of the census, 1966 (Karr, 1968), the oldest tree had only 49 growth rings. The canopy was closed, however, and the dominant tree species were eastern cottonwood (*Populus deltoides* Bartr.), silver maple, and sycamore. It is part of a continuous forest along the river.

Vermilion River Woods

In 1958 the University of Illinois purchased a tract of about 193 ha approximately 6.4 km southeast of Danville, Vermilion County, in the wooded strip on the east side of the Vermilion River (40° 5′ N, 87° 35′ W). Part of the area is used for an observatory containing parabolic radio-telescopes, but most of the area is undisturbed. Smock (1970) conducted a breeding bird census on 16 ha of the best part of the wooded area in 1969. About 56% of the study area is fairly level upland which had been exposed to grazing by domestic animals until 1959, and the remainder consists of fairly steep slopes to a branching intermittent stream that crosses the area. The principal dominant trees are, in order, red oak, hickory, white oak, and sugar maple. An understory, mainly of sugar maple and eastern hophornbeam (*Ostrya virginiana* (Mill.) K. Koch.), is scattered in the upland but dense on the slopes.

4. Methods of Censusing

Spot-mapping of Breeding Birds

A. S. Hyde (unpublished data) derived breeding bird populations in 1927 and 1928 from maps of the woods showing the location of nests or of birds that repeatedly showed solicitude for definite localities when the search for nests proved fruitless. Twomey (1945) visited the woods almost daily during the nesting seasons of 1934 and 1935 and mapped territories. Effort was also made from 1936 to 1939 to map the location of nesting pairs. The woods were gridded with stakes in 1939 at intervals of 50 m, each stake being numbered and lettered according to its position in vertical and horizontal rows. Following rows of stakes insured a uniform coverage of the whole area. Beginning in 1940, the size of the breeding bird population was obtained by the standard spot-mapping method (Williams, 1936; Kendeigh, 1944). I began to supervise and participate in the field work at this time. Censuses were taken yearly except for the breeding seasons of 1929–33 and 1938 (see Acknowledgments for participants).

The location of all birds observed on each trip was plotted on a separate map of the woods. Greatest attention was given to singing males, but the location of females and nests was also recorded. The routes which I took, usually with an assistant, follow the pattern shown in Figure 2. Censuses usually started at 0700 or 0730 hours and required 3–4 hours. Care was taken with dense populations to check simultaneous presence of neighboring males before mapping of additional birds. After nesting was over, a composite map was made for each species, showing the location of birds on all trips. These locations usually fell into groups which identified territories and were easily counted. Where males were concentrated, territories were not distinguished unless adjacent birds

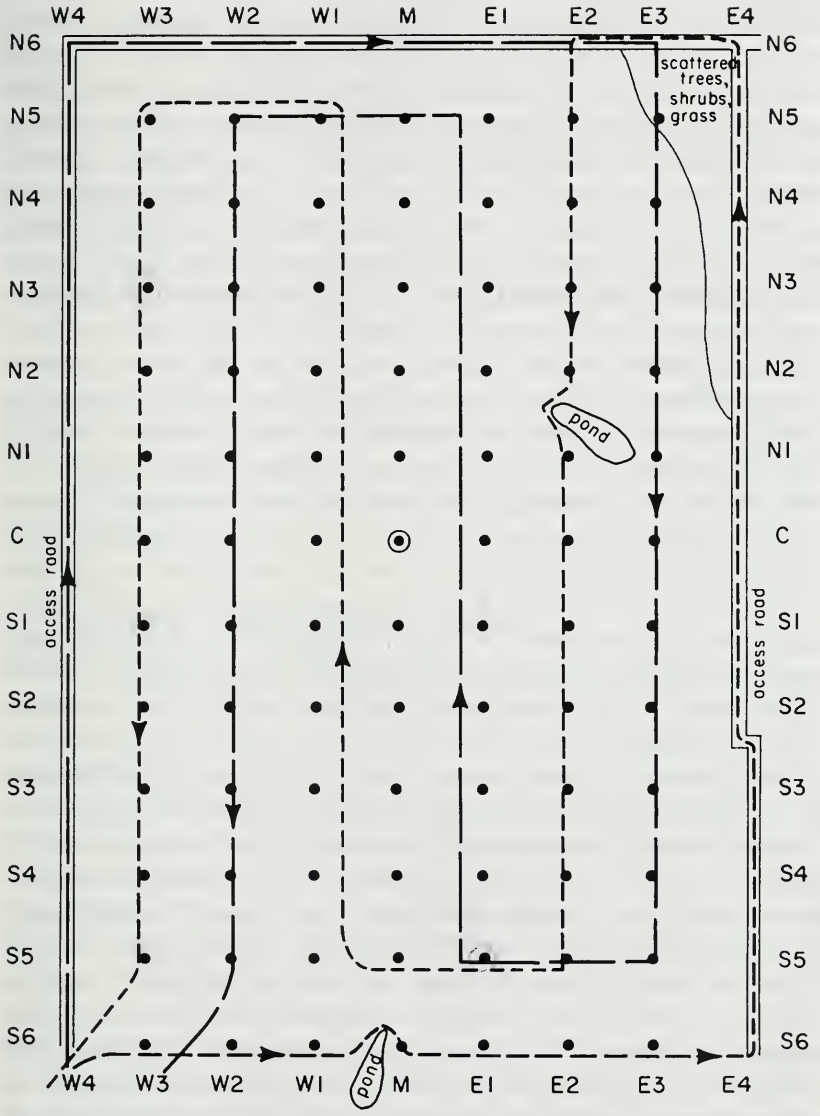


Fig. 2. Usual routes of two observers taking a bird count in William Trelease Woods. Stakes at 50-m intervals bear letters and numbers of horizontal and vertical lines.

had been simultaneously recorded on one or more dates. Each territory was assumed to represent a nesting pair (Appendix 1). Not all birds that were present were found on each trip. Single counts do not usually record over two-thirds of the birds later established to be present (Palmgren, 1930; Kendeigh, 1944; Stewart et al., 1952; Enemar, 1959; Preston, 1979). Greatest weight was placed on the number of territories established at the height of the nesting period for the species. For most hole-nesting species this was mid-April through May; for migrant species, the main nesting period was June; a few species delayed nesting until July and August. Some species raised two or more broods, but usually fewer nesting pairs were present during later months. This procedure followed closely that recommended by the International Bird Census Committee (Robbins, 1970).

The accuracy of the population estimates depends partly on the number of counts taken and their distribution through the nesting season. In 1941, a minimum of two counts each in April and May, three or four in June, one or two in July, and one in August was set, although this was not always attained. I made all the composite territory maps so that there was uniformity in interpretation of the data from year to year. Based on the frequency and distribution of counts, the censuses in 1939, 1945, and 1947 are evaluated as poor, although the species present and population levels measured appeared normal; those in 1927, 1928, 1936, 1937, 1940, and 1946 are rated as fair, while the rest are considered good.

The accuracy of the censuses varied with the species (Stewart et al., 1952). The counts for the less numerous species were probably total. With the more abundant species, it was not always possible to know whether scattered dates on composite maps represented one or more territories. The tendency was probably to underestimate rather than overestimate densities (Best, 1975). Blue jays were difficult to count because they appeared often to leave their territories. Starlings were most difficult of all, as their territories were only small areas around the nest. The density of this species was based on the number of tree sites on which birds were observed calling or perching. Although the spot-mapping method of censusing is subject to various shortcomings, it is the

most practical procedure available (Enemar, 1962; Slagsvold, 1973; Svensson, 1974; Berthold, 1976; Robbins, 1978).

The spot-mapping procedure does not necessarily measure the total number of birds that nest in an area during the season or insure that those present are actually nesting. This is shown by my studies with the house wren (Kendeigh, 1944) where all nests were located and all birds banded. The identity of individuals on a territory often changed during the season, especially between broods. Some males and females left the area by the end of the first nesting period, or earlier if their nesting attempt failed. Other birds appeared for the first time during the second nesting period. Some males with territories never secured mates. Other studies have shown that birds may be present that never attempt nesting during the season. This possible non-breeding population was not measured. I make no claim, therefore, for the complete accuracy of the yearly estimates of breeding populations at William Trelease Woods, but because the censuses were conducted in a nearly similar manner every year they are comparable, and major fluctuations in population size from year to year should have meaning.

Cruising for Wintering and Transient Birds

Blake (1926) states that in his winter census of William Trelease Woods in 1924–25, he covered the entire woods "at least weekly and frequently oftener." The winter bird counts of A. S. Hyde from 1926–27 to 1929–30 were less frequent. Twomey (1945) made two counts per week during the winters of 1933–34 to 1935–36 and more frequent counts during the migration periods. He gives a diagram of the way he cruised the woods. No counts were made in the winters of 1925–26, 1930–31 to 1932–33, and 1936–37. Since 1941, the routes which my assistant and I took followed the pattern shown in Figure 2. Two counts were ordinarily made each in December, January, and February, but the total number varied from four to seven. The counts were taken in the early morning and required 2–2.5 hours. Considerable dependence was placed on locating birds by their calls or songs. The place where each bird was found was marked on a map of

the woods, so that duplication of the same individual in counts was minimized, although difficulty was experienced with some conspicuous and wandering species, such as the blue jay. Individual birds or flocks of birds wandered from day to day throughout the woods, and some would leave for days or weeks at a time to feed in surrounding wooded areas and farmlands. The density index used was simply the mean number of birds observed per count (Appendix 2).

Transients during the migration periods were counted in the same manner as wintering birds, and populations indicate only the number observed on particular dates. Since migrant birds remained for only short periods, a few hours or a few days, I have no idea as to the total number of individuals that passed through the woods.

Christmas Bird Counts

Christmas bird counts were taken annually, beginning in 1941, in late December, by members of the Champaign County Audubon Society under my general direction. The correct interpretation of these counts involves many difficulties (Raynor, 1975). To reduce these difficulties and to make the counts comparable from year to year, the same areas, with some slight variation, were visited at the same time of day each year. The count began about 0800 hrs and terminated about 1630 hrs, with an hour out for lunch. The area covered extended from the Sangamon River valley near White Heath to Lake-of-the-Woods on the north, Brownfield and Trelease Woods on the east, and University South Farms and pine plantation on the south, about 450 km^2 (Fig. 1).

The data for each year were analyzed in terms of number of birds observed per party-day. A party-day consisted of 4.8 ± 1.0 hours ($\bar{X}$ ± SD) on foot covering approximately 9.7 km and about 2.5 hours in roadside observations by car covering about 55 km. Approximately 40% of effective censusing was in forest, 30% in forest edge and shrubby fields, 28% in farmland and along roadsides, and 2% over water. These percentages do not represent existing proportions of these habitats in the region. Farmland is heavily predominant.

The size of parties increased through the years but averaged 3.9 observers. The number of party-days involved in a count increased from about 2 in the early years to 6 in the later. With more party-days, there was more complete coverage of the area. Minor variations in the number of observers from year to year were largely compensated for by varying the size of parties. I can find no evidence that weather on the day of censusing significantly affected general trends in population size. One should exercise caution in interpreting the data, however, because the Christmas bird counts are for only one day early in the winter and are unlikely to represent average populations for the entire winter, as do the winter counts at William Trelease Woods.

5. The Avifauna of William Trelease Woods

The species composition and average population sizes of breeding birds are given for two years near the beginning and two years near the end of the period of study, since they were years of most extensive observations by Twomey (1945) and myself (Table 1).

The avifauna was both more varied and more numerous in the later period. Previous to 1952, the largest number of species recorded breeding in any year was 27; beyond this year there were never less than 28 species, generally over 30, with the largest number (38) in 1953 (Appendix 1). The total number of species of land birds recorded was 61 and the average number over 42 years, 28. One species of water bird, the great blue heron *(Ardea herodias),* started to build a nest near the pond on the east side of the woods in April 1958, but then left the area. It is not included in the statistics for the woods. Populations began to go consistently over 100 pairs per year in 1941, over 200 in 1959, and to drop below 200 again in 1967. Over the entire period, they averaged 165 pairs.

The woods avifauna has been divided into four categories corresponding to the biotope (biotic community and physical habitat combined) in which each species is found most characteristically. Forest-edge species (FE) are largely confined to the forest edge, mixtures of trees, shrubs, and grasses, or if they nest in the forest, do practically all of their feeding outside the forest (Johnston, 1947). Open-forest species (OF) are wide ranging, occurring along forest edges, openings in dense forest (e.g., treefalls), and in open woods. Closed-forest species (CF), a term suggested by C. S. Robbins (personal communication), spend most of their time in and under the forest canopy, and forest-interior species (FI) are

largely limited to extensive tracts of forest (see p. 66). The number of species in each of the first three categories at William Trelease Woods is approximately equal, with OF species having the most numerous pairs. The greater abundance of birds in 1974–75 compared with 1934–35 was owing to quadrupling of the number of forest-edge birds and to more than doubling of the open-forest birds. Why these changes in the biotope categories occurred will be brought out later in this monograph.

ble 1. Breeding pairs (excluding the brown-headed cowbird) in William Trelease Woods fore and after a 40-year interval

ecies	Status[1]	Biotope[2]	1934–35	1974–75
oper's hawk	SR	OF	0.5	0
d-tailed hawk	PR	FE	0	0.5
nerican woodcock	SR	OF	0	0.5
urning dove	SR	OF	1.0	6.0
llow-billed cuckoo	SR	OF	1.5	3.5
eat-horned owl	PR	CF	0	0.5
rred owl	PR	CF	1.0	0
by-throated hummingbird	SR	OF	1.0	0
mmon flicker	PR	OF	1.0	10.5
d-bellied woodpecker	PR	CF	0	4.0
d-headed woodpecker	PR	OF	3.0	5.0
iry woodpecker	PR	CF	1.0	1.0
wny woodpecker	PR	CF	4.5	4.0
eat crested flycatcher	SR	CF	4.5	3.0
stern wood pewee	SR	CF	3.5	5.0
ue jay	PR	OF	0	15.0
mmon crow	PR	FE	3.5	+[3]
rolina chickadee	PR	OF	0	0.5
fted titmouse	PR	CF	4.5	0
ite-breasted nuthatch	PR	CF	0.5	0.5
use wren	SR	OF	3.5	11.0
rolina wren	PR	CF	0	1.0
ay catbird	SR	FE	1.0	0.5
own thrasher	SR	FE	1.0	1.5
nerican robin	SR	OF	0	17.5
od thrush	SR	CF	3.0	2.5
rling	PR	FE	9.0	62.5

Table 1. (continued)

Species	Status[1]	Biotope[2]	1934–35	1974–75
Red-eyed vireo	SR	CF	6.0	4.5
Common yellowthroat	SR	FE	1.5	3.5
Northern oriole	SR	FE	0	1.0
Brown-headed cowbird	SR	——	(+)	(+)
Scarlet tanager	SR	FI	0	0.5
Cardinal	PR	OF	3.0	6.0
Rose-breasted grosbeak	SR	OF	0	0.5
Indigo bunting	SR	OF	21.5	8.0
American goldfinch	SR	FE	1.0	1.5
Rufous-sided towhee	SR	FE	0	1.5
Field sparrow	SR	FE	1.0	4.5
Song sparrow	PR	FE	1.0	0.5
Total species (excluding brown-headed cowbird):				
		FE	8	11
		OF	9	12
		CF	9	10
		FI	0	1
		Combined	26	34
Total pairs:		FE	19.0	77.5
		OF	36.0	84.0
		CF	28.5	26.0
		FI	0	0.5
		Combined	83.5	188.0

[1] SR, summer resident; PR, permanent resident.
[2] FE, forest edge; OF, open forest; CF, closed forest; FI, forest interior.
[3] + = Present, but nesting density too low to measure.

The wintering population included all the permanent residents, occasional summer residents such as the mourning dove and American robin, and winter visitors from the north. Winter visitors regularly included brown creeper, winter wren, dark-eyed junco, and tree sparrow. The ring-necked pheasant, a permanent resident in the region, commonly roosted in the woods in the winter but did not nest there. Flocks of juncos wandered throughout the woods but, along with flocks of tree sparrows, were more common on the forest edge. The total number of species recorded during

the 48 winters was 48, with an average of 20 species per year (Appendix 2). As with breeding birds, there were generally fewer than 20 species per year before the winters of 1949–50 to 1952–53 and more than 20 afterwards. The number of individual birds overwintering averaged 101, but was generally more than this number from 1953–54 through 1966–67, and less than this number both before and after this period.

The most common transients were several species of wood warblers, sparrows, thrushes, and blackbirds, two species of kinglets, and the yellow-bellied sapsucker.

6. The Yearly Cycle

In order to show how bird populations varied monthly throughout the year, bird counts were made from December 1973 through February 1975 at intervals of about two weeks during the autumn and winter and of seven to ten days during spring migration. These are combined with the breeding bird census of 1974 in Figure 3.

Populations of permanent resident species (Table 1, PR) were lower during the winter months than during the nesting season as birds dispersed into the surrounding farmlands. The starling is a permanent resident in the region but largely deserted the woods after nesting was over, except for clear sunny days in the winter when individuals or small flocks were observed at potential nest-sites. It is shown separately because of its large numbers.

The main influx of summer residents (Table 1, SR) occurred during April and May and the main exodus in August and September. The nesting population became well established by mid May or early June and remained fairly stable through July. Numbers did not increase as young birds left the nest. It appeared that both adults and young dispersed quickly out of the woods and presumably began their autumn migration. Such an exodus of birds in late summer was also observed by Williams (1936) for a deciduous forest tract in northern Ohio, by Stewart et al. (1952) at the Patuxent Research Refuge in Maryland, and by Holmes and Sturges (1975) at the Hubbard Brook Experimental Forest in New Hampshire.

The number of winter visitors was largest in February and March as birds wintering farther south passed through on their way northward and again in October and November as they returned southward.

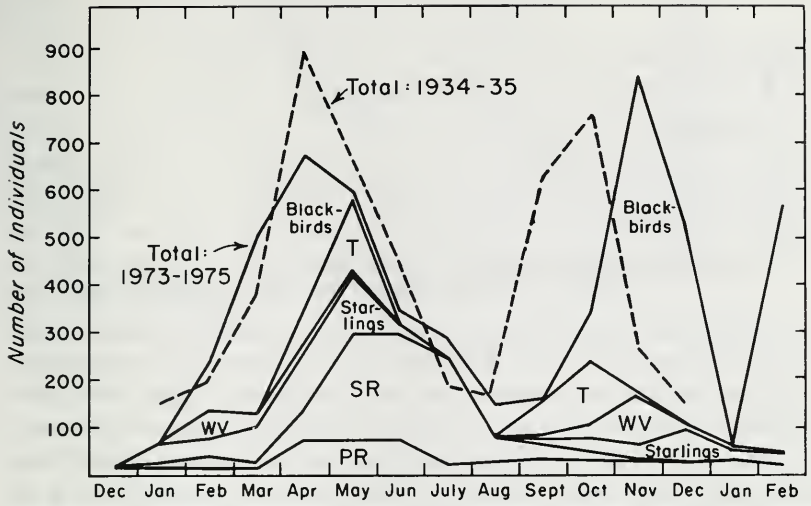


Fig. 3. Variations in mean number of birds per month in William Trelease Woods from December 1973 through February 1975. The data for 1934–35 are averages for two years (Twomey, 1945). PR, permanent residents; SR, summer residents; WV, winter visitors; T, transients.

Among the transients other than blackbirds, sparrows attained peak numbers a little earlier (late April and early May) than wood warblers (mid May) in the spring and significantly later in the autumn (October, compared with late August and September).

The earliest and latest migrants in the woods were blackbirds. Large flocks of common grackles, red-winged blackbirds, rusty blackbirds, brown-headed cowbirds, and, in recent years, Brewer's blackbirds occurred in the woods in early spring and late autumn. The common grackle persisted in the woods in small numbers during late spring and early summer and increased somewhat in numbers in late summer. It did not nest in the woods but did some feeding and roosting there. The cowbird remained common in the woods through June and did at least part of its feeding there. The red-winged blackbird nested in surrounding fields and sang from trees at the forest edge. Twomey (1945) did not mention the occurrence of these large transient flocks of blackbirds in the woods for the years 1934 and 1935, and no observations

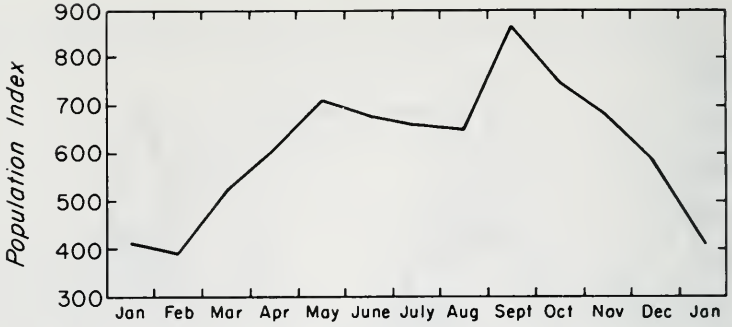


Fig. 4. Variation in approximate number of invertebrates per square meter during the course of 38 years in William Trelease Woods. Invertebrates in or on tree trunks were not censused. All other forms were largely restricted to the ground litter and soil from December through March, but occurred also in the herb, shrub, and tree foliage during the rest of the year. Counts were made weekly from April through October—and less frequently during the winter— of 0.1-m^2 ground samples and 48 sweeps with an insect net separately through herb, shrub, and lower tree strata (Kendeigh, 1979).

of them are reported from the 1940s. A large flock of approximately 2,000 common grackles was recorded on 28 March 1953. Systematic counts during other than breeding and winter months are generally lacking for the intervening years. It appears, however, that the stopping here of these species in such large numbers is a fairly recent development.

When blackbirds are included, peak populations of all species came in April and November. Excluding blackbirds, peak populations occurred in May and October. Total populations given by Twomey (1945) for 1934–35 are in round numbers only. Large flocks of transient sparrows in April and October helped to establish his population peaks. Spring populations, other than blackbirds, were higher than autumn populations. This was true also for Funk Forest (Calef, 1953), and in a hardwood forest in northern Ohio (Williams, 1936) if the large flocks of migrating robins that occurred there in the autumn are excluded. Lower peak populations in autumn are explained by summer residents' having dispersed elsewhere, by the more leisurely southward movements of the transients over a longer period, and perhaps also by the greater difficulty in censusing non-singing, less conspicuous birds. In the Patuxent Research Refuge in Maryland, Stewart et al.

(1952) found the highest number of species in the spring but the highest number of individuals in the autumn.

Birds depend considerably on animal food during the months when it is available. Monthly fluctuations in the invertebrate populations in William Trelease Woods (Fig. 4) agree well with fluctuations in bird populations, an increase beginning in March, peak numbers in May and again in September and October, a leveling out over the summer months, and a decline to lowest numbers during the winter. Many overwintering bird species are largely granivorous.

7. Fluctuations from Year to Year

Fluctuations in size of bird populations at William Trelease Woods were measured over a span of 50 years (Appendix 1, 2). Causes of these fluctuations were often difficult to ascertain, but correlations with weather, food supplies, changes in the vegetation, competition between species, and the occurrence of predators will be made and quantified whenever possible.

Weather

Mean monthly temperature during the principal breeding season (April, May, June) varied only about 5° C between extremes (Fig. 5). Mean temperature during the coldest month of the winter was below 0°C in all but three years and varied 12°C between extremes. Very low temperatures lasting only a day or two may sometimes cause considerable mortality, especially when the procurement of food is difficult. Since many birds feed on the ground, the amount and duration of snowfall are critical. Occasional winters had nearly 50 cm of snow in one month.

Food

Weekly population measures (less frequently over winter) of insects, spiders, other arthropods, and mollusks in William Trelease Woods (Kendeigh, 1979) showed a conspicuous surge in the size of these populations over the decade beginning in the early 1940s (Fig. 6).

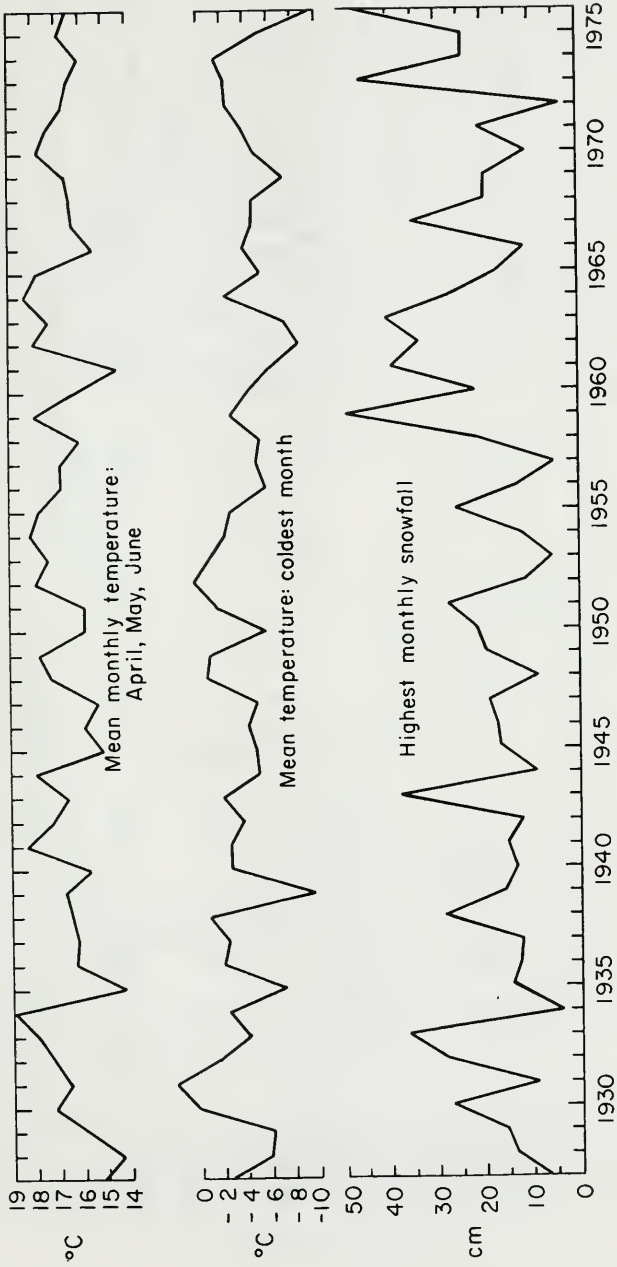


Fig. 5. Fluctuations in weather (U.S. Weather Bureau, Urbana).

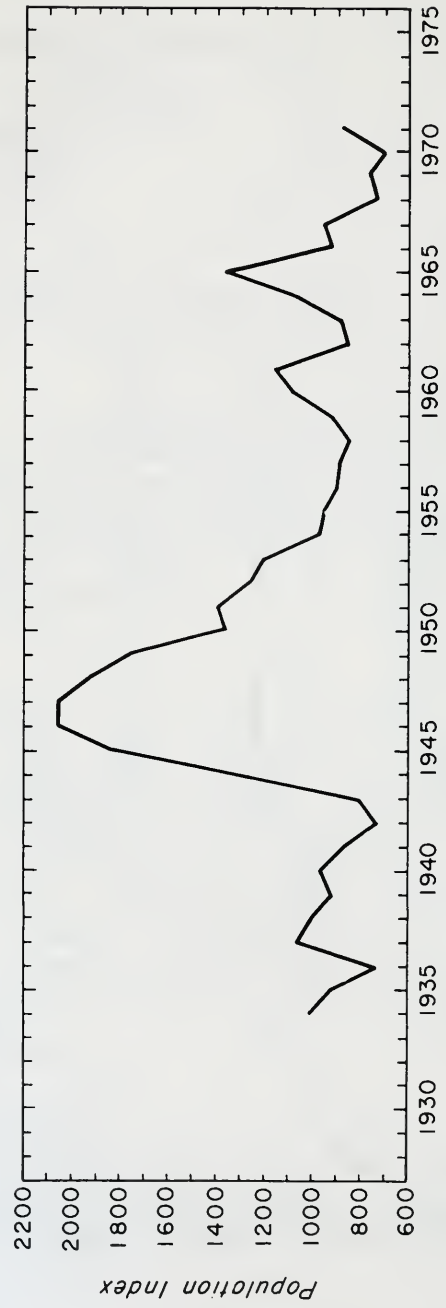


Fig. 6. Fluctuations from year to year in maximum monthly invertebrate population (mean number per square meter) at William Trelease Woods (Kendeigh, 1979).

Vegetation

Important for interpretation of fluctuations in bird populations from year to year is the time sequence in the destruction of elm trees that took place throughout the region. Within the city limits of Champaign-Urbana, the first mortality of trees was observed in 1944, when the American elm became infected with a mycoplasm-like organism that is spread by a leafhopper (*Scaphoideus luteolus* Van D.). This produces a phloem necrosis. Dutch elm disesase, caused by a fungus (*Ceratocystis ulmi* (Buism.) C.) and carried by a native bark bettle (*Hylurgopinus rufipes* Eichh.) and a European bark beetle (*Scolytus multistriatus* Marsh.) began to kill trees in 1951. All native elm species may be infected with the disease, but the American elm is most susceptible. Both diseases spread rapidly during the 1950s (Fig. 7). By 1961, more than 99%

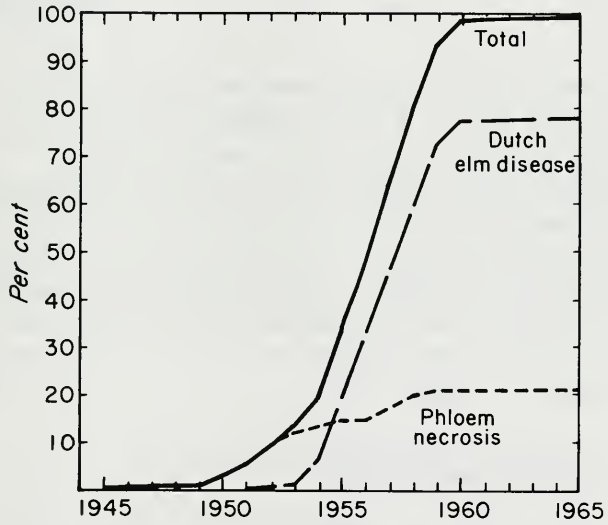


Fig. 7. Cumulative percentages of the original elm tree population in Urbana-Champaign lost through diseases (Carter and Carter, 1974).

of all elm trees were dead (Carter and Carter, 1974). In William Trelease Woods, scattered dead elm trees were first noticed in 1953, they became very conspicuous in 1954, and it was evident

in 1955 that the American elm tree population in the woods was doomed. Dead trees remained standing for several years; their bark peeled off, and they eventually fell. Their death opened up the forest canopy considerably, as they had covered 25% of the area. The forest canopy began to close again in the late 1960s but had not been completely restored by the end of the study period in 1976.

Hawks, Falcons

The Cooper's hawk (OF) nested in William Trelease Woods 11 times in the 17 years between 1927 and 1949 and then disappeared. It was generally absent from the region from early January to mid March. The red-tailed hawk (FE), a permanent resident, appeared in the woods in 1956 and nested during 10 of the following 20 years. The American kestrel (FE), a partial migrant, appeared only during some years when neither of the other two species was present.

Graber and Golden's (1960) analysis of Christmas bird counts for 22 localities in central Illinois between 1903 and 1955 showed major peaks in numbers of wintering red-tailed hawks from 1930 to 1933. Our Christmas bird counts in east central Illinois included 7–11 birds in 1945, 1947, 1950–51, and 1960–61 but smaller numbers in other years. In general, populations of red-tailed, red-shouldered, rough-legged, and marsh hawks and American kestrels were fairly well maintained until the early 1960s. Since then, numbers have declined, as they have in other states (Brown, 1971; Temple and Temple, 1976).

Bobwhite, Ring-necked Pheasant

The bobwhite (FE) and ring-necked pheasant (G) were present on surrounding farms but did not nest at the woods. They were observed more frequently along the forest edge during the winter and at times the pheasant sought shelter throughout the woods. Christmas counts indicated greater numbers of bobwhite in the region before 1955 than later when the ring-necked pheasant became more numerous. There was a peak in numbers of the

pheasant in east central Illinois and throughout the state in 1963. Preno and Labisky (1971) attribute the general decline after 1963 to a decrease in acreage of hay fields and increases in corn and soybeans.

Owls

The barred owl (CF) disappeared as a breeding bird in the woods after 1939 and the great horned owl (CF) first made its appearance in 1949, after which it was recorded almost every year. The screech owl (OF) may well have been present more frequently than recorded, as this species is easily overlooked in daytime censusing. The long-eared and saw-whet owls were caught in mist nets being used in another project.

Mourning Dove

The mourning dove (OF) nested only occasionally in the woods until 1953 but then increased rapidly to a peak of 17 pairs in 1959, after which it declined (Fig. 8). This corresponded to changes in the forest canopy with the death of elm trees. Graber and Graber (1963) reported populations in central Illinois to be about the same in 1957–58 as in 1907–9, but apparently there was a decline in numbers over the state in 1960 to a level about which it fluctuated during the next decade (Preno and Labisky, 1971).

Cuckoos

The yellow-billed cuckoo (OF) fluctuated in the woods between zero and six pairs throughout the half-century (Fig. 8). The black-billed cuckoo (FE) was rare.

Woodpeckers

Five species of woodpeckers occurred in William Trelease Woods throughout the year, each occupying a slightly different feeding and nesting niche (Lawrence, 1967; Willson, 1970; Reller, 1972; Williams, 1975; Williams and Batzli, 1979a, b). Populations varied

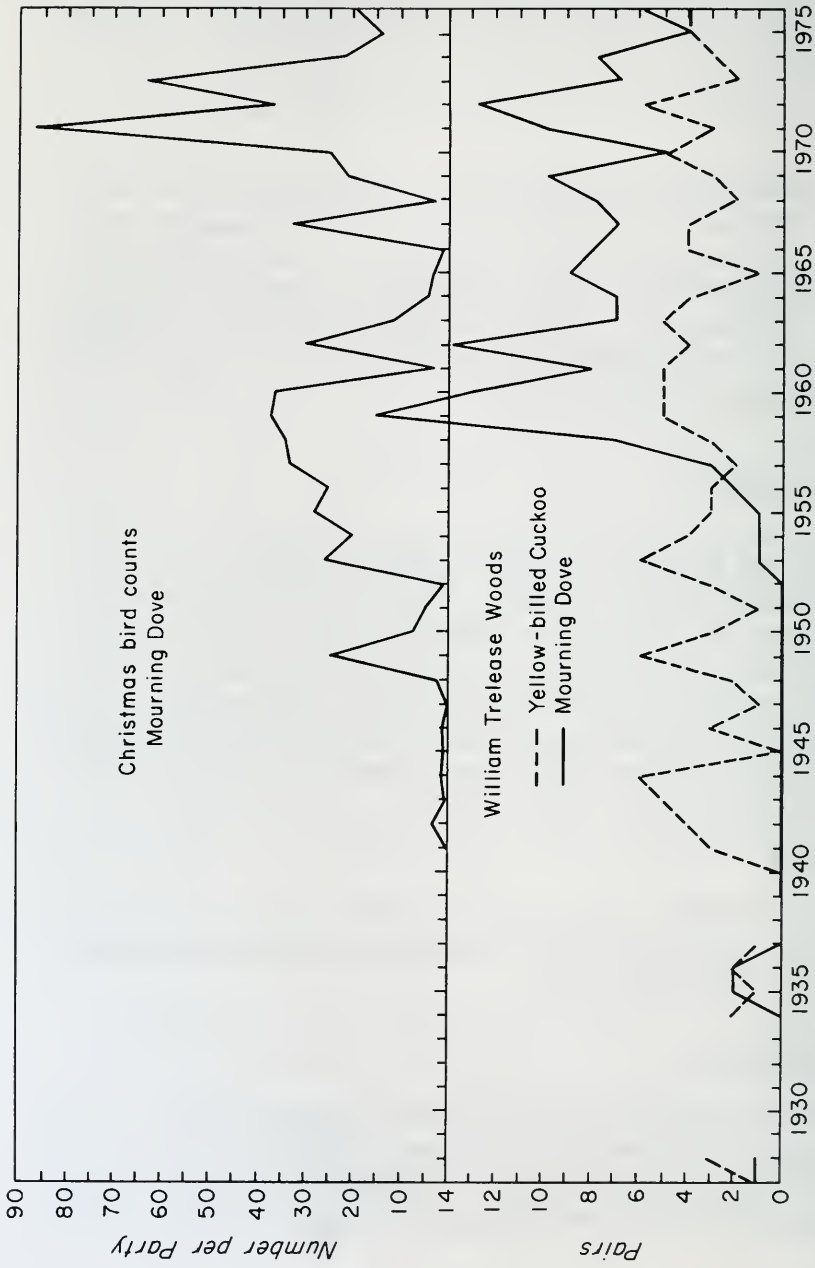


Fig. 8. Fluctuations in breeding (pairs) and early winter populations (number per party) of the mourning dove and yellow-billed cuckoo.

between summer and winter (Table 2). For the period before onset of the elm diseases, 1927–50, the overwintering population of the common flicker (OF), a partial migrant, was higher than during the summer. The population of red-bellied woodpeckers (CF) was about the same winter and summer, which means that only sufficient young birds remained in the woods to replace the mortality and dispersal of adults. The red-headed woodpecker (OF) was an irregular migrant, overwintering in large numbers some years, scarce or absent in others. There was dispersal of hairy and downy woodpeckers (CF) out of the woods in the winter.

With dying of elm trees in the 1950s, both nesting and overwintering population of all species increased except for the hairy woodpecker in the summer and perhaps the common flicker in the winter (Table 2). These increases were widespread in east central Illinois since they appeared also in the Christmas bird counts. Increases were greatest in the red-headed woodpecker. Peak populations were reached in different years in different species.

Increase in numbers of woodpeckers was probably a response to more insect food as the trees rotted and to abundant possibilities for excavating nesting and roosting cavities. The common flicker feeds mainly on ground insects, particularly ants, so its lack of significant increase in numbers overwintering is understandable. Since elm mortality was widespread through the region and state, the increase in woodpecker populations doubtless resulted from increased reproduction rather than from attraction of birds from elsewhere as sometimes occurs (Yeager, 1955).

Winter populations of red-headed woodpeckers fluctuated extensively, with peaks coming usually at intervals of two or three years. These peaks are better shown in the Christmas bird counts (Fig. 9). The species stores oak acorns for overwinter use (Williams and Batzli, 1979a). Quantitative collections of fallen acorns in a square-meter trap under a single bur oak at the south edge of William Trelease Woods indicated good crops in 1956, 1959, 1965, 1968, 1970, and 1971, but poor crops in the intervening years. In Robert Allerton Park there was a relatively poor acorn crop from white oak trees in 1973 and an abundant crop in

Table 2. Number of individual woodpeckers and starlings in William Trelease Woods before and after death of elm trees

Species	Biotope inhabited[1]	Mean, 1927–1950		Peak populations after 1950					
				Nesting			Overwintering		
		Nesting	Overwintering	Year	No.	Increase[2]	Year	No.	Increase[2]
Common flicker	OF	1.7 (2)[3]	2.6 (9)[3]	1964	28	16.5x	1952	4	1.5x
Red-bellied woodpecker	CF	1.9 (2)	2.0 (4)	1955–57	8[4]	4.2	1956	9	4.5
Red-headed woodpecker	OF	2.3 (5)	0.5 (5)	1965	58	25.2	1963	29	58.0
Hairy woodpecker	CF	2.0 (4)	1.4 (5)	——	2	1.0	1956	4	2.9
Downy woodpecker	CF	8.1 (6)	7.4 (12)	1959	26	3.2	1956	19	2.6
Starling	FE	35.6 (50)	3.4 (25)	1960	184	5.2	1965	47	13.8

[1] OF, open forest; CF, closed forest; FE, forest edge.
[2] Compared with mean populations, 1927–1950.
[3] Peak numbers in parentheses.
[4] 10 individuals (5 prs.) nesting in 1975 and 1976 are unexplained but not related to disturbances produced by death of elms.

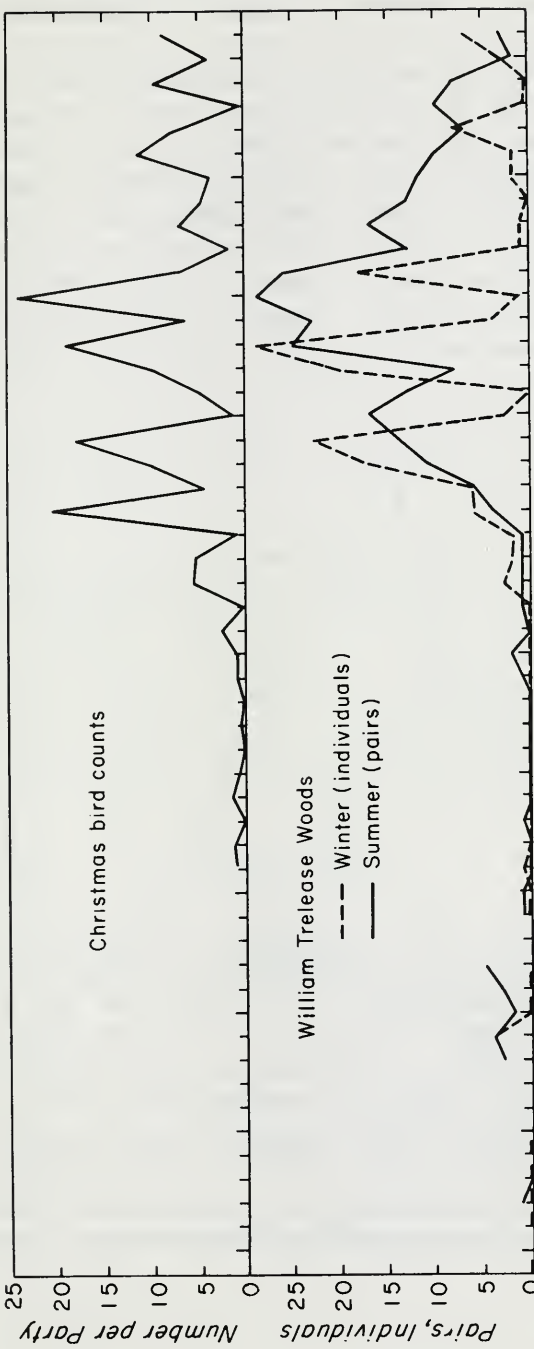


Fig. 9. Fluctuations in breeding (pairs) and overwintering populations (individuals, number per party) of the red-headed woodpecker.

1974 (Johnson, 1975). These peaks and troughs agree well with fluctuations in the red-headed woodpecker population, except for 1963.

Three-year moving averages were plotted (Fig. 10) to evaluate the possibility that competition between species may have caused peak populations to occur at different times. The starling was included because it competes with woodpeckers for nest cavities, usually successfully (Löhrl, 1956; Kilham, 1958; Troetschler, 1976). Populations of common flicker and downy and red-bellied woodpeckers were all on the increase by 1953 or 1954. The red-bellied woodpecker reached a peak in 1956, and the downy woodpecker maintained relatively large numbers from 1955

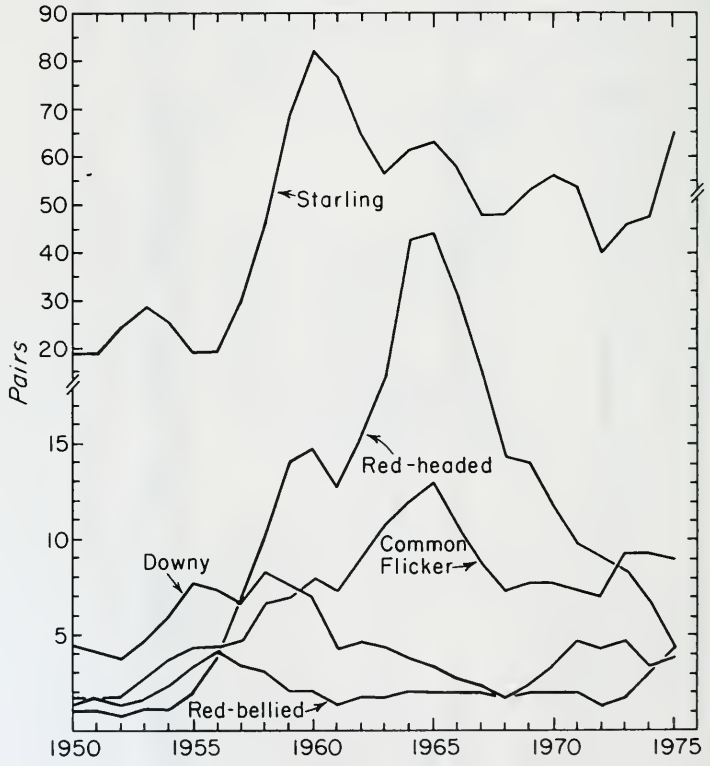


Fig. 10. Three-year moving averages of breeding populations of four species of woodpeckers and the starling in William Trelease Woods.

through 1960, after which it declined rapidly. Red-headed woodpeckers did not begin to increase until 1955 and the starling until 1957. The rapid and very large increases in these latter two species may have led to the decline of red-bellied and downy woodpeckers. The red-headed woodpecker is especially aggressive against these two species, sometimes forcing red-bellied woodpeckers to leave an area and restricting downy woodpeckers to foraging in the lower part of the tree canopy (Williams and Batzli, 1979a, b). Likewise, the red-headed woodpecker is more resistant to attacks by starlings than are other species of woodpeckers (Kilham, 1958). But the population rise of the red-headed woodpecker was interrupted between 1959 and 1961 when starlings were at peak numbers, and the rapid rise in numbers of red-headed woodpeckers from 1961 to 1964 coincided with a sharp decline of starlings. The decline in numbers of starling, red-headed woodpecker, and common flicker after 1965 was probably caused by falling of dead elm trees.

Troetschler (1976) calculated general trend lines (5-degree polynomial regressions using least squares fit) for populations of red-headed woodpeckers, common flickers, and starlings at William Trelease Woods and concluded that the presence of starlings seemed not to have caused a decrease in the numbers of the two woodpeckers. However, much is lost when fluctuations are smoothed over sequences of several years. Likewise, neither Troetschler's analysis nor ours shows how much greater the populations of woodpeckers would have been, had the starling not been present.

Flycatchers

The great crested flycatcher (CF), in contrast to the eastern wood pewee (CF), maintained a fairly constant population through the years (Fig. 11). The two species were about equally abundant until the late 1940s, but then the wood pewee doubled its numbers by the mid 1950s. There followed a fluctuating but progressive decline until populations were reached in the 1970s similar to those in the 1940s. The surge in the population of the wood pewee preceded the disruption of the forest canopy with the death of elm trees by about ten years, and, in fact, the population was declining when the canopy disruption was at its maximum. This evidence does not

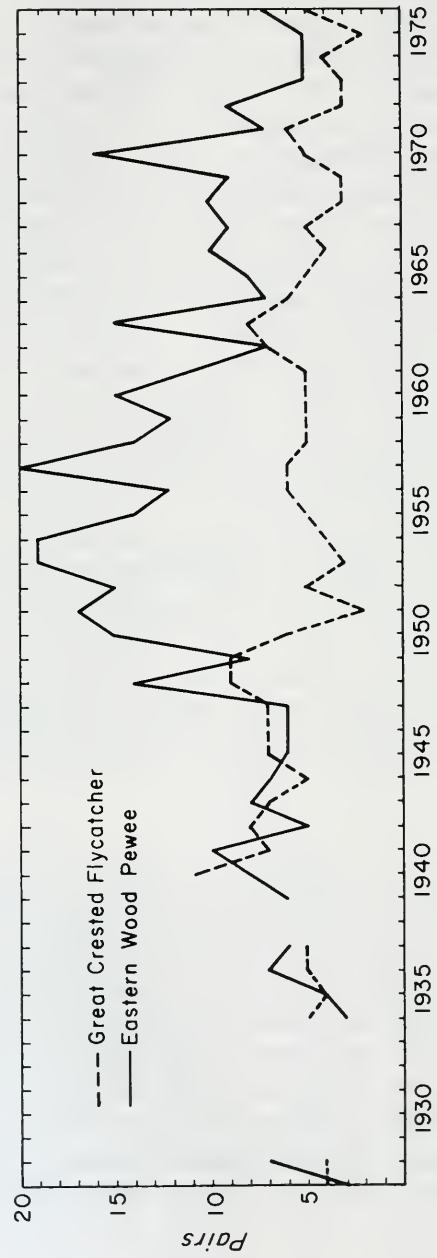


Fig. 11. Fluctuations in breeding populations of two flycatchers in William Trelease Woods.

indicate a preference of the species for open forests or treefalls as suggested by Hespenheide (1971). The population rise and decline, however, may have been influenced by the fluctuation of invertebrate populations (Fig. 6), if a lag in response of three to five years is allowed. I do not know why the great crested flycatcher did not respond similarly and can only suggest that the insect species on which it feeds did not experience an increase.

The Acadian flycatcher (FI) was seen only occasionally in the woods and the eastern kingbird (FE) only once. All the flycatchers are migratory.

Blue Jay, Common Crow

The blue jay (OF) nested only infrequently in the woods until the canopy was disrupted in the 1950s (Fig. 12). Its numbers then increased dramatically, and it became one of the more common nesting species, this despite the later closing of the canopy. The increases in breeding and wintering populations may have been simply a local phenomenon, because the Christmas bird counts do not show any similar changes in winter abundance. Increases or peaks in abundance during the winter in both woods and region coincided with five of the seven years of high acorn production (p. 31). Mast is commonly used as food during this season.

The common crow (FE) nested regularly in the woods to 1952, with peak numbers from 1943 through 1947. The steady decline thereafter was correlated with the appearance of the great horned owl. Crows were frequently observed "mobbing" the owl during the daytime.

Chickadees, Tufted Titmouse, Nuthatches

Blake (1926) listed the black-capped chickadee (OF) as present in the winter of 1924–25, A. S. Hyde in 1927–28; and A. C. Twomey's original records show black-capped chickadees in the woods in 1933–34. The only chickadee that I have heard singing in the woods since the winter of 1951–52 has been the Carolina chickadee. There is no record of chickadees in the woods during the interim. There

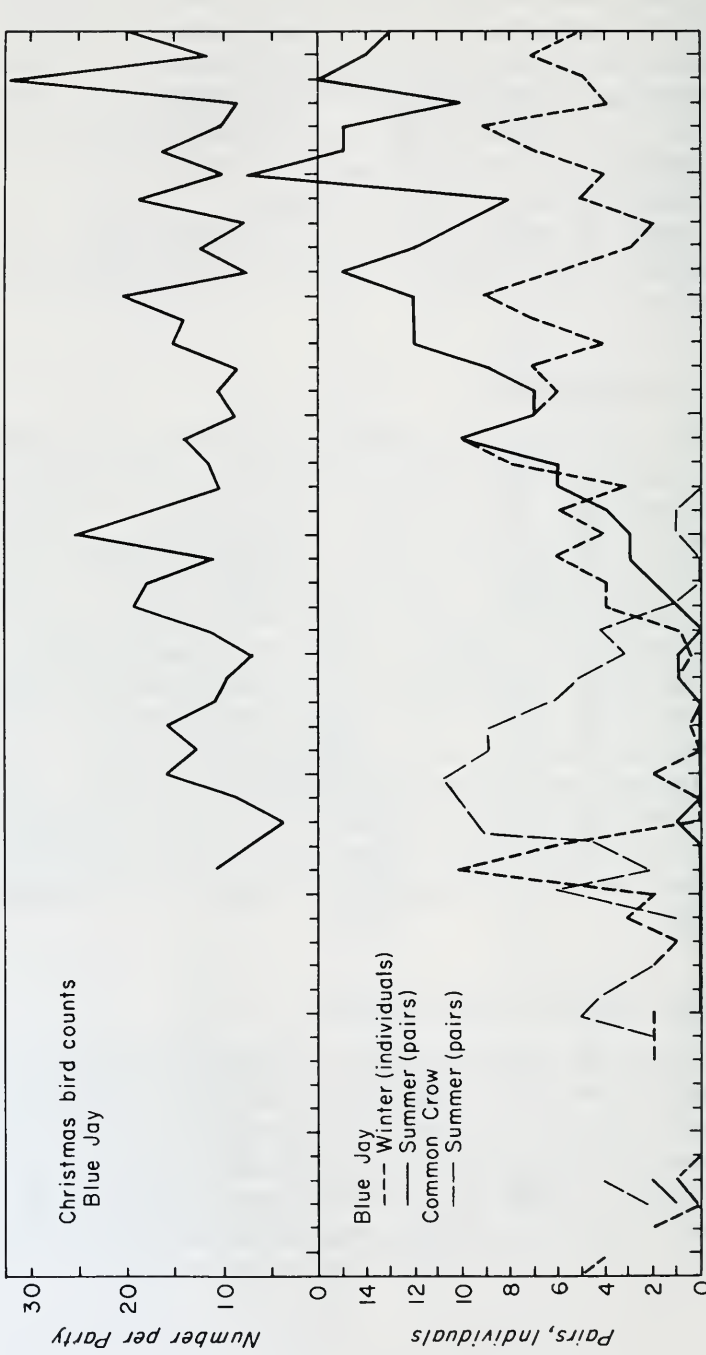


Fig. 12. Fluctuations in breeding (pairs) and overwintering populations (individuals, number per party)(blue jay and common crow).

has been a general decline in numbers of black-capped chickadees in the Christmas bird counts since 1963.

The tufted titmouse (CF) was a common breeding and overwintering species in the woods until the early 1960s (Fig. 13). It disappeared as a nesting species in 1966 and was seen only sporadically during the winter until it also disappeared during the winter of 1970. There has been a general decline over the region since the early 1950s.

The white-breasted nuthatch (CF) was recorded in William Trelease Woods more frequently in the winter than in the nesting season. Christmas bird counts indicate a general decline in the region since 1966. The red-breasted nuthatch was recorded in the woods during only two winters.

The cause of declines in these three species is not known, but since all are hole-nesters, there may have been harassment from the increased numbers of starlings and woodpeckers. The white-breasted nuthatch and tufted titmouse also come into conflict with red-headed woodpeckers in the winter for stored mast supplies (Kilham, 1958; Williams and Batzli, 1979a).

Brown Creeper, Kinglets

The brown creeper occurred fairly regularly in William Trelease Woods during the winter and the golden-crowned kinglet less frequently. As shown by the Christmas bird counts, there was a regional irruption of the golden-crowned kinglet in the winter of 1948–49, but this did not include William Trelease Woods. The ruby-crowned kinglet was recorded four times in the Christmas bird counts (1954, 1972, 1973, 1976).

Wrens

The Carolina wren (CF) occurred in William Trelease Woods as a permanent resident (Fig. 32), the winter wren as a sporadic winter visitor, and the house wren (OF) as a regular summer resident.

House wrens were scarce in the woods during the early years (Fig. 14) but became the most abundant species in all but three

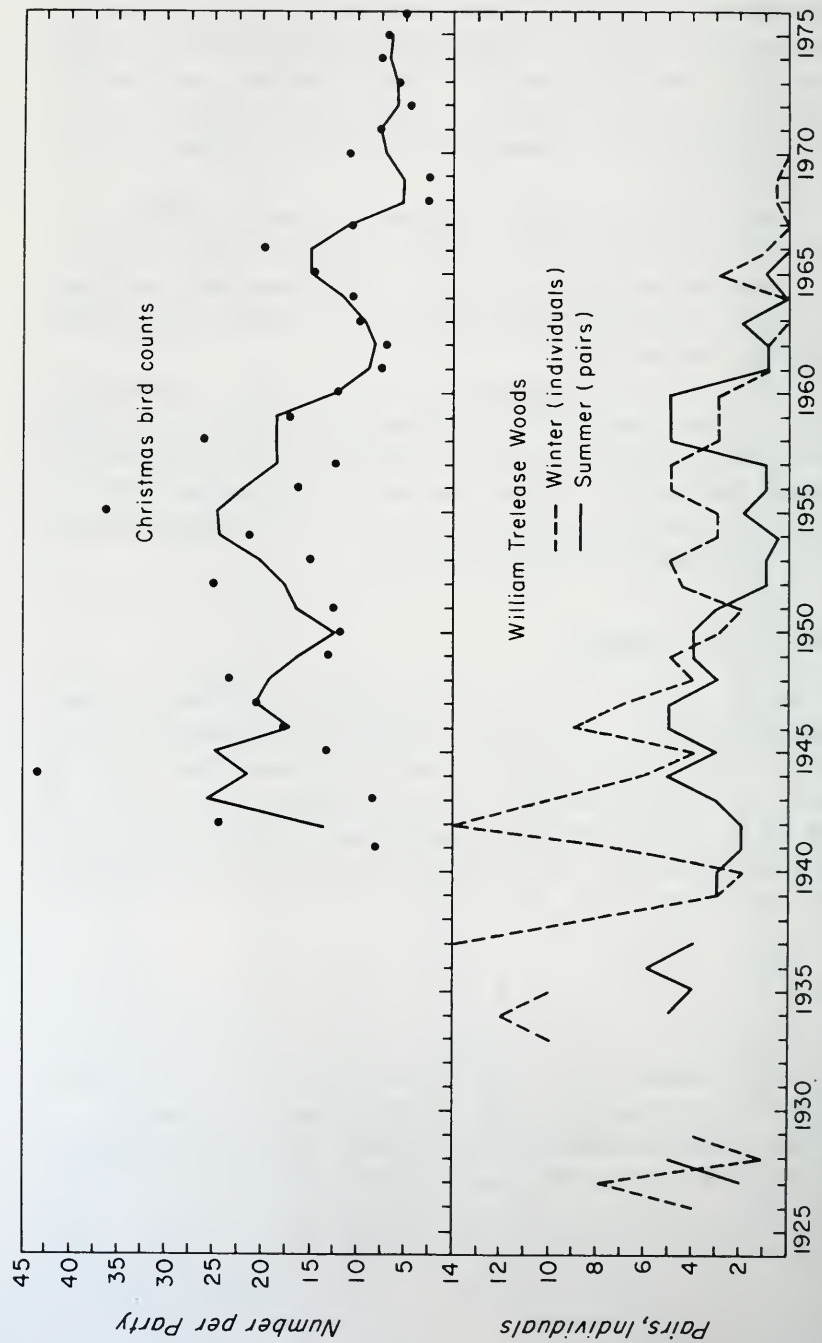


Fig. 13. Fluctuations in breeding (pairs) and overwintering populations (individuals) of the tufted titmouse in William Trelease Woods (below) and three-year moving averages (number per party) of early winter populations (above).

of the 16 years from 1942 to 1957 (for a map of house wren territories in 1942 see Kendeigh 1944: 92). These large populations began before and extended beyond the increase in invertebrate populations (Fig. 6) and cannot be correlated with the death of elm trees, or with June temperatures, or June and July precipitation.

The species, however, is sensitive to drops in temperature below zero during the winter (Kendeigh, 1934), and low temperatures could also have affected their arthropod food supply. To determine the relation between winter temperatures and population size, mean temperatures during the coldest month each year were averaged for five localities in the wren's wintering range: Tampa and Jacksonville in Florida, Savannah in Georgia, and Montgomery and Mobile in Alabama. The peak population of 1949 coincided with the highest temperature during the preceding winter for any year between 1933 and 1976 (Fig. 14). Lesser peaks in 1943 and 1957, but not in 1955, correlated with peaks in temperature. The wren population, however, did not respond to the warm winter of 1952. The extremely cold winters of 1940 and 1958 coincided with low nesting populations the following summers. Likewise, declining populations from 1960 to 1971 correlated with winter temperatures persisting below normal. Statistical analysis shows that the correlation between breeding population and temperature in the wintering range the preceding winter is highly significant ($P < 0.001$), and the coefficient of determination ($r^2 = 0.54$) indicates that over half of the fluctuation in population size is accounted for by the temperature factor. As a postscript, no house wrens nested in William Trelease Woods in 1977, following a winter with the lowest temperature (ave. 5.8°C) during the period of study.

Any correlation between fluctuations in the local breeding population and mean temperature over the extensive wintering range must mean that fluctuations in population size of the house wren at William Trelease Woods reflect to some extent fluctuations in the species' population over its entire breeding range in eastern United States. Evidence from *Audubon Field Notes* (now *American Birds*) indicates that populations were generally depressed in 1940 and 1958.

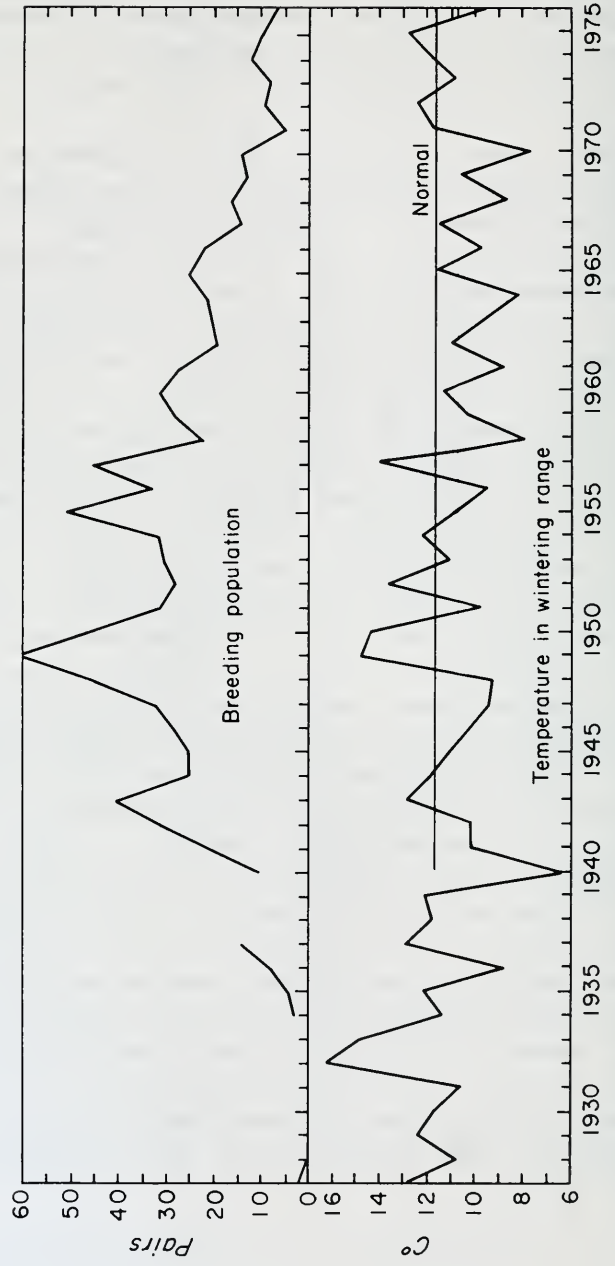


Fig. 14. Fluctuations in breeding populations of house wrens in William Trelease Woods and in mean temperature of the coldest month of the preceding winter (December through February) on the species' wintering range. The horizontal line is the normal temperature for the coldest month, i.e., the mean of all available records.

Gray Catbird, Brown Thrasher

These forest-edge (FE) species were present almost every year since the early 1950s, rising to peak numbers in 1968 and 1969 (Fig. 15). Deterioration of the forest canopy allowed these birds to extend their territories farther into the forest, but in nearly all instances territories were observed to have at least one boundary on the forest edge.

American Robin, Wood Thrush

The American robin (OF) was rarely found inside the woods until the forest canopy began to open in the early 1950s, but then continued to increase in abundance to a peak in 1974 despite reclosing of the canopy (Fig. 16). In this latter year, only the starling was a more abundant nesting species in the woods. The wood thrush (CF) was present fairly regularly and was apparently unaffected by changes in the forest canopy.

Starling

The first report of starlings (FE) in east central Illinois is for February 1922 (Smith, 1922). Twomey's (1945) original notes indicated their presence in William Trelease Woods during October and November 1933, and he reported eight pairs nesting the next spring. None was reported in 1927–28, so the species presumably invaded the woods in the interval. It used the woods only for nesting, doing all its feeding in the surrounding countryside.

Breeding populations increased abruptly in 1958, following a winter when more than usual numbers came into the woods (Fig. 10). Since 1958 breeding populations have averaged three times the size they were preceding that year, and winter populations have also been higher. The increase was probably the result of dead elm trees providing abundant natural cavities for nesting. The starling also competes, often successfully, for cavities excavated by woodpeckers.

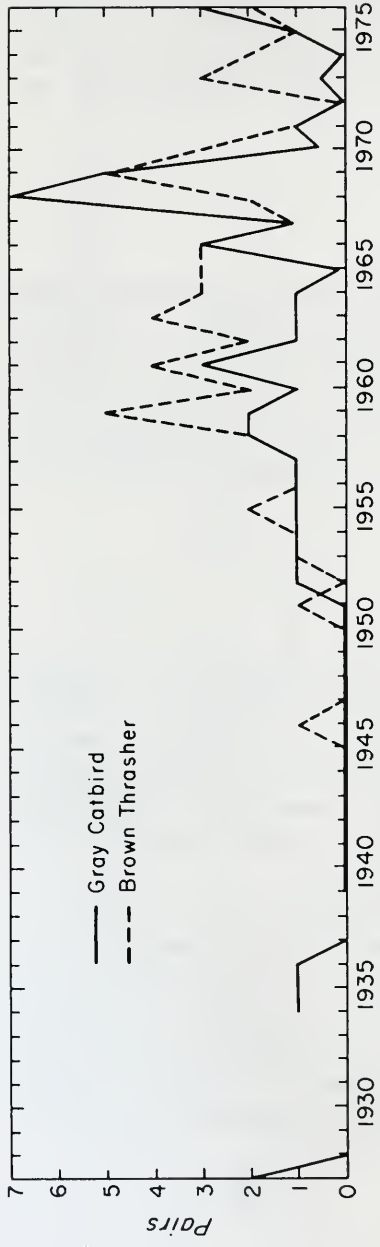


Fig. 15. Fluctuations in breeding populations of gray catbird and brown thrasher in William Trelease Woods.

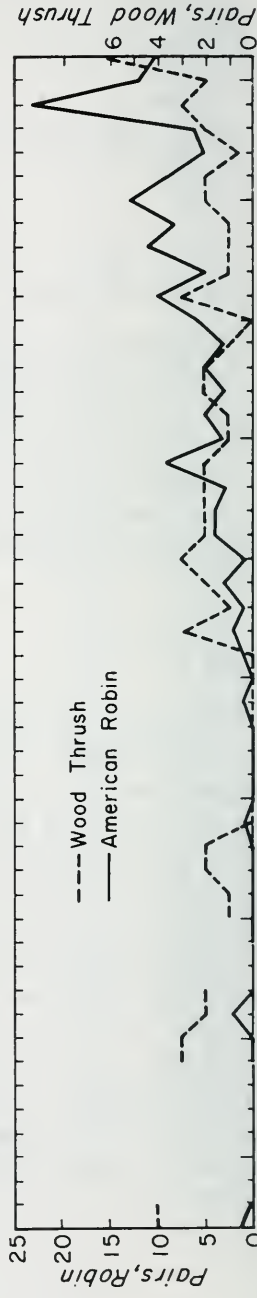


Fig. 16. Fluctuations in breeding populations of wood thrush and American robin in William Trelease Woods.

Red-eyed Vireo

The red-eyed vireo (CF) increased in numbers in the late 1940s, lagging behind the increase in abundance of invertebrates by about four years, and decreased after the population of invertebrates had declined and as the forest canopy became disrupted (Fig. 17). Since 1960 its numbers have been comparable to those in the mid 1930s.

Common Yellowthroat

The common yellowthroat (FE) showed an increase in the late 1950s, along with other forest-edge species, and since then has maintained populations averaging about double what they were before 1950 (Fig. 17). The species was not recorded in 1927 and 1928.

House Sparrow

The invasion of a forest-edge species into the woods with the opening of the canopy in the late 1950s and its virtual disappearance as the canopy again became closed is probably best shown by the house sparrow (FE) (Fig. 18). The house sparrow nested in cavities in the dead elm trees and probably roosted in them during winter nights.

Cardinal

Breeding populations of cardinals (OF) were significantly higher after the break in the forest canopy than before. The average population ($\overline{X} \pm SD$) after 1955 was 5.4 ± 1.9 ($n = 21$) and earlier, 2.7 ± 1.0 ($n = 23$).

Large numbers of cardinals overwintered in the woods in 1926 and 1927 and again in 1933 and 1934, but in later years fewer birds wintered than nested there (Fig. 19). Large numbers of cardinals were found in the Christmas bird counts in the early winter of 1961. This correlates with a small peak in the nesting population of the woods, but a larger peak of nesting birds in 1970 does not show in the Christmas bird counts.

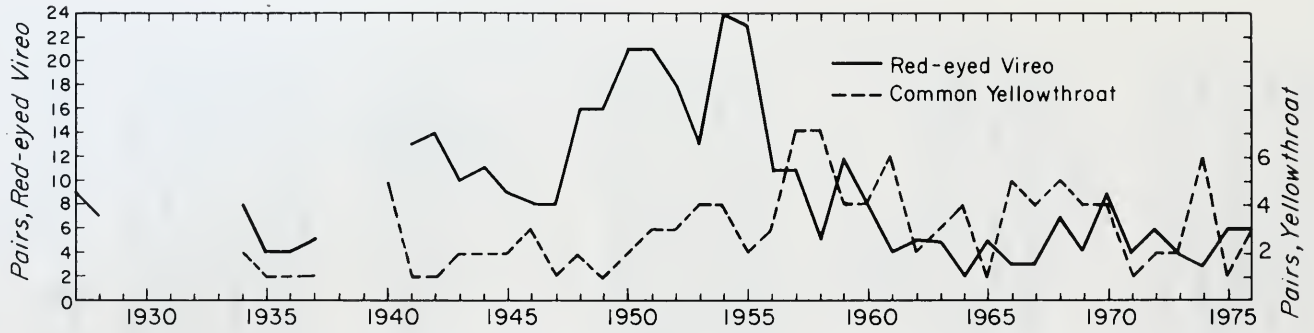


Fig. 17. Fluctuations in breeding populations of red-eyed vireo and common yellowthroat in William Trelease Woods.

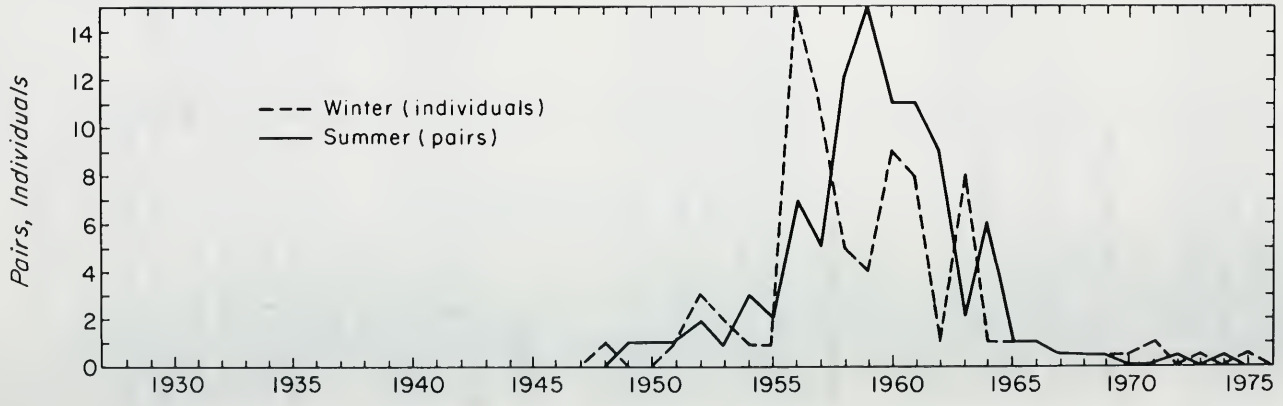


Fig. 18. Fluctuations in breeding (pairs) and overwintering (individuals) populations of the house sparrow in

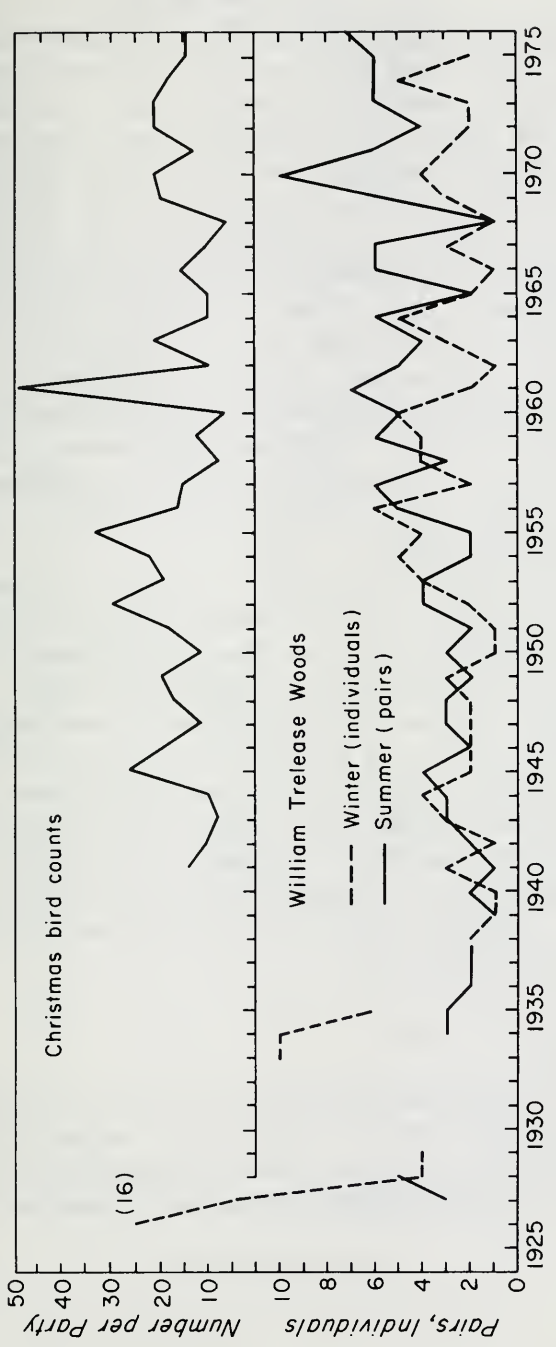


Fig. 19. Fluctuations in breeding and overwintering populations of the cardinal in William Trelease Woods.

Indigo Bunting, Rufous-sided Towhee, Field Sparrow

Populations of indigo buntings (OF) in William Trelease Woods are larger than have been found elsewhere (C. S. Robbins, personal communication). They nested in the shrub stratum in semi-openings throughout the woods as well as along the forest edge (see territory map for 1942 in Kendeigh 1944:91). Twomey (1945), in a special study of this species, found 41 nests in 1934 and 1935. During the 1940s and to 1951, the indigo bunting was second to the house wren as the most abundant species in the woods (Fig. 20). The peak population of 1950 followed a year after that of the house wren (Fig. 14) and may have been in response to the high population of insects and spiders prevailing at that time. The indigo bunting regularly feeds insects to its young, and when insects are plentiful the adult birds also feed on them (Twomey, 1945). Although preferring a semi-open biotope, its numbers declined for some unknown reasons through the 1950s and 1960s when the forest canopy was disturbed.

The rufous-sided towhee (FE) is a shrub and ground inhabitant, although often singing from lower branches of trees. It did not appear at the woods until the elm tree disaster and reached a peak in 1959 (Fig. 20). Its presence has been irregular since 1960.

The field sparrow (FE) may nest and sing on the forest edge but roams out into grassy fields for many of its activities. It increased in abundance in the late 1950s (Fig. 20), but probably not in response to the opening of the forest canopy, because the species did not penetrate into the forest. Although absent in 1961 and 1962, the generally greater abundance of the species during the last two decades probably resulted from the addition to the size of the forest-edge area (pp. 5–6).

Northern Sparrows

The dark-eyed junco nests within the spruce-fir forest in the north, while the tree sparrow nests at tree line where spruce-fir forest contacts Arctic tundra. Peaks in overwintering populations of both species, but more conspicuously in the tree sparrow, came at inter-

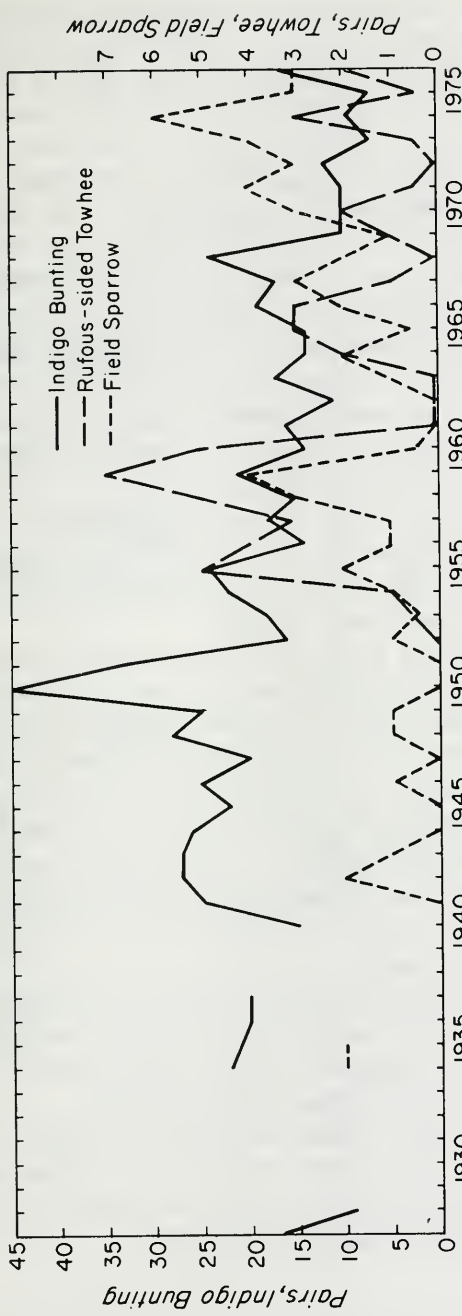


Fig. 20. Fluctuations in breeding populations of indigo bunting, rufous-sided towhee, and field sparrow in William Trelease Woods.

vals of three or four, rarely two or five, years and often coincided (Fig. 21). These intervals are the same duration as for the cycle of lemming mice and other small mammals that occur in the Arctic tundra (Kendeigh, 1974), which may indicate that some general factor affected their reproductive success at intervals. However, prevalence of these species during winter in east central Illinois may also depend on the amount of snow cover, since heavy persisting snow may induce these ground-feeding birds to migrate farther south to pass the winter. High populations in each species were present when snowfall was less than 10 cm and low populations when snowfall was more than 20 cm in the most severe month, in 64% of the instances. The amount of snowfall in December may be more important in determining overwintering populations than that for January or February. Snowfall in December was high in 1942–45, 1950–51, 1960–63, 1967, 1969, and 1973–75. These highs coincided with lows in the tree sparrow populations with the single exception of 1961 and in the junco with the exception of 1944 and 1969. During intervening years with low snowfall, populations in both species were often high.

The white-crowned and white-throated sparrows also nest in the north, the white-crowned sparrow at tree line. Both species were recorded in the Christmas bird counts more frequently after 1955 than earlier (Fig. 22) but have not been found during the winter at William Trelease Woods. It is of interest that the 1960 and 1964 and the 1972 and 1976 peaks of the white-crowned sparrow came at four-year intervals. The peaks of 1960 and 1964 came a year earlier than the corresponding peaks of the tree sparrow but the 1972 peak coincided. If there is a four-year "cycle" in this species, the peak for 1968 was missed.

The fox sparrow, another northern species, was found only occasionally (Fig. 23). A few swamp sparrows nest in the region, but most of the winter birds probably came from the north. Numbers have increased significantly in recent years (Fig. 23).

The song sparrow (FE) nested irregularly at William Trelease Woods. There were influxes of birds in the winter and numbers were especially high in the early 1960s and early 1970s at the woods but not elsewhere in the region (Fig. 24).

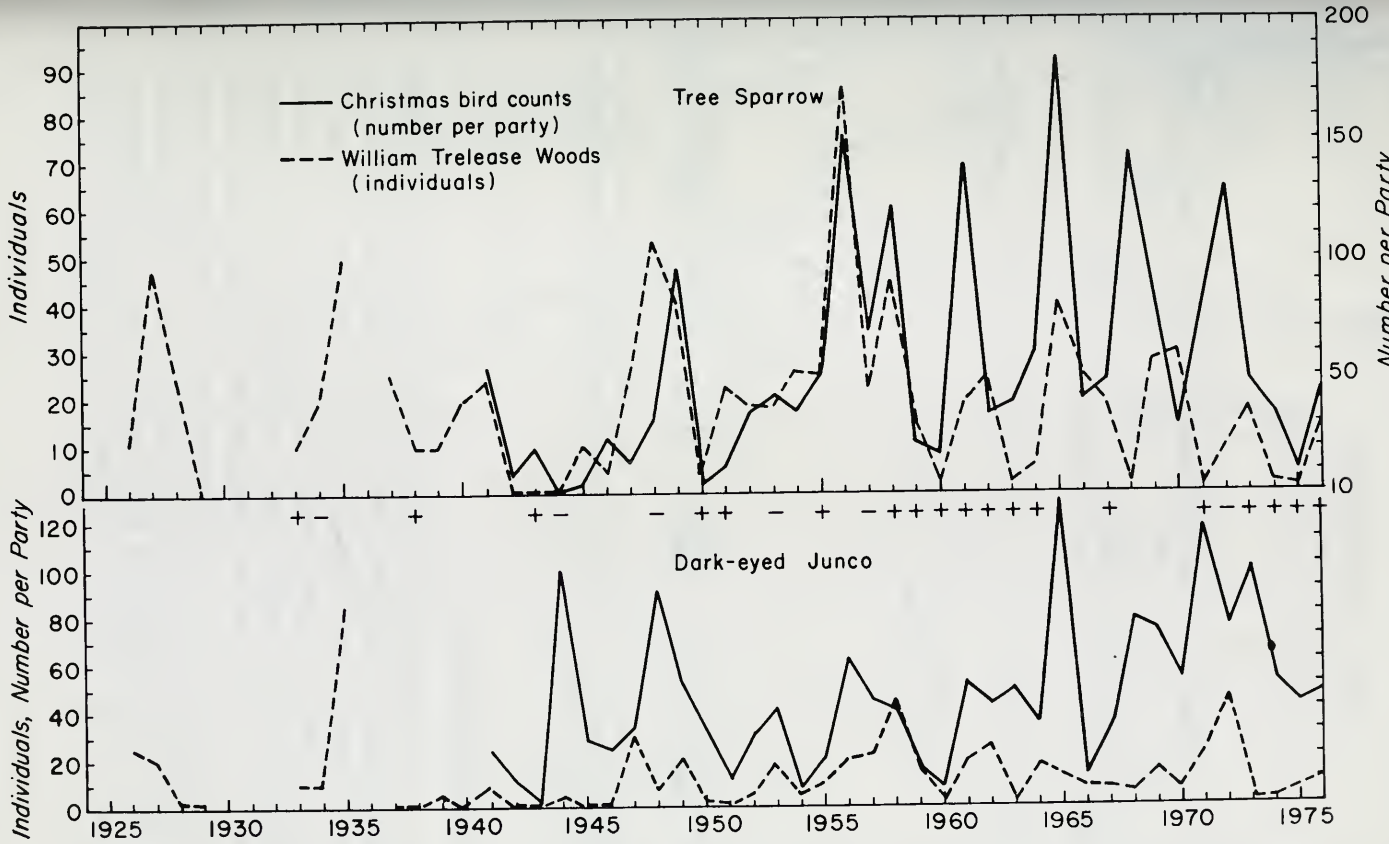


Fig. 21. Fluctuations in number of overwintering tree sparrows and dark-eyed juncos (+, greatest monthly snowfall > 20 cm; −, greatest monthly snowfall < 10 cm). William Trelease Woods.

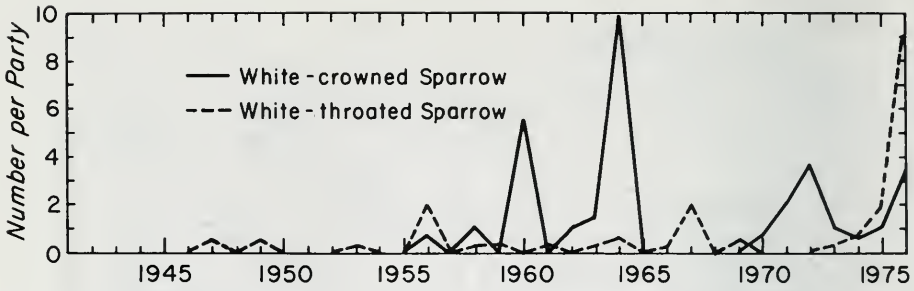


Fig. 22. Fluctuations in numbers of two northern sparrows (white-crowned and white-throated) (Christmas bird counts).

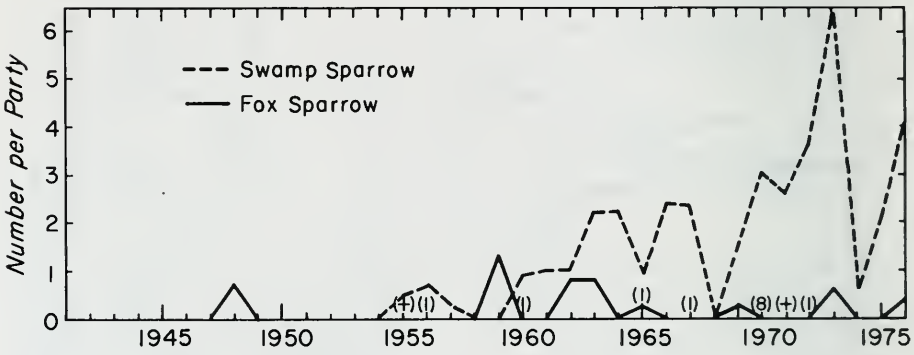


Fig. 23. Fluctuations in numbers of two northern sparrows (swamp and fox) (Christmas bird counts). Numbers in parentheses are for swamp sparrows overwintering in William Trelease Woods.

Total Bird Populations

Some of the differences between species in the manner in which their populations fluctuated over the years are related to the biotopes occupied. Closed-forest (CF) and open-forest (OF) species increased during the late 1940s (Fig. 25). Nothing in the weather fluctuations of the region (Fig. 5) explains these rises in population size, but this does not eliminate the possibility that weather during migration or on the wintering grounds of migrant species may have been involved. These increases, however, coincided with the rise in the invertebrate food supply (Fig. 6), if allowance is made for a lag of three or four years in the response of the bird

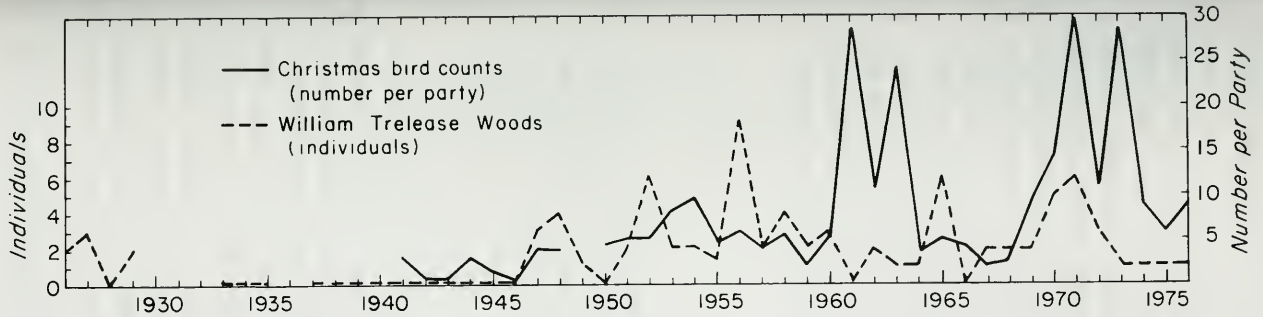


Fig. 24. Fluctuations in number of overwintering song sparrows in William Trelease Woods.

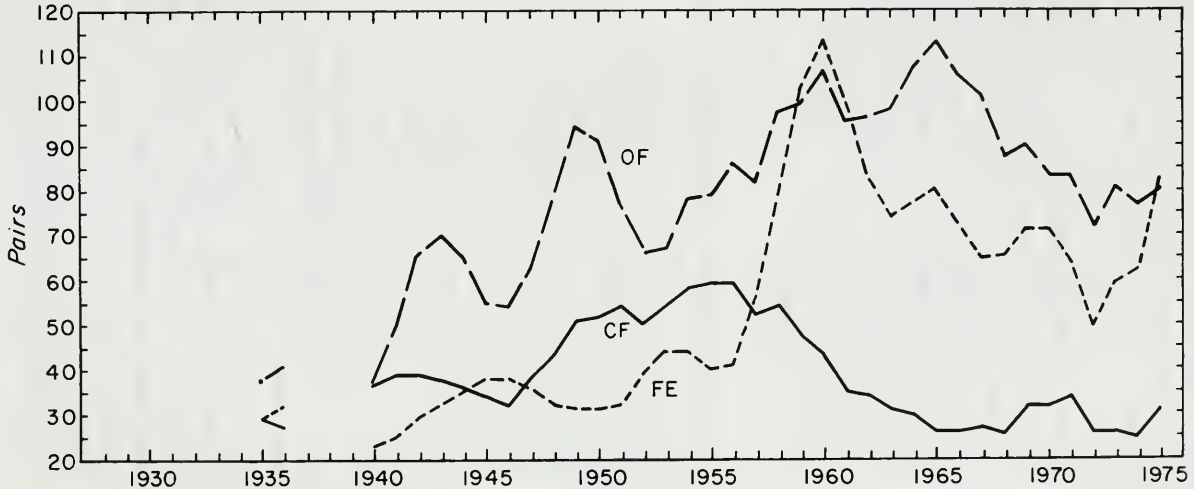


Fig. 25. Moving three-year averages of breeding populations of forest-edge (FE), open-forest (OF), and closed-forest (CF) species in William Trelease Woods. Invertebrates were most abundant from 1944 to 1953; elm trees died, 1950–60.

populations. The decrease from 1950 to 1952 in OF species followed by about two years the decrease in the invertebrate populations.

Decrease in CF species did not come until the late 1950s and correlates more significantly with disruption of the forest canopy caused by death of elm trees, which reached its maximum effect (25%) during this period (Fig. 7). Open-forest species, however, showed a steady increase from the early 1950s to at least 1960. Forest-edge (FE) species, which appeared not to respond to the increase in the invertebrate populations within the woods in the late 1940s, exhibited a spectacular increase from 1956 to 1960. With the closing again of the forest canopy in the 1960s, OF and FE species declined in numbers but not to the levels present before the disturbance of the vegetation. Closed-forest species had not shown any recovery of previous population levels by the end of the study period.

Invasion, Extinction, and Turnover Rates

The composition of species nesting in William Trelease Woods, as well as their population sizes, fluctuated appreciably from year to year (Appendix 1). The presence of great horned and barred owls and of Cooper's and red-tailed hawks depended on their use of outside areas for at least part of their feeding, and in some years they nested elsewhere. Open-forest (OF) and forest-edge (FE) species moved in and out of the woods. Even the CF species did not continuously saturate all favorable biotopes in east central Illinois, so that the presence of the less common species in this small local area was partly a matter of chance. William Trelease Woods is analogous to an ocean island surrounded by water, as it is isolated in a large area of farmland, and on small islands individual species are often unable to establish high enough population levels to avoid extinction at times. The avifauna of an island is stable only when invasion of new species equals the rate at which formerly established species disappear, and both invasion and extinction rates are generally higher than on mainland areas (MacArthur and Wilson, 1967).

Invasion and extinction rates were calculated for all species in

William Trelease Woods and separately for the different biotope categories for the periods before (1928–49), during (1950–64), and after (1965–76) the period of greatest disturbance to the forest canopy (Table 3). An invasion was counted as occurring when a species was present one year (even with "+" pairs) but not the preceding year and an extinction when a species was absent after being present the preceding year.

Considering the entire period, 1928–76, the avifauna at William Trelease Woods is in near balance with an annual flux of about 3.0 species. The flux in FE species was greatest and in CF and FI species the least. During the period of disturbance, 1950–64, invasion rates exceeded extinction rates, especially for FE and OF species. During the recovery period, 1965–76, the extinction rate for FE species exceeded the invasion rate but OF species invaded faster than they disappeared.

A better way of evaluating the degree of stability of species composition is in their comparative percentage of turnover. The higher the turnover rate, the lower the stability. Percentage annual turnover may be calculated as one hundred times the sum of total invasions and extinctions divided by two times the total number of species (Diamond, 1969). Whitcomb et al. (1976) calculated the average turnover rate for William Trelease Woods for the years 1934–75 as 13.6%, ranging between 5.3 and 27.3% for particular years.

Table 3. Average yearly bird invasion and extinction rates (species per year) at William Trelease Woods before, during, and after destruction of elm trees

Inclusive time intervals	Invasion					Extinction				
	FE[1]	OF	CF	FI	Total	FE	OF	CF	FI	Total
1928–49	0.64	1.14	0.43	0.57	2.79	0.86	1.14	0.71	0.14	2.86
1950–64	1.60	1.00	0.40	0.47	3.47	1.27	0.73	0.40	0.60	3.00
1965–76	1.17	0.33	0.83	0.50	2.83	1.33	0.33	0.92	0.50	3.08
1928–76	1.15	0.85	0.54	0.51	3.05	1.15	0.76	0.66	0.41	2.98

[1] FE, forest-edge; OF, open-forest; CF, closed-forest; FI, forest-interior species.

Table 4. Percentage of yearly turnover of bird species at William Trelease Woods

Inclusive time intervals	FE[1]	OF	CF	FI	Total
1928–49	13.8	16.2	7.5	62.5	13.6
1950–64	14.5	9.0	4.6	66.7	11.0
1965–76	15.8	3.6	9.8	85.7	11.1
1928–76	14.7	9.3	7.0	70.4	11.7

[1] FE, forest-edge; OF, open-forest; CF, closed-forest; FI, forest-interior species.

My calculations show (Table 4) an average turnover rate of 11.7% for the entire period, with CF species the most stable and FI species highly unstable. Forest-interior (FI) species seldom persisted for more than one year at a time, although one pair of Kentucky warblers was present every year but one between 1949 and 1954. Especially notable in these statistics is the way OF species changed from the least stable to the most stable element in the avifauna from the first to the last period.

8. Intra-regional Variations in Forest Populations

The ten forested areas censused (pp. 3–9) were of different sizes, with different amounts of contact with surrounding open country, in different habitats, and located along different river systems (Figs. 1, 26, 27). Consequently there were differences in their avifaunas.

In order to compare populations in census areas of different sizes, densities were converted to number of pairs per 40 ha (really 40.47 ha). Although convenient for statistical purposes, converted values are not truly representative for areas of this size. As will be shown below, number of species recorded commonly increases with size of area censused. Correcting for this discrepancy presents difficulties and was not undertaken. Calculating pairs/40 ha by a multiple determined by the ratio of 40 ha to the number of hectares censused is justified for OF, CF, and FI species but is inaccurate for FE species. The length of forest edge in large tracts is proportionately less than in small tracts of the same shape. In Tables 5, 6, 10 that follow, population sizes have been adjusted by multiplying the number of pairs of FE species by the square root of the multiple used for forest species. This adjustment was not made where the census plot was a solid block of forest-edge vegetation or when forest-edge vegetation was contained within the boundaries of the plot.

Another consideration in comparing different populations is in the number of years of censuses that have been combined. There is value in knowing the mean population size over a period even though a species may have zero population during some years. The total number of species recorded over a period of time will almost always be more than the number present during any one year. In Tables 5, 6, 10, counts over two years averaged 2.7 more species than the mean for those years, counts over three years averaged

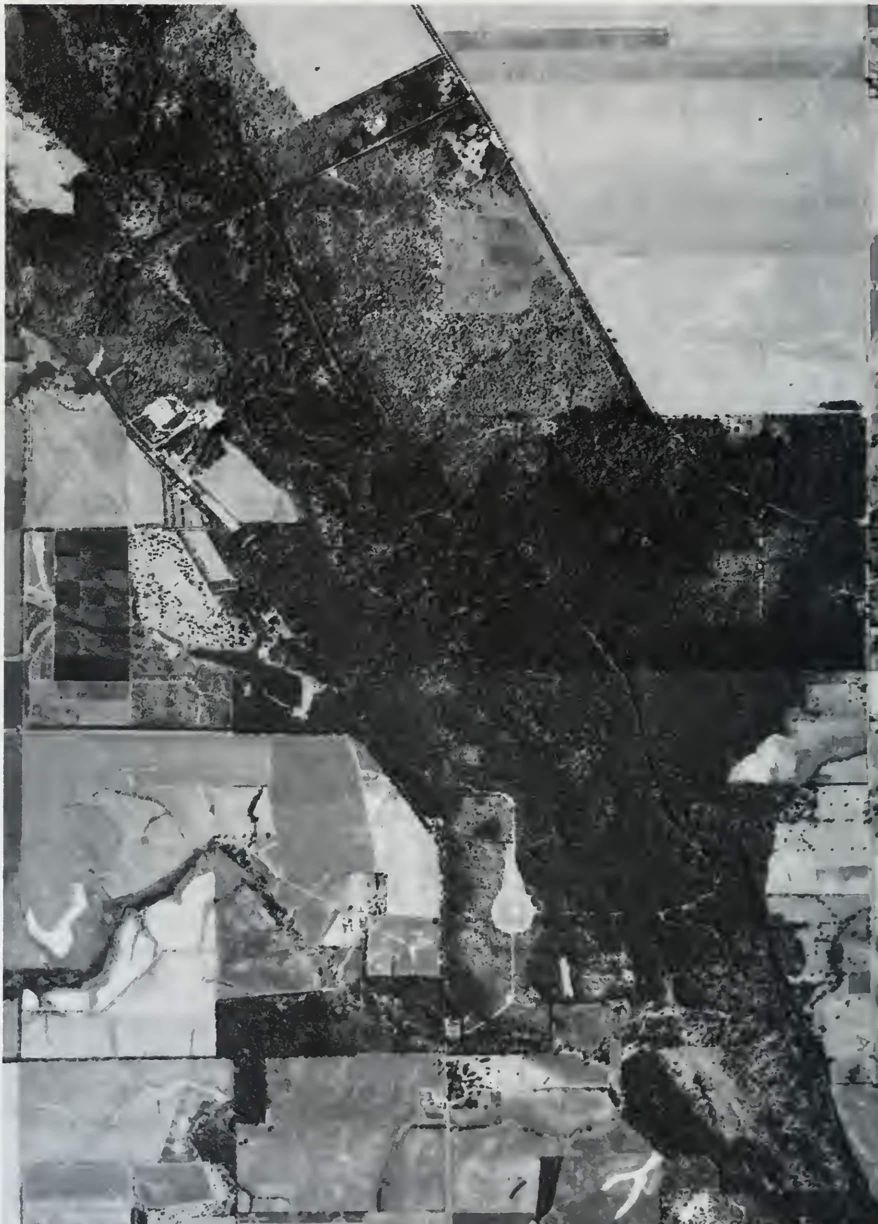


Fig. 26. Composite aerial photograph of Robert Allerton Park, 1966 (courtesy U.S. Department of Agriculture). Compare with Fig. 27.

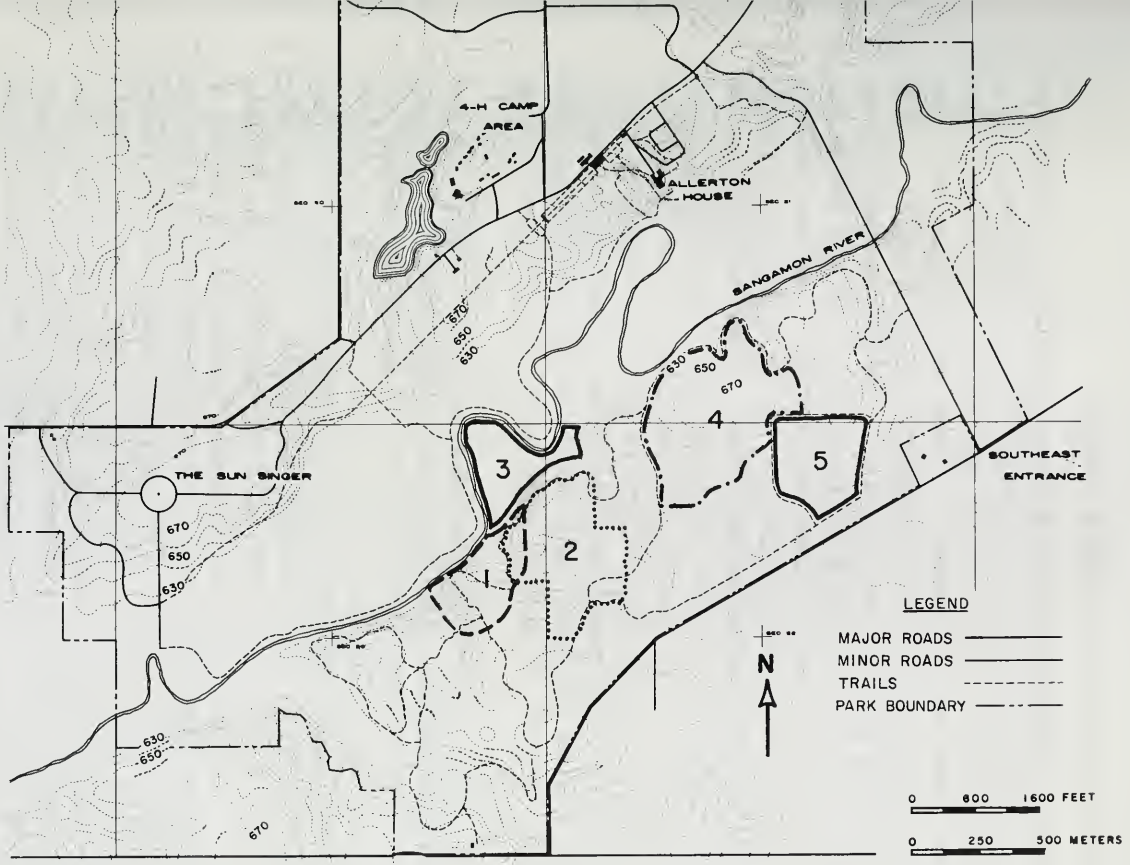


Fig. 27. Study areas at Robert Allerton Park: 1, upland forest area censused by Allison; 2, upland forest area censused by others; 3, floodplain forest census area; 4, forest-edge census area; 5, area of restored prairie. Elevation of contour lines are given in feet (1 foot = 0.30 m). Base map courtesy of W. M. Keith, Director, Robert Allerton Park.

5.3 more species, over four years 8.2 more, over seven years 8.6 more, and for 42 years at William Trelease Woods, 33 more. Both total and mean number of species are given in Table 10.

Effects of Size and Surrounding Contacts

The two smallest upland census areas averaged 8.2 ha and the two largest, 24 ha (Table 5). According to Graber and Graber (1976), with this difference in size and assuming similarity in biotope, there should have been an increase in number of nesting species in the larger tracts of 73%. For isolated tracts, Galli et al. (1976) provide an equation that indicates the increase should have been 70%. Actually the increase in average annual number of nesting species was only 27%. For floodplain areas, varying from 5 to 20 ha (Table 6), there was no consistent increase, although Graber and Graber (1976) would have predicted an increase of 65%. Simberloff (1978) states that island faunas of many kinds occurring in the same-sized areas tend to have smaller numbers of species than do continental ones. The entirely isolated William Trelease Woods had an average of 27 species, the partially isolated Funk Forest of the same size had 30 species, while the Robert Allerton upland tract of only about half the size but part of a continuous forest of several hundred hectares had 29 species.

Of greater importance, the isolation of areas affected the proportion of species with different biotope preferences. In four years at William Trelease Woods (Table 1), FE species constituted 36% of the total populations, OF species 44%, CF species 20%, and FI species +. In contrast, the upland area in Robert Allerton Park from 1949 to 1951 (3 years) contained FE species 1%, OF species 25%, CF species 46%, and FI species 28%. Furthermore, the turnover rate for all species at William Trelease Woods before the onset of the elm diseases (Table 4) was 13.6%, compared with 9.7% at Robert Allerton Park. Bond's (1957) data for forest tracts in southern Wisconsin show similar differences in biotope preferences. Seven species that belonged to FE and OF biotopes decreased in frequency of being recorded and 15 CF and FI species increased from Bond's smallest plots (6–14 ha) to middle-sized plots (16–32 ha), but then maintained essentially the same frequency in the largest plots (>32

Table 5. Breeding bird populations (pairs/40ha) in upland forest; adjusted populations in parentheses (see text)

	Biotope[1]	Funk Forest	Robert Allerton Park		Hart Memorial Woods	William Trelease Woods[2]	Vermilion River
			Allison	Others			
Size of area (ha)		24	7.3	12.6	9.1	24	16
Years record		2	1	6	4	4	1
Wood duck	FE	1.6 (1.3)					
Cooper's hawk	OF					0.4	
Red-tailed hawk	FE	1.6 (1.3)				0.4 (0.3)	
American woodcock	OF			0.5		0.4	
Mourning dove	OF	2.4		0.7	2.0	5.8	
Yellow-billed cuckoo	OF	2.4	11.2	2.8	3.5	4.2	
Great horned owl	CF	0.8		+[3]		0.4	
Barred owl	CF	0.8	2.8	0.3		0.8	
Whip-poor-will	FI		5.6	1.8			10.0
Ruby-throated hummingbird	OF		5.6	4.8		0.8	5.0
Common flicker	OF	2.4		2.5	9.0	9.6	10.0
Red-bellied woodpecker	CF	11.0	15.4	9.0	8.8	3.3	5.0
Red-headed woodpecker	OF			15.2	22.5	6.7	
Hairy woodpecker	CF	10.3	5.6	4.7	1.5	1.7	1.2
Downy woodpecker	CF	11.5	18.2	8.0	8.0	7.1	7.5
Great crested flycatcher	CF	10.2	25.3	7.7	11.7	6.3	2.5
Acadian flycatcher	FI		11.2	5.2			25.0

Table 5. (Continued)

	Biotope[1]	Funk Forest	Robert Allerton Park		Hart Memorial Woods	William Trelease Woods[2]	Vermilion River
			Allison	Others			
Size of area (ha)		24	7.3	12.6	9.1	24	16
Years record		2	1	6	4	4	1
Eastern wood pewee	CF	12.3	42.0	26.2	23.7	7.1	17.5
Blue jay	OF	4.0		5.7	29.2	12.5	3.8
Common crow	FE	+	+	+	+	2.9 (2.3)	+
Black-capped chickadee	OF	11.1		5.2	1.0		
Carolina chickadee	OF					0.4	3.8
Tufted titmouse	CF	6.0	12.6	15.2	20.2	3.8	18.5
White-breasted nuthatch	CF	8.7	11.2	6.2	3.5	0.8	2.5
House wren	OF	5.6			1.3	12.1	15.0
Carolina wren	CF	6.4		2.8		0.8	2.5
Gray catbird	FE				1.3 (0.6)	1.3 (1.0)	5.0 (3.2)
Brown thrasher	FE				2.0 (1.0)	2.1 (1.6)	5.0 (3.2)
American robin	OF	1.6			10.0	14.6	
Wood thrush	CF	10.7	5.6	4.8	15.7	4.6	7.5
Blue-gray gnatcatcher	FI			2.3			2.5
Starling	FE					59.6 (46.1)	
Yellow-throated vireo	FI		16.8	5.2			
Red-eyed vireo	CF	7.1	20.2	18.8	3.3	8.8	25.0
Black-and-white warbler	FI						2.5

Table 5. (Continued)

Cerulean warbler	FI		11.2	1.3			
Ovenbird	FI	11.1	43.4	23.2	2.0		2.5
Louisiana waterthrush	FI		15.4				
Kentucky warbler	FI	1.2	3.4	9.8	3.3		10.0
Common yellowthroat	FE	2.4 (1.9)				4.2 (3.2)	
American redstart	FI	0.8	28.0	12.7			5.0
Northern oriole	FE					0.8 (0.6)	
Brown-headed cowbird	——[4]	(+)	(+)	(+)	(+)	(+)	(+)
Scarlet tanager	FI	2.0		2.7	0.7	0.4	2.5
Summer tanager	FI		5.6				
Cardinal	OF	3.2	16.8	16.0	15.2	7.5	9.8
Rose-breasted grosbeak	OF	5.2			11.3	0.4	
Indigo bunting	OF	2.0	1.4	2.8	10.3	24.6	
American goldfinch	FE					2.1 (1.6)	
Rufous-sided towhee	FE			2.0 (1.0)	6.0 (2.9)	1.3 (1.0)	5.0 (3.2)
Field sparrow	FE					5.4 (4.2)	
Song sparrow	FE					1.2 (1.0)	
Totals (excluding brown-headed cowbird)							
Species: total		30	24	33	27	38	28
mean		28.5	——	26.8	20.0	27.2	——
Pairs		157+ (156+)	334+	226+ (225+)	227 (222)	227 (209)	213+ (208+)

[1] FE, forest edge; OF, open forest; CF, closed forest; FI, forest interior.
[2] Density based on Table 1.
[3] Present, but nesting density too low to measure.
[4] Ubiquitous

Table 6. Breeding bird populations (pairs/40 ha) in floodplain forests; adjusted populations in parentheses (see text)

		Robert Allerton Park[2]		White	Hart Memorial	Salt Fork
	Biotope[1]	1949–51	1963,67	Heath	Woods	Area
Size of area (ha)		10.1	10.1	20	5.1	6.2
Years record		3	2	1	4	1
Wood duck	FE	1.3 (0.6)	+[3]			13 (5)
Mourning dove	OF				4.5	
Yellow-billed cuckoo	OF	7.3	10.0	8	5.5	6
Barred owl	CF	+	+	2		
Ruby-throated hummingbird	OF	2.7	3.0	2		3
Common flicker	OF	+	11.0		20.2	23
Red-bellied woodpecker	CF	10.0	18.0	6	8.5	19
Red-headed woodpecker	OF		24.0		63.8	16
Hairy woodpecker	CF	3.0	4.0	2	2.8	13
Downy woodpecker	CF	13.3	8.0	10	10.5	23
Great crested flycatcher	CF	8.7	21.0	10	21.3	13
Acadian flycatcher	FI	10.7	12.0	4		23
Eastern wood pewee	CF	20.7	21.0	12	11.3	19
Blue jay	OF	9.7	6.0	+	14.2	13
Common crow	FE	+	+	2 (1)		
Black-capped chickadee	OF	10.0	10.0	10	5.5	
Carolina chickadee	OF					29
Tufted titmouse	CF	15.3	18.0	4	22.8	26
White-breasted nuthatch	CF	8.0	16.0	2	1.8	6
Brown creeper	FI		3.0			
House wren	OF		8.0		16.7	
Carolina wren	CF	7.3	9.0	2	7.5	3
Gray catbird	FE		7.0 (3.5)		25.0 (8.9)	
Brown thrasher	FE				1.3 (0.5)	
American robin	OF				9.0	6
Wood thrush	CF	8.7	+	8	10.3	10
Eastern bluebird	FE			2 (1)		
Blue-gray gnatcatcher	FI		6.0			13
Starling	FE		1.0 (0.5)			32 (12)
Yellow-throated vireo	FI	0.7	6.0			
Red-eyed vireo	CF	6.7	24.0	12	14.0	13
Warbling vireo	OF					26

Table 6. (Continued)

	Biotope[1]	Robert Allerton Park[2] 1949–51	Robert Allerton Park[2] 1963,67	White Heath	Hart Memorial Woods	Salt Fork Area
Size of area (ha)		10.1	10.1	20	5.1	6.2
Years record		3	2	1	4	1
Prothonotary warbler	FE	13.3 (6.7)		2 (1)		13
Northern parula warbler	FI		+			13
Cerulean warbler	FI	11.3	12.0	2		13
Yellow-throated warbler	FE		4.0 (2.0)			
Louisiana waterthrush	FI	1.3				
Kentucky warbler	FI	5.3	2.0		3.7	26
Common yellowthroat	FE		4.0 (2.0)		12.7 (4.5)	6 (2)
Yellow-breasted chat	FE		3.0 (1.5)			
American redstart	FI	58.7	35.0	12		32
Northern oriole	FE					6 (2)
Brown-headed cowbird	——	(+)	(+)	(+)	(+)	(+)
Scarlet tanager	FI	2.0	+	2	2.0	
Cardinal	OF	12.0	24.0	14	22.0	
Rose-breasted grosbeak	OF				22.7	
Indigo bunting	OF	22.3	36.0	12	28.0	13
American goldfinch	FE					6 (2)
Rufous-sided towhee	FE				2.8 (1.0)	
Song sparrow	FE				3.8 (1.4)	
Totals (excluding brown-headed cowbird)						
Species: total		28	36	24	28	31
mean		24.7	33.0	——[4]	21.3	——
Pairs		270+ (263+)	366+ (356+)	142+ (138+)	374 (345)	476 (436)

[1] FE, forest edge; OF, open forest; CF, closed forest; FI, forest interior.
[2] The five censuses are separated into two groups, one before death of the elms and one afterward.
[3] Present, but nesting density too low to measure.
[4] Data for only one year.

ha). That changes of a different sort may also occur has been pointed out by Forman et al. (1976), who showed that the proportion of insectivorous to herbivorous and omnivorous species increased as the size of areas increased.

Except for the wood duck which is dependent on the river, all new species at Robert Allerton Park not present in William Trelease Woods are what Robbins (1979) calls "area-sensitive forest interior species" in that they nest only in large tracts of forest. He estimates that the Acadian flycatcher and Kentucky warbler require at least 30 ha to sustain breeding populations while other species may require 100 ha or more. Robbins also lists scarlet tanager, found infrequently in William Trelease Woods; black-and-white warbler that occurs in the extensive forest along the Vermilion River; and northern parula warbler, present in the floodplain forest at Robert Allerton Park. The blue-gray gnatcatcher, cerulean warbler, and summer tanager, not mentioned by Robbins, are listed by Webster and Adams (1972) for old-growth deciduous forest of the Midwest. The yellow-billed cuckoo, wood thrush, and red-eyed vireo, designated FI species by Robbins, were common in William Trelease Woods and hence may more properly be called OF or CF species.

Several FI species were found intermittently through the years at William Trelease Woods without establishing a stable population there (Appendix 1). One or two FI species were recorded every year from 1949 through 1956 during and immediately after the surge in invertebrate populations there. Likewise, FI species were recorded off and on throughout the successional progress on abandoned farmland at Robert Allerton Park (Appendix 4). These doubtless represent a spillover from adjacent forest populations.

Effect of Habitat

Floodplain forests are frequently inundated at high water, often for days at a time, so they present unfavorable habitat for ground-nesting birds. Oxbows or sloughs may retain water until mid or late summer. Of 39 species breeding in upland forests and 35 species in floodplain forest, excluding FE species, 31 were found in both communities (Table 5, 6). American woodcock, whip-poor-will, black-and-white warbler, and ovenbird, ground-nesting species, were restricted to upland forests. Prothonotary and yellow-throated warblers are characteristically river-edge species, and the northern parula warbler and warbling vireo are, in my experience, more often found in bottomland forests. The brown creeper is a rare summer

resident in Illinois (Kendeigh, 1970). The presence of several FE species in both upland and floodplain was the result of disturbance of the forest canopy by the elm diseases.

The annual number of breeding species (26) averaged the same in the upland (n = 17) and floodplain forests (n = 10) in east central Illinois. Average populations, however, tended to be larger in floodplain forests (332 pairs/40 ha) than in upland forests (224 pairs). Graber and Graber (1976) found populations to be larger on floodplains than in uplands throughout Illinois, and, based on a broad survey of the literature, Udvardy (1957) indicates that upland temperate deciduous forests commonly contain 100–300 pairs whereas mixed bottomland and floodplain forests have 300–500 pairs/40 ha.

9. Successional Changes

A much larger percentage of east central Illinois is unforested than is forested. The original prairie has been almost completely converted to farmland; parts of the region have been strip-mined for coal; urban areas, parks, country homes, railroad and highway waylands, and industrial sites present a variety of environments occupied by different bird communities. All these situations represent stages in succession from bare ground to climax forest that are held in check only by man's activities. Knowing how the succession would proceed, stage by stage, will help us to orient the various bird communities to each other and to explain why species are distributed as they are.

Succession of bird communities has been commonly inferred by comparing avifaunas in different types of vegetation of known seral sequence, such as my study in northern Michigan (Kendeigh, 1948) and those of Odum (1950), Haapanen (1965, 1966), Ferry and Frochot (1970), and Głowacinski and Weiner (1977). Three such studies in "old fields" in North America, with which I am here concerned, are those of Johnston and Odum (1956), Shugart and James (1973), and Speirs and Orenstein (1975). The present study differs from those cited, in that changes in bird populations were followed on the same area over a period of 26 years correlated with the succession of vegetation. But this study, carried out at Robert Allerton Park, was started several years after succession began, so that the early sequence of bird communities had to be sought elsewhere.

Early Years in the Succession

Plant succession begins quickly on the fertile farmland of east central Illinois, once farming operations cease. We need to examine first, however, bird populations on the farms themselves. Miller (1955) measured bird populations on 389 ha of active farmland in 1949. The area was located approximately 2.3 km southeast of Urbana. Species were identified with the kind of crop or field in which they nested, although they often foraged more widely. The variety of species and their populations were few and small except in bluegrass pastures (Table 7). On a plot in the Phillips Tract northeast of Urbana (Frontispiece), covered partly by bluegrass and partly by alfalfa, the eastern meadowlark was less numerous in 1969–70 than in the bluegrass pasture censused by Miller, but there were three new species (Willson, 1974). A bluegrass area in Robert Allerton Park (Fig. 27:5 in part) contained all species except the red-winged blackbird found in the other bluegrass areas, and had an additional species (Allison, 1947).

Graber and Graber (1963) showed, in respect to breeding birds on farmland, that during approximately the first half of the present century, red-winged blackbirds spread in large numbers from marshes into upland grassy fields, horned larks increased considerably because of the greater prevalence of bare ground in fields, while FE species decreased with the practice of "clean farming" or cultivating close to fences.

Black (1937) made a few winter bird counts on open farmland in Champaign County in 1935–36; the most numerous species were the Lapland longspur, tree sparrow, dark-eyed junco, horned lark, and common crow, in that order. In our Christmas bird counts, the Lapland longspur was quite numerous in 1956 and 1966 but scarce during other years. The horned lark was exceptionally numerous in 1956, 1961, 1966, 1968–69, and 1972–74.

Annuals and biennials commonly predominate after the cultivation of row crops or small grains ceases. Willson (1974) censused birds on 12 ha of fallow fields on the Phillips Tract for the first two years after cultivation stopped (Table 8). The birds found were all grassland species except for the common yellowthroat (FE) and all occur also on farmland. Karr (1968) censused several areas in and near Kickapoo State Park in the eastern part of our

Table 7. Breeding bird populations (pairs/40 ha) on farmland

Authority	Miller (1955)							Willson (1974)	Allison (1947)
Cover type	Bare fields	Corn	Soybeans	Oats	Wheat	Alfalfa	Bluegrass pasture	Alfalfa & bluegrass	Bluegrass
Census area (ha)	268	191	74.7	44.4	26.8	16.6	12.1	6.9	10.9
Ring-necked pheasant						12			
Killdeer	+[1]	+		1					
Horned lark	8			7					
Bobolink					3		13		4
Eastern meadowlark				1	3	7	37	4	8
Red-winged blackbird								15	
Dickcissel			1					18	8
Grasshopper sparrow								3	4
Henslow's sparrow									4
Lark sparrow						2			

[1] Present, but nesting density too low to measure.

Table 8. Breeding bird populations (pairs/40 ha) in early seral stages on abandoned farmland and striplands (Karr, 1968; Willson, 1974; Allerton Park)

	Biotope[1]	Fallow fields			Restored prairie	Grassland-shrub	Early shrubs	Late shrubs
Years since disturbance		1	2	3	——	——	12	44
Census area (ha)		12	12	10.1	6.1	6.9	8.7	8.7
Bobwhite	FE						12	5
Killdeer	G			6				
Mourning dove	OF				3		19	16
Yellow-billed cuckoo	OF						5	2
Common flicker	OF							16
Red-headed woodpecker	OF							5
Downy woodpecker	CF							9
Eastern kingbird	FE							2
Great crested flycatcher	CF							7
Willow flycatcher	FE						19	
Eastern wood pewee	CF							5
Horned lark	G	3		6				
Blue jay	OF							16
Carolina chickadee	OF							9
Tufted titmouse	CF							9
House wren	OF							30
Gray catbird	FE						36	16

Table 8. (Continued)

	Biotope[1]	Fallow fields			Restored prairie	Grassland-shrub	Early shrubs	Late shrubs
Years since disturbance		1	2	3	——	——	12	44
Census area (ha)		12	12	10.1	6.1	6.9	8.7	8.7
Brown thrasher	FE						12	14
American robin	FE							14
Wood thrush	CF							7
Eastern bluebird	FE					6		5
Bell's vireo	FE					14	9	
Warbling vireo	FE							12
Yellow warbler	FE						36	9
Common yellowthroat	FE		3			14		5
Yellow-breasted chat	FE						9	
Eastern meadowlark	G	2			10	10		
Red-winged blackbird	G		32	8			19	19
Northern oriole	FE							7
Brown-headed cowbird	——	(+)	(+)	(+)	(+)	(+)	(14)	(9)
Cardinal	OF						5	16
Indigo bunting	OF						31	14
Dickcissel	G	13	73		3			
American goldfinch	FE						19	9
Rufous-sided towhee	FE						9	14
Grasshopper sparrow	G	7	2		3			

Table 8. (Continued)

	Biotope[1]	Fallow fields			Restored prairie	Grassland-shrub	Early shrubs	Late shrubs
Years since disturbance		1	2	3	—	—	12	44
Census area (ha)		12	12	10.1	6.1	6.9	8.7	8.7
Vesper sparrow	G	3			6			
Field sparrow	FE				36	51	28	21
Song sparrow	FE			2	3	6	26	14
Totals (excluding brown-headed cowbird):								
Species:	G	5	3	3	4	1	1	1
	FE		1	1	2	5	11	13
	OF				1		4	10
	CF							5
	Total	5	4	4	7	6	16	29
Pairs:	G	28	107	20	22	10	19	19
	FE		3	2	39	91	215	133
	OF				3		60	138
	CF							37
	Total	28	110	22	64	101	294	327

[1] G, grassland, FE, forest edge; OF, open forest; CF, closed forest.

region (Fig. 1). One area had been strip-mined three years previously. The soil was sterile, with only some 8% of the ground covered with forbs and grasses, but there were a few small trees not more than two years old. Shrubs and trees commonly invade fallow fields almost immediately, although shrubs do not become prominent for 5 years and trees not for 15 to 20 years (Beckwith, 1954). The occurrence here of the song sparrow represents the appearance of another FE species. Five of the nine species occurring in the fallow fields of Illinois also occurred during the first years after restoration of strip-mined areas in West Virginia. Of the six species occurring there, only the savannah sparrow *(Passerculus sandwichensis)* was not found in our areas (Whitmore, 1980).

A restored prairie tract at Robert Allerton Park (Fig. 26, 27:5), overlapping the bluegrass area studied by Allison (Table 5), was censused in 1967 and 1968 by Willson (1974). The area had been disturbed by the introduction of prairie grasses *(Andropogon, Panicum, Sorghastrum)* and succession retarded by controlled burning, but clumps of *Prunus* and brier thickets were present. The census is of interest in showing decreased populations of grassland species and increased abundance of FE species, notably the field sparrow. An adjacent unburned area lacked the planted prairie grasses but had several species of shrubs *(Rhus, Rubus, Prunus)* and small trees, including *Crataegus.* Censuses in 1967 and 1968 showed a predominance of FE species. While the chronological age since cessation of cultivation of these two fields is much greater, possibly over 40 years, their ecological age and position in the fallow field sere are intermediate between the 3- and 12-year areas shown in Table 8.

The "early shrub" stage on the strip-mine area (Karr, 1968) was only 12 years old, but shrubs and small trees covered more than one-third of the area. The "late shrub" stage, abandoned about 44 years (41–46 years) earlier, still had some bare ground but was nearly two-thirds covered with shrubs and small trees. In listing the birds in these stages (Table 8), species are excluded whose occurrence was clearly dependent on adjacent bodies of water (spotted sandpiper, *Actitis macularia*) or artificial plantings of trees (common grackle). The predominance of FE species is evident, but OF species had become more important and a few CF species had made their appearance.

Middle Years in the Succession

Allison (1947), who initiated the long-term study of succession at Robert Allerton Park in 1946, marked out an area of 18 ha, but the following year it was increased to 24.3 ha (Fig. 27:4). Altogether, 25 yearly censuses of bird populations were made to 1971, skipping only 1970. Censuses were made by the spot-mapping method and mostly by graduate students working for M.S. degrees (see Acknowledgments). Bird counts were started in early spring and often extended into mid autumn. During the peak of nesting, counts were usually made three or four times a week. I checked over all the students' species summary maps at the end of the season to give uniformity to estimating the number of nesting pairs. During years when no student was available (1952, 1954, 1956–58, 1961), an assistant and I made the census, but then time did not permit taking more than about five complete counts at the height of the nesting season instead of the minimum of eight that is generally considered adequate. The area was first gridded at 30- to 50-m intervals with waterproofed numbered cards attached to trees, but in 1953 numbered metal stakes replaced the cards.

The Allerton Park area was well drained, with intermittent streams leading into the Sangamon River. A narrow one-way road marked the boundaries on the upper half of the east side and on the north and west sides, while the south border was an artificial irregular line. The area was bordered on the north by floodplain forest, on the upper east and west by second-growth upland forest, in the southeast corner by grassland, and elsewhere by similar forest-edge vegetation.

The agricultural history of the plot cannot be fully documented, but an older resident recalled that the area was cultivated until 1925 when it was converted into pasture for domestic animals, probably cattle. The abundance here of briers and hawthorns indicated that grazing probably continued until a few years before the University acquired the park in 1946. There had been mowing of the grass in open areas up to this time, but since 1946 there has been little disturbance.

The principal grass of the area was Kentucky bluegrass, *Poa pratensis* L. Brier patches and thickets were composed of wild

blackberry (*Rubus allegheniensis* Porter), black raspberry (*Rubus occidentalis* L.), poison ivy, and smooth sumac (*Rhus glabra* L.). Tree species, listed in 1966 (Roth, 1967), were, in order of importance (percentage of total density plus percentage of total basal area divided by 2): shingle oak (*Quercus imbricaria* Michx.), 24.8; wild black cherry (*Prunus serotina* Ehrh.), 20.6; both species of elm, 20.6; hawthorn, 10.0; and 10 other species.

The earliest aerial photograph of the area that I have seen was taken in 1936, 12 years after cultivation ceased. Brier patches, thickets, and small trees were scattered in a diffuse manner over a considerable portion of a grassy area but there was no forest. Aerial photographs, together with ground observations, allowed preparation of vegetation maps in 1946, 1953, 1957, 1959, and 1967. Portions of the area were mapped as grassland if they contained at least 0.2 ha covered with grasses and forbs without large trees or shrubs; forest edge if the grassland contained scattered clumps of briers, shrubs, and trees; and forest if trees made a closed canopy over at least 0.2 ha (Borst, 1967). The amount of area covered by each biotope was then expressed in percentages for preparing Figure 28. It was obvious that as forest-edge vegetation increased in

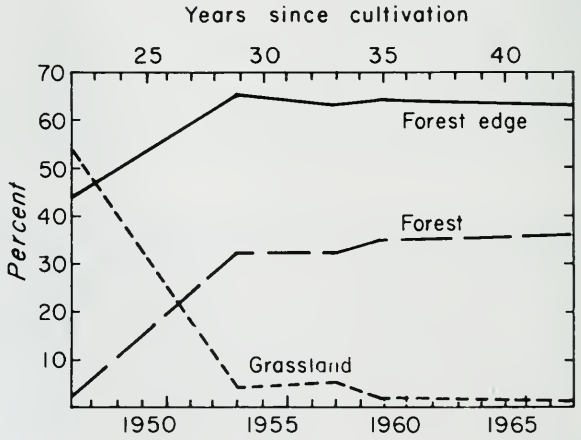


Fig. 28. Changes in percentage of area covered by each of three biotopes at Robert Allerton Park as determined from aerial photographs and vegetation maps.

density, grassland was crowded out. Forest invaded slowly, first along the north and east margins, then encroached inward. With protection of the area from disturbance, both forest and forest edge expanded rapidly from year 22 to year 29, but thereafter changes came quite slowly.

The amount of time required for the entire area to be covered with climax forest similar to that elsewhere in the park can be only estimated. A study done in another part of Robert Allerton Park estimated that 75 years would be required from cutting of the original forest to development of a relatively stable young white oak–red oak–hickory forest (F. L. Johnson, personal communication). The succession on the bird study area, however, will take longer because an additional intermediate stage of different tree composition occurs. On the Piedmont Plateau of North Carolina, a good oak-hickory understory to pine requires about 110 years to develop (Oosting, 1942).

At the time of the last analysis of the vegetation on the study area at Robert Allerton Park, 42 years after cessation of cultivation, forest still covered less than 40% of the ground. When forest comes to cover the entire area, the avifauna will probably be similar to that of the Salt Fork area (Table 6) studied by Karr (1968) which developed on an area that was strip-mined 60 (56–66) years previously. Being located on the floodplain of the Salt Fork River, the forest was dominated by rapidly growing trees. More than half of the area contained an understory of shrubs. The first forest developing on the bird study area at Robert Allerton Park is composed principally of species different from those in the Salt Fork area, but these trees also grow rapidly and are succeeding shrubs. The final or climax stage will doubtless be composed predominantly of oaks, hickories, and sugar maples, similar to the upland study plot at Robert Allerton Park (Table 5). For the purpose of our analysis, I am assuming that the final stabilized study area at Robert Allerton Park is at least 100 years old.

Bird censuses spanned a period from 22 to 47 years after cultivation (Appendix 4). Grassland species persisted throughout the period (Fig. 29). There was a gradual decrease in populations of FE species and increases in OF and CF species. The most numerous FE species were yellow-breasted chat, rufous-sided towhee,

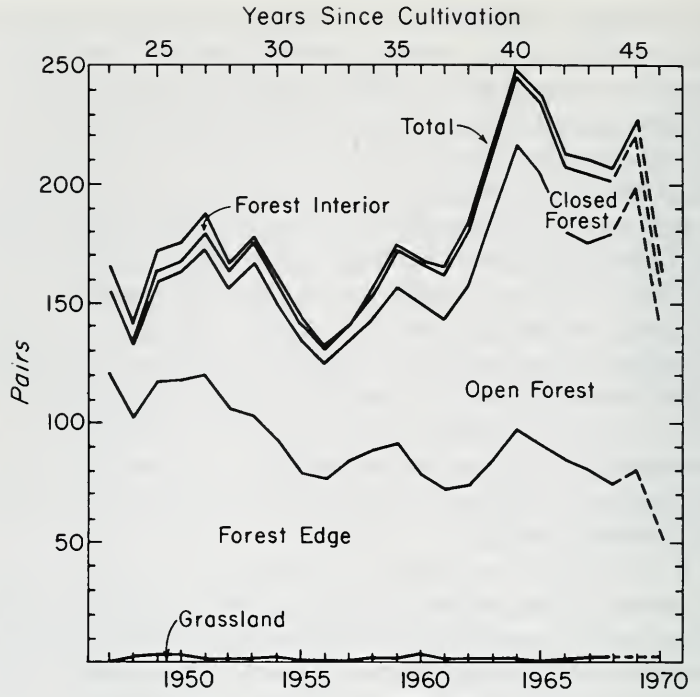


Fig. 29. Three-year moving averages showing changes in number of breeding birds in different biotopes at Robert Allerton Park. Data for 1969 are averages for 1968 and 1969; for 1970, averages of 1969 and 1971.

and field sparrow, and the most abundant OF species were mourning dove and indigo bunting. Peak or near-peak numbers for many species occurred in the mid 1960s, while a decline in numbers for several species occurred between 1969 and 1971. The larger populations of FI species before 1952 rather than later was caused by overflow from large populations of American redstarts in the adjacent forest at that time (Appendix 3).

The Complete Sere

The increase in number of species and total populations correlated with succession of vegetation from fallow field to forest has been pointed out by Karr (1968). When the various census areas in this

study are arranged in order of decreasing G and FE species and increasing CF and FI species (Table 10), a rough correlation is evident between chronological age and increase in mean number of species and population size to the late shrub and early forest stages. That the correlation is not more precise and does not continue into older forests is explained by variations in habitat, differences in rapidity of vegetational development, and proportion of forest edge to forest interior. If one could quantify the succession of bird communities on an adequately sized area over 100 or more years, one would undoubtedly find progressive predominance in turn of G, FE, OF, CF, and FI species. The gradual increase in numbers of OF species to a maximum followed by a decline is characteristic of populations in each group except for FI species.

Yearly population sizes of individual species, when plotted against time, commonly assumed distribution curves skewed positively in relation to the biotope occupied by each species (Fig. 30). The dickcissel (G) quickly became abundant after a field was abandoned, and decreased gradually as shrubs increased in density. The field sparrow (FE) appeared with the first shrubs, soon reached a peak, and slowly disappeared as shrubs became replaced by forest. The blue jay (OF) lagged behind the field sparrow both in invading the forest edge and in reaching a peak. Its numbers decreased as the forest matured. The tufted titmouse (CF) lagged behind the blue jay in first appearing and reaching a peak, but then maintained high numbers. The curves of OF and CF species resemble those obtained by Bond (1957) for frequency of occurrence of species plotted against a continuum index extending from xeric to mesic forests. Ferry and Frochot (1970) found in forest succession after logging that many species showed a preference for initial low shrub stages and then disappeared, a few species reached optimum abundance in intermediate stages, and other species became common only in the late subclimax stage.

The time schedule for invasion and extinction of bird species on abandoned farmland varies with the type of vegetation that comes in. In an "old field" succession in Michigan, juniper (*Juniperus communis* L.) was a common species (Evans, 1978). Field sparrows were well established when the study began, approximately 24 years after cessation of cultivation, as was true in my study area,

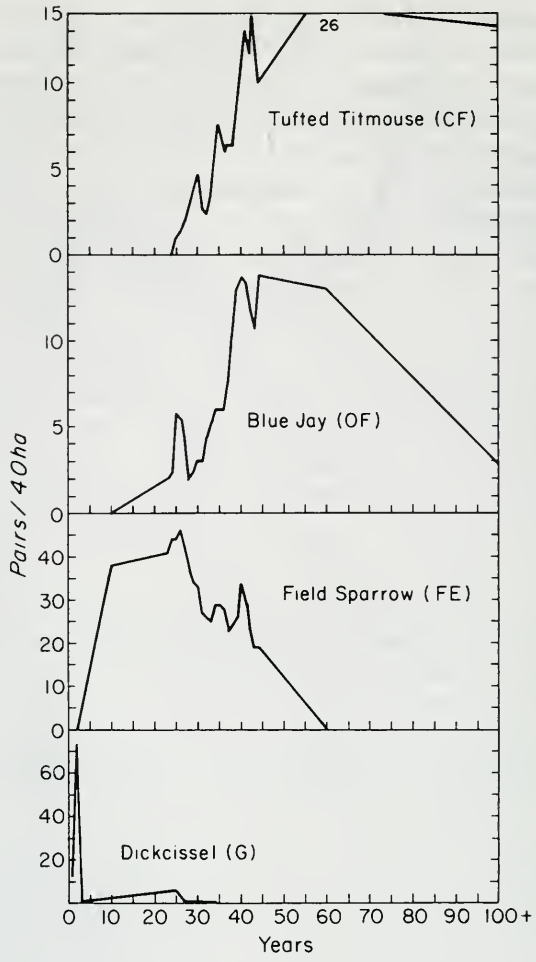


Fig. 30. Characteristic changes with time in population size of representative grassland (G), forest-edge (FE), open-forest (OF), and closed-forest (CF) species. The number of pairs of nesting birds each year is based on three-year averages except for year 60 (Salt Fork area) and 100+ and for the dickcissel (Tables 5, 8, Appendix 4). The data for year 10 are averages of the census for year 12 on the strip mine area and two censuses on areas of somewhat earlier ecological age at Robert Allerton Park. The data for year 44 are averages for three years at Robert Allerton Park and one year in the strip mine area. The data for year 100+ (minimum estimated time to complete sere, see text) are for the upland forest at Robert Allerton Park. The data for the dickcissel are plotted on a yearly basis because of the rapid changes in population size.

but then the species increased in numbers to at least year 50, by which time they had almost disappeared from my area. One reason for this increase in Michigan, apparently, is that the birds shifted from nesting chiefly on the ground in the early years to nesting in the increasingly abundant junipers.

It is not possible to date accurately the first appearance in the sere at Robert Allerton Park of most FE and OF species because of the lack of data before year 22. The order in which these species reached peak populations, however, is interesting (Table 9). Based

Table 9. Order of appearance and peaking in populations of bird species in years after termination of cultivation at Robert Allerton Park; data in parentheses are for other areas

	First appearance	Regular occurrence	Peak(s)
Forest-edge Species			
Song sparrow	(3)		(12±)
Black-billed cuckoo			22
Cedar waxwing			22
American goldfinch			22, 24
Brown thrasher			22, 26, 36
Field sparrow			23, 26
Yellow-breasted chat			25
Common yellowthroat	(2)		26, 29
Bell's vireo			28, 30–31
Gray catbird			29, 34, 41
Rufous-sided towhee			34
White-eyed vireo			44
Open-forest Species			
American woodcock			22
Mourning dove			22, 30, 41, 44
Indigo bunting			26, 39–40, 45
Ruby-throated hummingbird		25	27–28, (100)
Cardinal			28, 40
Black-capped chickadee		25	28, 35, 42
Rose-breasted grosbeak	23	36	39
Blue jay			40
House wren		27	41

Table 9. (Continued)

	First appearance	Regular occurrence	Peaks(s)
Common flicker	29	31	44, (60)
Red-headed woodpecker		36	44, (60)
Yellow-billed cuckoo			45
American robin	39		(60)
Closed-forest Species			
Great crested flycatcher	22	26	
Tufted titmouse		26	
Eastern wood pewee	22	33	
Downy woodpecker	27	35	
Red-bellied woodpecker	35	36	
Wood thrush	26	38	
White-breasted nuthatch	28	39	
Carolina wren	26	43	
Red-eyed vireo	25		
Hairy woodpecker	30		
Forest-interior Species			
Whip-poor-will	22	42	

on studies in other areas, it is assumed that the common yellowthroat and song sparrow were the first FE species to appear. The song sparrow attained its highest recorded population in the 12-year strip-mine area and was last recorded in the Robert Allerton Park study area in year 26. The yellowthroat did not peak until this latter year. Several other species appeared to be at or near their peaks when the censuses began in year 22. The white-eyed vireo was the last FE species to peak—at year 44. Most of the species listed were still present when the study was concluded in year 47, but the Bell's vireo was last found in year 34, the black-billed cuckoo in year 38, and the cedar waxwing in year 39. These three species, as well as the song sparrow, became irregular in occurrence before they disappeared entirely. Some OF species peaked early, but most of them reached their maxima later than did the FE species. Some species exhibited large populations also in the 60-year forest stages on the Salt Fork.

The invasion of CF species can be followed with some accuracy. Their incursions were usually sporadic at first, being recorded present but not definitely nesting some years and entirely absent other years, before they became established in the nesting avifauna. Eight CF species began to appear regularly between years 26 and 43. The recording of FI species depended to a large extent on their presence and abundance in the neighboring forest. The whip-poor-will may be the first real FI invader, since the species was present in good numbers annually, beginning in year 42.

Mean number of species (36) and populations (248 pairs/40 ha) reached peaks at Robert Allerton Park 39–41 years after cultivation stopped. This is to be compared with 27 species and 241 pairs/40 ha in the adjacent mature forest.

10. Variations in Community Structure

In previous sections, community structure has been analyzed in respect to the preferences of species for particular biotopes. We are here concerned with other aspects of community structure, and population statistics for all communities studied in this region have been brought together in Table 10.

There is a weak statistical correlation between total populations (unadjusted pairs/40 ha) and total numbers of species ($r^2 = 0.25$), and a stronger one between total populations and mean population size (p/s = pairs/species/40 ha) ($r^2 = 0.50$). Variation in total populations among different communities depends to some extent on the number of niches available for different species, but to a greater extent on the degree to which they are occupied.

In his analysis of 20 censuses in several types of forest vegetation, Udvardy (1957) showed that the 62.8% of species with less than 10 pairs/40 ha each provided 22.8% of the total populations while only 4.6% of the commonest species, with 40+ pairs each, provided about the same proportion, 23.5%. This represents a positively skewed distribution of population sizes; that is, the median and mode p/s are smaller than the arithmetic mean.

The extent of skewness (g_1) in our bird communities was calculated from the total number of species and mean populations in each area, using equation 7.7 from Zar (1974):

$$g_1 = \frac{\Sigma(x_1 - \bar{x})^3}{(n-1)(n-2)(sd)^3 n}$$

where $x_1 = p/s$ for a species, $\bar{x}$ is the mean p/s, n is number of species, and sd is standard deviation. Whether the skewness was significantly different ($p \leqslant 0.05$) from a normal or symmetrical distribution ($g_1 = 0$) was determined from Table D25 in Zar (1974).

With a symmetrical distribution, species populations appear well-balanced; with a highly skewed distribution, a few species are very numerous while others are poorly represented (Fig. 31). The NS skewness of the four populations shown in Table 10 varied only between 0.18 and 0.45.

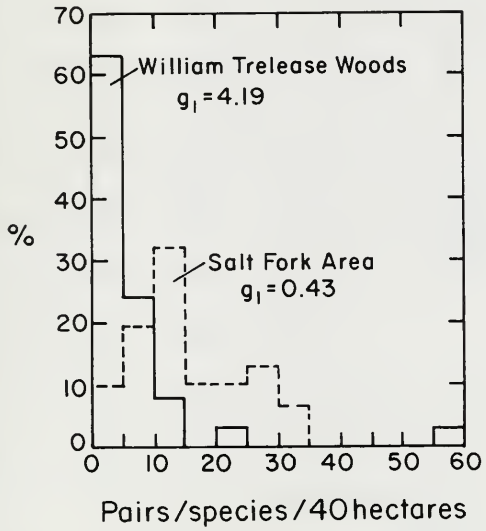


Fig. 31. Percent total number of species at different population levels. The distribution of species populations in William Trelease Woods is highly skewed; in the Salt Fork area, they approach a symmetrical distribution.

Highly skewed distributions of mean populations size ($g_1 > 2.0$) for fallow fields resulted from abundance of dickcissels; for grassland-shrub and 22–24 year seral stages, field sparrows; for the 39–41 year seral stage, field sparrows, cardinals, and indigo buntings; for Hart Forest floodplain forest, red-headed woodpeckers; for Hart Forest upland forest, blue jays; for Robert Allerton Park floodplain forest (1949–51), American redstarts; and for William Trelease Woods, starlings. Starlings are an exotic species introduced into this country by man. When they are omitted for William Trelease Woods, g_1 drops from 4.19 to 2.07. Indigo buntings were

Table 10. Population statistics

Vegetation/Source of data	Age in years	Size (ha)	Years record	Number, species Total	Mean
Fallow field Phillips Tract & Hart Forest, Willson (1974) Strip-mined area, Karr (1968)	1–3	10–12	3	8	4.3
Grassland-shrub Phillips Tract & Hart Forest, Willson (1974)	(?)	6–7	2	10	6.5
Early shrubs Strip-mined area, Karr (1968)	12	8.7	1	16	
Abandoned farmland Allerton	22–24	24.3	3	29	22.0
Late shrubs Strip-mined area, Karr (1968)	44+	8.7	1	30	
Late shrubs (omitting starlings) Strip-mined area, Karr (1968)	44+	8.7	1	29	
Abandoned farmland Allerton	39–41	24.3	3	43	35.7
Upland forest (Table 1) Trelease	virgin	24.0	4	38	27.2
Upland forest (Table 1) (omitting starlings) Trelease	virgin	24.0	4	37	26.2
Floodplain forest Phillips Tract & Hart Forest, Willson (1974) Hart Forest, Blem & Blem (1975)	?	5.1	4	28	21.3
Upland forest Phillips Tract & Hart Forest, Willson (1974) Hart Forest, Blem & Blem (1975)	125+	9.1	4	27	20.0[2]
Floodplain forest (Salt Fork) Strip-mined area, Karr (1968)	60+	6.2	1	31	
Floodplain forest White Heath area, Fawver (1947)	(?)	20.0	1	24	
Floodplain forest (1949–51) Allerton	virgin	10.1	3	28	24.7
Floodplain forest (1963, 1967) Allerton	virgin	10.1	2	36	33.0
Upland forest Vermilion River area, Smock (1970)	(?)	16.0	1	28	
Upland forest Funk Forest, Calef (1953)	virgin	24.0	2	30	28.5
Upland forest Allerton	125+	11.8	7	35	26.4

[1] Calculated from "mean pairs/40 ha."
[2] Average of 3 years with complete censuses.
[3] NS = not statistically significant.

Pairs/40 ha		Percentage of pairs in biotope[1]					Pairs/species/40 ha			Skewness
Mean	Adjusted	G	FE	OF	CF	FI	Mean	Adjusted	Annual	(g_1)
53		98	2				6.6		12.3	2.07
82		19	79	2			8.2		12.6	2.89
294		6	73	20			18.4			NS[3]
165			73	21		6	5.7		7.5	2.75
364		5	47	40	8		12.1			1.44
327		6	41	42	11		11.3			0.83
248		+	39	48	12	2	5.8		6.9	2.12
227	209		36	44	20	+	6.0	5.5	8.3	4.19
167			13	60	27	+	4.5		6.4	2.07
374	345		12	57	30	2	13.4	12.3	17.6	2.40
227	222		4	51	43	3	8.4	8.2	11.4	2.47
476	414		21	23	30	25	15.4	13.4		NS
142	138		3	33	50	14	5.9	5.8		NS
270	263		5	24	38	33	9.6	9.4	10.7	3.21
366	356		6	36	38	21	10.2	9.9	10.5	1.10
212	208		7	22	42	28	7.6	7.4		1.45
157	156		4	26	61	10	5.2	5.2	5.5	NS
241	241		1	22	46	31	6.9	6.9	8.8	1.66

the second most abundant species in the woods with 12.2 *p/s*. Skewed distributions indicate full or nearly full occupancy of a highly available niche but this condition is sometimes of relatively short duration. The excessive abundance of red-headed woodpeckers and starlings depended on the temporary presence of dead elm trees. In the Robert Allerton Park floodplain forest, American redstarts had decreased and several other species increased between 1951 and 1963 (Appendix 3).

Near symmetrical distributions (g_1 = NS) were associated with both high and low values of *p/s* and with both seral shrub and climax or near-climax floodplain and upland forests. They likewise occurred with various combinations of FE, FO, CF, and FI species. There is no correlation between g_1 and number of species. There is a tendency for g_1 to vary negatively with total pairs/40 ha and *p/s* but the coefficients of correlation are not statistically significant.

Considering only tracts (n = 3) with skewed populations less than 2.0 (actually <1.70), the upland deciduous forest of east central Illinois in presettlement time may have had a relatively stable bird population on areas averaging 17.3 ha of about 31 species annually, total populations of 203 pairs/40 ha, *p/s* annually of 7.3, and g_1 of 1.10. Distribution according to biotopes would have been FE, 4%; OF, 23%; CF, 50%; and FI, 23%. The two floodplain forests censused with symmetrical distribution of species population varied too widely to warrant such a generalization of community structure.

11. Northward Dispersal: Variations in Rates and Routes

How avifaunas have become modified as the result of dispersal of exotic species, such as house sparrow, starling, and ring-necked pheasant, into the region has been considered. Local avifaunas have also been affected by dispersal of native species from the south northward, and the routes they have taken in this dispersal. I have left this section to the last, as it involves species in both forest and seral communities and variations in community structure.

East central Illinois is near the northern limits in the dispersal of Carolina wrens and mockingbirds. Both are permanent residents but their prevalence in the region fluctuates depending, at least in part, on winter weather.

The Carolina wren was first recorded in William Trelease Woods during the winter of 1928–29, then again in 1942–43, and fairly regularly beginning in 1949–50. As a breeding bird, it was recorded in 1934, 1943, and more frequently beginning in 1951 (Fig. 32). The species feeds mostly on or near the ground, and numbers of nesting birds were generally reduced following winters with much snow. Low temperatures may also have been critical.

The mockingbird had extended its range northward into central Illinois by the 1880s but was known to fluctuate in abundance correlated, in some cases at least, with winter weather (Graber et al., 1970). Christmas bird counts in east central Illinois indicated a progressive rise in early winter populations to a peak in 1969 and then a decline (Fig. 32).

Dispersal of forest and forest-edge birds appears to have occurred along river systems. One principal route extended in a roundabout way from the Mississippi, Illinois, and Sangamon Rivers into the western part of the region and another from the Ohio, Wabash, Vermilion, and Salt Fork Rivers into the eastern part (Fig. 1). The

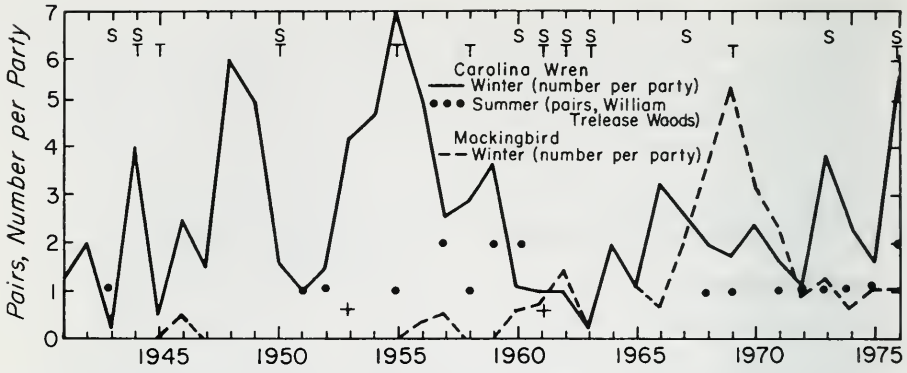


Fig. 32. Fluctuations in breeding (pairs) and wintering (number per party, Christmas bird counts) populations (Carolina wren and mockingbird) (S, snowfall over 12.5 cm above normal and T, temperature more than 5° C below normal during either December, January, or February.

latter route is more direct and shorter since it is oriented in a north-south direction. Although these river systems are separated from each other by only a few kilometers, intervening tallgrass wet prairie in presettlement time served to prevent free inter-dispersal. Only the sparsely wooded headwaters of the Kaskaskia and Embarras Rivers occur between the two major river systems. The different census plots in Tables 5 and 6 are listed progressively from the extreme west to the extreme east.

According to Brewer (1963), the black-capped chickadee originally prevailed over the region but is now being displaced by the Carolina chickadee which is expanding its range northward. This displacement has not yet occurred along the Sangamon and upper Kaskaskia Rivers but is nearly complete along the Embarras and Vermilion-Salt Fork Rivers. In 1910, the black-capped chickadee nested along the Embarras River near Philo, and Twomey's original notes indicated this species in William Trelease Woods the winter of 1933–34. Only the Carolina chickadee nests at these localities now. The greater prevalence of willow flycatcher, mockingbird, warbling vireo, yellow warbler, northern oriole, and song sparrow in the eastern parts of the region (Tables 5, 6, 8) is not so easily explained because their present ranges extend far north of this region.

Differences in community structure are conspicuous. In the early shrub (12 years) and late shrub (44 years) stages along the Vermilion River, pairs/40 ha averaged 329, *p/s* 15.2, and g_1 0.94. In corresponding stages along the Sangamon River in Robert Allerton Park (22–24 and 39–41 years) pairs/40 ha averaged 206, *p/s* 5.8, and g_1 2.44. Similar differences, although statistically insignificant, occurred between forest bird populations in the two river systems. Regional differences in community structure probably depended on the particular species compositions in each region, but to explain why the species composition varied as it did requires further study.

12. Discussion

The principal finding of this study is that the avifauna is in continual flux correlated with time and space. Populations fluctuate in yearly cycles, from year to year, and less conspicuously over decades and longer intervals. Variations occur intra-regionally in species composition and population sizes. Changes in community structure accompany these fluctuations and variations.

The yearly cycle relates to migration, nesting, and overwintering and is apparently regulated by photoperiod, weather, growth and fruiting of plants, and the yearly cycle of the invertebrate food supply.

An increase over a period of years followed by a decrease in abundance, correlated with a surge in their invertebrate food supply, was best shown by eastern wood pewee, red-eyed vireo, and indigo bunting. Fluctuations in bird numbers lagged three to five years behind the fluctuation in insects, spiders, and other arthropods. A lag in response is to be expected, as all three species are migratory, and changes in population level presumably resulted from differences in the percentage of young birds attracted back to the vicinity of where they hatched and of adults from elsewhere into the area. No correlation was found between fluctuations in weather in the region and the number of nesting birds of these species, and since all three species overwinter in the tropics or subtropics, weather was probably not involved there also, although this was not documented.

The delay in response of bird populations to the increase in the invertebrate food supply is longer than has been found elsewhere. In the Hubbard Brook Experimental Forest of New Hampshire, a defoliating moth destroyed 44% of the annual leaf production in

the second year of its outbreak. Some insectivorous species began to increase after a lag of only one to two years and continued to increase for two years after the peak population of the insect had passed (Holmes and Sturges, 1975). The almost immediate response of some northern birds to outbreaks of spruce budworm (*Choristoneura fumiferana* (Clem.)) in New Brunswick is related to the 8,000-fold increase in the insects over only a two-year period. But two species of warblers did not peak in numbers until three years after that of the budworm (Morris et al., 1958). In an outbreak of larch sawfly (*Pristiphora erichsonii* (Htd.)) in Manitoba some bird populations began to increase when the insect population reached 1200/ha, but for other species not until the insect population attained levels of one to two and one-half million per hectare (Buckner and Turnock, 1965). In William Trelease Woods, the less than 10-fold increase in invertebrates over a three-year period was less spectacular. It appears that the speed with which bird populations respond to increases in their food supply varies not only with the rate at which the food supply increases but also with the species of the bird.

Yearly fluctuations in some bird populations are affected by the weather, either directly or through the availability of their food supply. The Carolina wren and mockingbird, at the northern boundary of their ranges, fluctuated in abundance related to winter temperatures and snowfall locally. With house wrens, variations in temperature in the Gulf states where they winter affected the number that survived and returned north to their breeding grounds. Wintering populations of tree sparrows, dark-eyed juncos, and perhaps other species that show a more or less four-year cycle of abundance may have been determined by fluctuating conditions affecting reproductive success in the north, by fluctuating snow cover in this region, or by both.

Species varied in their biotope requirements according to their relation to grassland (G), forest edge (FE), open forest (OF), closed forest (CF), and forest interior (FI) biotopes. These relationships affected their responses to changes in the environment, especially in the vegetation. The response of many OF and FE species to the opening and closing of the forest canopy resulting from the death of elm trees at William Trelease Woods is clearly shown by the bell-shaped or normal curves of the red-headed woodpecker (Fig. 10)

and house sparrow (Fig. 18). Some species, such as the gray catbird, brown thrasher, and common yellowthroat, had skewed curves in that they increased rapidly to a peak in abundance but then decreased more slowly. Still other species, such as mourning dove, blue jay, American robin, starling, and cardinal, after once gaining peak numbers, appear now to have become established throughout the forest tract. Not all FE and OF species responded to these changes in the forest. The ruby-throated hummingbird, yellow-breasted chat, American goldfinch, field and song sparrows were unaffected (Appendix 1).

There may well be disagreement among observers as to the proper biotope for assignment of some species. Using a statistical cluster analysis of the distribution of species in eastern Kansas in relation to 10 environmental factors, Johnston (1979), for instance, puts the indigo bunting, American robin, and cardinal in with a group of forest-edge species, while I call them OF species. There are some other discrepancies, particularly since he did not distinguish between OF, CF, and FI categories. C. S. Robbins (personal communication) considers the indigo bunting strictly a FE, rather than an OF species. Differences among observers in their assignment of species may not be entirely a matter of judgment, since species may vary locally in their apparent biotope requirements, depending on subtle differences in vegetation, inter-species competition, or prevailing climate.

With changes in vegetation, inter-species competition for territories, nesting sites, and food supplies in William Trelease Woods greatly influenced population levels attained by starlings, various species of woodpeckers, and perhaps white-breasted nuthatch and tufted titmouse. The replacement of bobwhite by ring-necked pheasant and black-capped by Carolina chickadees probably involved inter-species competition, but I have no direct evidence that the replacement of Cooper's hawk by red-tailed hawk and barred owl by great horned owl was the result of competition. If competition between these latter species occurred, it would have been elsewhere in the region, because several years elapsed between their occurrences at William Trelease Woods.

In succession of vegetation on abandoned farmland, G species were predominant in the early stages, followed in turn by FE, OF,

and CF species. Individual species appeared, reached a peak in numbers, and then, unless they belonged to the climax, disappeared. Total populations increased from single-layered grassland to two- and three-layered shrub and forest vegetation. This was clearly correlated, as has been shown elsewhere (Udvardy, 1957), with an increase in number of species that found suitable niches in the more diversified vegetation. However, after establishment of these bird communities in complex vegetation, our data indicate that variation in total populations from one stand to another depended not so much on number of species as on the extent and occupancy of the niches available. Udvardy's (1957) study of 130 samples of temperate deciduous forest also indicated the greater importance of mean population size. Reconstructing data from a curve that he gives shows that an increase in total populations of 150% (180 to 450 pairs/40 ha) was correlated with an increase of only 35% in number of species (20 to 27) but 86% in *p/s* (9.0 to 16.7).

The equitability index or evenness in the population size of different species within a community (Sheldon, 1969) is a component, along with species richness, of Shannon and Weiner's species diversity index (Pielou, 1966). Although these indices are in common use in comparing community structure, skewness (g_1) is a better criterion than equitability for showing how species populations are distributed. As discussed elsewhere (Kendeigh and Fawver, 1981), biological measurements are commonly distributed symmetrically around a mean similar to a normal or Gaussian curve. Seldom if ever are measurements of a structure or function exactly uniform. It is more logical to indicate the degree to which the distribution of measurements departs from symmetry than from a condition that never occurs. All bird communities that I have analyzed have had a positively skewed distribution of population sizes, to a greater or lesser extent. However, nearly symmetrical distributions, where g_1 is not statistically different from zero, appear to be typical of undisturbed stabilized communities; and highly skewed distributions result from special, often temporary, conditions.

This study provides information on two practical problems of present-day concern. The reliability of the Christmas bird counts as quantitative samples of regional bird populations has been questioned. Several figures in this paper show good agreement for par-

ticular species between yearly fluctuations in these counts and fluctuations in breeding and wintering populations at William Trelease Woods. The Christmas bird counts were of importance in showing that populations of certain species were affected throughout the region in the same manner as they were at William Trelease Woods. Care needs to be exercised with the Christmas bird counts, however, to cover the same areas in the same manner each year and to make proper allowances for possible effects of weather conditions on the day of the counts.

There is controversy as to the best size of areas that are to be made into bird preserves. Simberloff and Abele (1976) suggest that relatively small preserves will contain more species than a single preserve of the equivalent combined areas. Whitcomb et al. (1976), however, point out that the species assemblage on small isolated areas will often be different and may include exotic or "weedy" species. Diamond et al. (1976), Robbins (1979), and others have also emphasized the importance of large tracts of forest containing hundreds or perhaps thousands of hectares for insuring the preservation of stable populations of forest interior species.

William Trelease Woods is a relatively small isolated area surrounded by farmland. Compared with the continuous forests of Robert Allerton Park, its bird community has a greater percentage of FE and OF species, no permanent FI species, a high turnover rate, and a higher g_1. William Trelease Woods and its bird life represents a reasonably good sample of the ecotone between deciduous forest and what was formerly tallgrass prairie and should be preserved for this reason. In presettlement time, this ecotone contained many small isolated tracts of forest. The avifauna of the woods, however, is poorly representative of that found in continuous forest. The upland and floodplain forests of Robert Allerton Park, in contrast, are good examples of what formerly occurred along the streams in the region. The Vermilion River Woods and Kickapoo State Park deserve preservation because they contain avifaunas resulting from dispersal northward along the Wabash-Vermilion River systems and differences in species composition, p/s, and g_1, from avifaunas along the Sangamon River.

13. Summary

Fluctuations in species composition and population sizes of the avifauna in William Trelease Woods were followed for more than 50 years and in several other plots in east central Illinois for shorter periods. Breeding bird censuses were taken by the spot-mapping method and wintering counts by cruising over known distances (Christmas bird counts) and areas (William Trelease Woods). Yearly fluctuations in Christmas bird counts were in general agreement with fluctuations in breeding and wintering populations of permanent resident species determined by the spot-mapping procedure.

Nesting populations in William Trelease Woods consisted typically of about 17 permanent and 21 summer resident species. They are classified according to their preference for forest-edge, open-forest, closed-forest, and forest-interior biotopes. Wintering populations included four regular winter visitors in addition to the permanent residents. Transients were most numerous from March through May in the spring and from September through October in the autumn, with some species, especially blackbirds, persisting into early January.

Increases and then decreases in nesting populations of wood pewee, red-eyed vireo, and indigo bunting in William Trelease Woods during the 1940s and early 1950s followed, after a lag of 3 to 5 years, a surge in the size of invertebrate populations.

Diseases that eliminated elm trees from the forest canopy in William Trelease Woods during the 1950s brought decreases in forest-interior species and increases in open-forest and forest-edge species. These changes were temporary with most species, but high populations persisted with mourning dove, blue jay, American robin, and cardinal after the forest canopy had again become closed in the late 1960s.

Woodpeckers and starlings were especially favored by the death of the elms, and fluctuations in their numbers were apparently also correlated with inter-species competition. Decline in numbers of black-capped chickadee, white-breasted nuthatch, and tufted titmouse may be related to harassment from woodpeckers and starlings.

The starling and house wren invaded William Trelease Woods as regular breeders about 1934. The house wren became the most abundant nesting species between 1942 and 1957 and then declined to complete absence in 1977. Variations in abundance of house wrens were correlated with temperature conditions in the Gulf States where the species winters.

The avifauna of William Trelease Woods is similar to an island fauna in having an approximate balance of species invading and disppearing. Invasion and extinction rates varied with the different biotope categories but were highest during the period of disturbance of the forest canopy, 1950–64.

Bird populations in upland forests within the region contained the same number of species but lower populations than in floodplain forests. Some upland ground-nesting species were apparently prevented from nesting in the lowland forests because of occasional flooding, while some species restricted to floodplain forests frequent the river's edge for nesting.

Christmas bird counts indicated a decline in numbers of several species of hawks, increase in overwintering populations of mourning doves and sparrows, and possible cyclic fluctuations in the populations of wintering dark-eyed juncos, tree sparrows, and white-crowned sparrows.

In the succession of avifaunas and vegetation on abandoned farmland, grassland species were predominant for the first few years, followed in turn by forest-edge, open-forest, and closed-forest species. The invasion and decline in populations of certain grassland, forest-edge, and open-forest species, when plotted against time, exhibit positively skewed distribution curves.

Variations in size of total bird populations in well-developed shrub and forest communities were correlated to some extent with number of species present but to a greater extent with number of pairs per species. Distribution of pairs per species within each com-

munity was positively skewed, but the degree of skewness was minimal, approaching a symmetrical or normal distribution, in certain relatively undisturbed, stabilized seral shrub and climax forest stands. Bird communities with a skewness greater than 2.0 contained one or more species with disproportionately large populations.

The avifauna has changed during the past half-century as the result of dispersal of exotic species (ring-necked pheasant, starling, house sparrow) into the region and the tendency of several southern species (Carolina chickadee, Carolina wren, mockingbird) to extend their ranges northward. The avifauna along the more direct and shorter dispersal and migration route of the Ohio, Wabash, Vermilion, and Salt Fork River System in the eastern part of the region contains several species that are uncommon along the Mississippi and Sangamon River System in the west. Total populations and pairs per species were higher and skewness lower in the eastern than in the western portions of the region. Persistence of these differences may be related to tallgrass prairie in the upland area in early days and now farmland preventing easy inter-dispersal between the two river systems.

Breeding populations in the isolated 24-ha William Trelease Woods were composed of approximately one-third forest-edge, one-half open-forest, and one-fifth closed-forest and forest-interior species. This contrasts with the avifauna of a similar stand in the extensive forest tract at Robert Allerton Park where more than three-fourths of the birds were closed-forest and forest-interior species. Species turnover rates and skewness in the distribution of population sizes within the bird community of William Trelease Woods were higher than in census plots within continuous forests. These factors require consideration in selecting representative areas for nature preserves.

Appendices

Appendix 1: Breeding Bird Populations (number of male territories or pairs) at William Trelease Woods (24 ha)

	Species	Biotope	1927	1928	1934	1935	1936	1937	1939	1940
1	Cooper's hawk	OF	1	1		1				
2	Red-tailed hawk	FE								
3	American kestrel	FE						1		
4	Bobwhite	FE								
5	Ring-necked pheasant	G								
6	American woodcock	OF								
7	Mourning dove	OF	1	1		2	2			
8	Yellow-billed cuckoo	OF	1	3	2	1	2	1		
9	Black-billed cuckoo	FE								
10	Screech owl	OF								
11	Great horned owl	CF								
12	Barred owl	CF	1	1	1	1	1	1	1	
13	Ruby-throated hummingbird	OF	1	1	1	1	1	1	1	1
14	Common flicker	OF	1		1	1	2	1	1	
15	Red-bellied woodpecker	CF	1	1			1		1	1
16	Red-headed woodpecker	OF	1		4	2	3	5	1	1
17	Hairy woodpecker	CF	1	2	1	1	1		1	1
18	Downy woodpecker	CF	2	3	5	4	2	4	1	4
19	Eastern kingbird	FE								
20	Great crested flycatcher	CF	4	4	5	4	5	5	–[1]	11
21	Acadian flycatcher	FI								
22	Eastern wood pewee	CF	3	7	3	4	7	6	6	8
23	Blue jay	OF	1	2						
24	Common crow	FE	2	4	2	5	4	2	1	6
25	Carolina chickadee	OF								
26	Tufted titmouse	CF	2	5	5	4	6	4	3	3
27	White-breasted nuthatch	CF			1		1			
28	House wren	OF	1		3	4	8	14	–	10
29	Carolina wren	CF			1					
30	Mockingbird	FE								
31	Gray catbird	FE	2		1	1	1			
32	Brown thrasher	FE			1	1	1			
33	American robin	OF	1				2			
34	Wood thrush	CF	4	4	3	3	2	2	–	1
35	Eastern bluebird	FE								
36	Blue-gray gnatcatcher	FI		1						
37	Cedar waxwing	FE								

Appendix 1 (continued)

Species	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952
1	1	1	1		1	1	1	1	1			
2												
3												
4				6								
5												1
6												
7												
8	3	4	5	6		3	1	2	6	3	1	3
9												
10												
11									1	1	1	1
12												
13	1	1	1			1	1	1	1	2	2	1
14		1	1	1	2				1	2	1	2
15	1		1	1	1	1	1	2	2	2	1	2
16			1						1	2		1
17	1	1	1	1		1	1	1	1	2	1	1
18	5	5	6	6	6	4	4	3	5	4	4	4
19												
20	7	8	7	5	7	7	7	9	9	6	2	5
21									1	1		
22	10	5	8	7	6	6	6	14	8	15	17	15
23			1						1	1		1
24	2	4	9	10	11	9	9	6	5	3	4	1
25												
26	2	2	3	5	3	5	5	3	4	4	3	1
27												
28	20	31	40	25	25	28	32	45	61	46	31	28
29			1								1	1
30												
31												1
32						1					1	
33				1					1		1	2
34	1	2	2									3
35				1						1		1
36												
37												

Appendix 1 (continued)

Species	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964
1												
2				1	+[2]			1			1	
3					1	1			+			1
4			1	+						+		
5	+	+	1	+	+	+	+	+	+		+	
6												1
7	1	1	1	2	3	7	17	13	8	14	7	7
8	6	4	3	3	2	3	5	5	5	4	5	4
9				1		+	+		1	+	1	+
10	1									1		1
11	+	1	1	1	1	1	1	1	1	1	1	1
12												
13	2	2	1		1							
14	2	4	5	4	4	6	10	5	9	8	10	14
15	1	2	4	4	4	2	3	1	2	1	2	2
16	1	1	1	4	6	11	14	17	13	8	25	23
17	1	1	1	2	1	1	1		1	1		
18	3	7	8	8	6	6	13	4	4	5	5	3
19												1
20	3	4	5	6	6	5	5	5	5	7	8	6
21	1			1		1					+	+
22	19	19	14	12	20	14	12	15	11	7	15	7
23	2	3	3	4	6	6	10	7	7	9	12	12
24	+	+	1	1	+	+	+	+	+	+	+	+
25		1								1		
26	1	+	2	1	1	5	5	5	1	1	2	
27	1	1	1									
28	30	31	51	32	45	22	28	31	27	19	30	21
29	+		1		2	1	2	2	+			
30										+		
31	1	1	1	1	1	2	2	1	3	1	1	1
32	1	1	2	1	1	2	5	2	4	2	4	3
33	1	3	1	4	4	3	9	3	5	3	5	3
34	1	2	3	2	2	2	2	1	1	2	2	1
35			1									
36												
37		2										

Appendix 1 (continued)

Species	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976
1												
2	1			+		1	1	1	1	1	1	
3		1	1	+								
4	+	+	1	1	2	+	+		+			
5			+	+	2	+	+	+	+	+		+
6	+			1	1				+	1		
7	9	8	7	8	10	5	10	13	7	8	4	6
8	1	4	4	2	3	5	3	6	2	3	4	4
9		+		+								1
10												+
11	1	1	1	1	1	1		1	1	1		+
12												
13		1							+			
14	12	13	7	6	9	8	6	8	7	13	8	6
15	2	2	2	2	1	3	2	1	1	3	5	5
16	29	26	13	17	13	12	10	7	10	8	2	3
17	1	1	1	1	1		1			1	1	2
18	3	4	1	2	2	3	5	6	2	6	2	3
19												
20	5	4	5	3	3	5	6	3	3	4	2	5
21		1				1	+					
22	8	10	9	10	9	16	7	9	5	5	5	7
23	12	15	12	10	8	19	15	15	10	16	14	13
24	+	+	+	+	+	+	+	+	+	+	+	+
25									+	1		
26	1											
27							1		+	1	+	+
28	25	22	14	16	13	14	5	9	8	12	10	7
29				1	1		1	1	1	1	1	2
30							+					
31		3	1	7	5	+	1		+		1	3
32	3	3	1	2	5	3	1		3	2	1	2
33	6	10	5	11	8	13	9	5	6	23	12	10
34		3	1	1	1	2	2	+	2	3	2	6
35												
36												
37												

Appendix 1 (continued)

Species		Biotope	1927	1928	1934	1935	1936	1937	1939	1940
38	Starling	FE	–	–	8	10	25	16	–	9
39	Yellow-throated vireo	FI								
40	Red-eyed vireo	CF	9	7	8	4	4	5	–	–
41	Ovenbird	FI						1		
42	Kentucky warbler	FI		1						
43	Common yellowthroat	FE			2	1	1	1	–	5
44	Yellow-breasted chat	FE								
45	American redstart	FI		1						
46	House sparrow	FE								
47	Red-winged blackbird	G								
48	Orchard oriole	FE								
49	Northern oriole	FE								
50	Brown-headed cowbird	–	–	–	–	–	–	–	–	–
51	Scarlet tanager	FI								
52	Summer tanager	FI								
53	Cardinal	OF	3	5	3	3	2	2	1	2
54	Rose-breasted grosbeak	OF								
55	Indigo bunting	OF	17	9	22	21	20	20	–	15
56	Dickcissel	FE								
57	American goldfinch	FE	–	–	2	–	10(?)	–	–	–
58	Rufous-sided towhee	FE								
59	Vesper sparrow	G								
60	Field sparrow	FE			2	2				
61	Song sparrow	FE			1	1				
Totals (excluding brown-headed cowbird):										
		Species	22	20	25	24	25	19	–	–
		Pairs	60	63	88	82	114	92	–	–

[1] Species omitted from census.

Appendix 1 (continued)

Species	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952
38	16	17	22	16	20	29	21	16	22	20	13	22
39												
40	13	14	10	11	9	8	8	16	16	21	21	18
41			1									
42						1			1	1	1	1
43	1	1	2	2	2	3	1	2	1	2	3	3
44				1		1	1	1	2	1	1	2
45												
46									1	1	1	2
47												
48												
49												
50	–	–	–	–	–	–	–	–	–	–	–	–
51												
52												
53	1	2	3	3	4	2	3	3	2	3	2	4
54												
55	25	27	27	26	22	25	20	28	25	45	33	16
56												1
57	4	1	3	–	–	–	–	2	1	4	3	1
58												
59												
60		2	1			1		1	1			1
61		1									1	1
	18	20	24	19	14	20	17	19	27	25	25	33
	114	130	157	134	119	137	122	156	181	193	150	147

Appendix 1 (continued)

Species	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964
38	39	25	13	21	25	44	70	92	85	52	57	61
39	1											
40	13	24	23	11	11	5	12	8	4	5	5	2
41												
42		1										+
43	4	4	2	3	7	7	4	4	6	2	3	4
44	1	1	1	1	1			1	+			
45												
46	1	3	2	7	5	12	15	11	11	9	2	6
47						2						
48												+
49									1	1	1	1
50	—	—	—	—	—	—	—	—	—	—	—	—
51			1	1				1				
52												
53	4	2	2	5	6	3	6	5	7	5	4	6
54									2	2		
55	18	22	24	14	18	15	21	14	16	11	17	14
56	+	1	1									
57	2	2	2	1	1	2			+	+	+	
58	+	1	5	4	3	5	7	5				2
59	1											
60	+	1	2	1	1	3	4	+			1	2
61	1	1	+			+	2	+				
	38	36	37	34	33	34	30	31	32	32	30	33
	164	179	191	164	195	199	285	260	240	182	216	210

[2] + = present, but nesting density too low to measure.

Appendix 1 (continued)

Species	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976
38	66	62	44	38	62	59	47	55	18	64	61	70
39									+			
40	5	3	3	7	4	9	4	6	4	3	6	6
41								+	+			
42	1				1	2	+					
43	1	5	4	5	4	4	1	2	2	6	1	3
44												
45												
46	1	1	+	+	+			+		+		
47					+				+		+	+
48	+											
49						1				1	1	1
50	–	–	–	–	–	–	–	–	–	–	–	–
51								+			1	
52									1			
53	2	6	6	1	6	10	6	4	6	6	6	7
54							+	+			1	1
55	14	19	17	24	10	10	10	12	7	9	7	16
56												
57		+			1	+	+	1	+	2	1	+
58	3	3	1		1	2	+		+	3	+	2
59												
60	+	2	3	2	1	3	4	3	4	6	3	3
61			1								1	1
	29	31	29	31	32	30	33	28	36	32	32	34
	212	233	165	179	188	211	158	168	111	213	164	195

Appendix 2: Wintering Bird Populations (average number of individuals) at William Trelease Woods (24 ha)

	Year	1924-1925	1926-1927	1927-1928	1928-1929	1929-1930	1933-1934	1934-1935	1935-1936	1937-1938
	Number of counts	18	?	10	?	?	16	19	14	4
1	Cooper's hawk									
2	Red-tailed hawk	1	2	2	1		2	2	1	1
3	Rough-legged hawk			1						
4	American kestrel									
5	Bobwhite	+[1]								13
6	Ring-necked pheasant									
7	Mourning dove								10	
8	Screech owl									
9	Great horned owl									
10	Barred owl		2	2	2	2				
11	Common flicker	5	4	7	6	9	2	8	4	3
12	Red-bellied woodpecker	1	1	2	1	1				3
13	Red-headed woodpecker						3	4		+
14	Hairy woodpecker	2	2	2	1	1				2
15	Downy woodpecker	3	2	3	3	3	6	5	10	7
16	Blue jay	5	2		1		2	2	2	2
17	Common crow	5	3	12		4	2	20		8
18	Black-capped chickadee	2		1			2			
19	Carolina chickadee									
20	Tufted titmouse	8	4	8	1	4	10	12	10	14
21	White-breasted nuthatch	1	1	4	3		2	2	4	2
22	Red-breasted nuthatch									
23	Brown creeper		2	1	2				10	
24	Winter wren									
25	Carolina wren				1					
26	Mockingbird									
27	Brown thrasher									
28	American robin									
29	Eastern bluebird									
30	Golden-crowned kinglet	1		2						
31	Cedar waxwing									
32	Starling								20	2
33	House sparrow	+								
34	Red-winged blackbird									

Appendix 2 (continued)

	1938-1939	1939-1940	1940-1941	1941-1942	1942-1943	1943-1944	1944-1945	1945-1946	1946-1947	1947-1948	1948-1949	1949-1950	1950-1951
	7	6	5	5	5	5	5	5	4	6	5	6	5
1													
2	1	1	1	1	1			1		1		1	+
3													
4													
5		3	6				16		17	8		1	2
6										+	1	+	
7	6	14										1	7
8													
9											1	+	1
10	1												
11	5	1		2						1	1	2	+
12	3	1	2	2	3	2	2	3	3	3	3	4	1
13	+			1									
14	1	2	1	2	2	2	2	2	1	1	2	2	2
15	11	7	8	9	10	8	8	6	8	6	9	12	9
16	1	3	2	10	6			2		1		1	+
17	6	10	18	5	6	6	8	15	6	12	26	7	9
18													
19													
20	8	3	2	7	14	10	6	4	9	7	4	5	3
21	2	2		2	2	2	2	1	2	2	+	2	
22				1									
23	4	3	2	3	3	5	2	2	1	6	3	3	2
24													2
25					1					+		1	2
26													
27													
28												2	3
29													
30	1						2			1			
31													
32	2	1									3	25	1
33											1		
34													

Appendix 2 (continued)

	1951-1952	1952-1953	1953-1954	1954-1955	1955-1956	1956-1957	1957-1958	1958-1959	1959-1960	1960-1961	1961-1962	1962-1963	1963-1964
	6	6	6	6	7	6	6	4	5	6	5	5	5
1													+
2	+	1		1		1	1	1	1	1	2	2	1
3		+	+							+	1	+	
4							+				+		+
5				4			1		2	6	2		
6	1		+	7	4	3	2	14	11	6	48	9	2
7	7	1	17	11	45	12	16	6	38	16	21	17	20
8													+
9		1	1	1	1	1	1	1	1	1	1	1	1
10							1	1					
11	2	4	3	3	1	1	3	2	3	+	2		3
12	2	3	4	7	7	9	7	4	5	5	4	2	3
13			3	2	2	6	6	17	23	3		20	29
14	2	2	1	2	3	4	3	2	3	1	2	1	1
15	6	12	10	13	14	19	10	9	8	6	5	4	2
16	1	4	4	6	4	6	3	8	10	7	6	7	4
17	28	+	+	+	+	+	2	6	1	+	16	+	+
18													
19	1		1	3	2		1	1		2	3		1
20	2	4	5	3	3	5	3	3	3	3	1	1	
21		1	3	2	1	2	3	1	1		3	1	2
22							3		+				
23	4	3	4	3	1	1	1	5	1	4	1	1	2
24				+		1		+					
25	1	1	+	1	1	4	2	2	2				
26											+		
27											+		
28		1			1		10		1			1	
29							+						
30		1	+		+						+		
31													
32	+	6		8	1	14	30	22	38	20	18	+	36
33	1	3	2	1	1	15	11	5	4	9	8	1	8
34						+	1						6

Appendix 2 (continued)

	1964-1965	1965-1966	1966-1967	1967-1968	1968-1969	1969-1970	1970-1971	1971-1972	1972-1973	1973-1974	1974-1975	1975-1976	1976-1977
	5	5	5	5	7	5	5	6	6	6	6	6	5
1	+					+							
2	1		1	+	+	+	2	+	+	1	+	+	
3			+	+	+	+							
4	+			+									
5			1		2	3	2						
6	3	1	9	1	5	16	18	16	4	3	1	+	3
7	22		+	+	+	1		2	1	10	1	1	
8													
9	1	1	1	2	1	1	1	1	1	1	1	1	1
10													
11	3	1	2	3	1	+	1	1	1	+	+		+
12	6	4	2	5	3	3	4	4	2	2	4	2	2
13	4	1	18	1	1		2	2	8	+		3	7
14	2	2	1	2	2	1	1	1	1	1	+		+
15	7	5	3	3	5	6	5	6	4	4	7	4	6
16	7	9	6	3	2	5	4	7	9	4	5	7	5
17	+	+	+	+	+	+	+	+	+	+	+	+	+
18													
19	+	2			+				2	1	2	+	+
20		2	1		+	+							
21	3	2	1	+	2	1	1		1	+	1	1	1
22													
23	5	2	1	2	3	4	3	6	+	1	1	2	3
24	1					1	1	1	+	+	+		1
25				1	1	+	+		+	1	1	1	1
26				+		+	+			+	+		
27													
28	+		1	+		1		1	2	+	+	+	+
29													
30		+			+				+			+	1
31	+												
32	18	47	42	33	6	25	18	13	18	24	38	29	10
33	1	1	1	+	+	+	+	1		+		+	
34								+	+	+			+

Appendix 2 (continued)

		Year	1924-1925	1926-1927	1927-1928	1928-1929	1929-1930	1933-1934	1934-1935	1935-1936	1937-1938
		Number of counts	18	?	10	?	?	16	19	14	4
35	Rusty blackbird										
36	Common grackle										
37	Brown-headed cowbird										
38	Cardinal		7	16	12	4	4	10	10	6	2
39	Evening grosbeak										
40	Purple finch			7	2						
41	Common redpoll		+					10			
42	American goldfinch		+		8		3				
43	Rufous-sided towhee										
44	Dark-eyed junco		15	25	20	3	1	10	10	85	
45	Tree sparrow		10	11	47	25		10	20	50	25
46	Fox sparrow				2	1	2				
47	Swamp sparrow										
48	Song sparrow			2	3		2				
	Totals:	Species	18	16	20	15	12	13	11	12	14
		Individuals	66	86	141	55	36	68	95	212	84

[1] + Species present, but average number of individuals less than 0.5.

Appendix 2 (continued)

	1938-1939	1939-1940	1940-1941	1941-1942	1942-1943	1943-1944	1944-1945	1945-1946	1946-1947	1947-1948	1948-1949	1949-1950	1950-1951
	7	6	5	5	5	5	5	5	4	6	5	6	5
35													
36													
37													
38	2	1	1	3	1	3	4	2	2	2	2	3	1
39													
40										+			
41													
42													1
43													
44		5		9			4			30	7	20	2
45	10	10	20	24				10	5	25	53	40	4
46													
47													
48										3	4	1	
	17	16	11	15	11	8	11	11	10	19	16	21	20
	64	67	63	81	49	38	56	48	54	109	120	133	52

Appendix 2 (continued)

	1951-1952	1952-1953	1953-1954	1954-1955	1955-1956	1956-1957	1957-1958	1958-1959	1959-1960	1960-1961	1961-1962	1962-1963	1963-1964
	6	6	6	6	7	6	6	4	5	6	5	5	5
35			3		+	+	14	1				+	14
36										+			
37											+		7
38	1	2	4	5	4	6	2	4	4	5	2	1	3
39								2					
40			1			1		+		+			
41													
42		+			+	2	1		1	+		+	
43			2										
44	1	5	18	6	10	20	10	16	13	2	8	10	+
45	23	19	18	26	25	85	22	45	15	2	19	25	2
46					+								
47					+	1				1			
48	2	6	2	2	1	9	2	4	2	3		2	1
	19	23	25	24	27	27	31	27	25	26	26	23	26
	85	80	106	117	132	228	172	182	191	103	173	106	148

Appendix 2 (continued)

	1964-1965	1965-1966	1966-1967	1967-1968	1968-1969	1969-1970	1970-1971	1971-1972	1972-1973	1973-1974	1974-1975	1975-1976	1976-1977
	5	5	5	5	7	5	5	6	6	6	6	6	5
35	+	+		+						+			
36									+	+		1	+
37				+									
38	5	2	1	3	1	3	4	3	2	2	5	2	2
39													
40													
41													
42	+	+	3	1	1		+	3					+
43	1												
44	17	12	7	7	5	14	6	22	45	2	3	8	11
45	6	40	26	19	2	28	30	1	10	18	2	1	14
46													
47		1		1			8	+	1				
48	1	6		2	2	2	5	6	3	1	1	1	1
	28	23	23	28	26	26	24	23	26	27	22	22	24
	114	141	128	89	45	115	116	97	115	76	73	64	69

Appendix 3: Breeding Bird Populations (number of male territories or pairs) in Forest Plots at Robert Allerton Park

		Upland (12.6 ha)						Floodplain (10.1 ha)				
Species	Biotope[1]	1949	1950	1951	1962	1964	1966	1949	1950	1951	1963	1967
Wood duck	FE									1	+	+
American woodcock	OF				1							
Mourning dove	OF				1	+[2]	0.2					
Yellow-billed cuckoo	OF	+	2	1	1	1	0.5	2	1.5	2	2.5	2.5
Great horned owl	CF		+			+						
Barred owl	CF		+		+		0.5		+	+	+	+
Whip-poor-will	FI	1.5	1	1								
Ruby-throated hummingbird	OF	1	3	1	1	+	3	1	0.5	0.5	1	0.5
Common flicker	OF				1	2	2			+	2.5	3
Red-bellied woodpecker	CF	2.5	3	2.5	4	1	3.8	2	2.5	3	6	3
Red-headed woodpecker	OF				3	8	17				6	6
Hairy woodpecker	CF	1.5	+	1	2.5	2	2	1	0.3	1	1	1
Downy woodpecker	CF	2.5	4	1	2.5	2	3	3	4	3	2	2
Great crested flycatcher	CF	1.5	3	2	1.5	3	3	3.5	2	1	7	3.5
Acadian flycatcher	FI	2	4	1	2	1	+	2	4	2	3	3
Eastern wood pewee	CF	4.5	9.5	5.5	3.5	8	17.2	7.5	5	3	7	3.5
Blue jay	OF	1	0.5	1	2	3	3	1	2	4	2	1
Common crow	FE	+	+		+	+	+		+	+	+	
Black-capped chickadee	OF	1	2	1	1	4	1	1	4	2.5	3	2
Tufted titmouse	CF	2.5	8	2	3	5	7.8	4	5	2.5	6	3
White-breasted nuthatch	CF	2.5	2	1	2	3	1.2	2	2.5	1.5	5	3
Brown creeper	FI										1	0.5
House wren	OF										1	3
Carolina wren	CF	3	2		+		0.2	3	2.5		2	2.5

[1] FE, forest edge; OF, open forest; CF, closed forest; FI, forest interior.
[2] + = present, but nesting density too low to measure.

Appendix 3 (continued)

Species	Biotope	Upland (12.6 ha)						Floodplain (10.1 ha)				
		1949	1950	1951	1962	1964	1966	1949	1950	1951	1963	1967
Gray catbird	FE										1	2.5
Wood thrush	CF	1	1	1	2	2	2.5	3	1.5	2	+	
Blue-gray gnatcatcher	FI	0.5	2		1		1				1	2
Starling	FE											0.5
Yellow-throated vireo	FI	1	1	0.5	+	3	4	+	0.5		2	1
Red-eyed vireo	CF	5.5	9	5.5	5	5	5	1	3	1	9	3
Prothonotary warbler	FE							2.5	4.5	3		
Northern parula warbler	FI											+
Cerulean warbler	FI		0.5	1	1		+	3	4.5	1	3	3
Yellow-throated warbler	FE										1	1
Ovenbird	FI	6.5	8	7	7	10	4.2					
Louisiana waterthrush	FI							+	1			
Kentucky warbler	FI	4	6	2.5	4		1.8	1	2	1	1	
Common yellowthroat	FE										1	1
Yellow-breasted chat	FE										1	0.5
American redstart	FI	6.5	8	6	3			21.5	15	7	10	7.5
Brown-headed cowbird	–	(+)	(+)	(+)	(+)		(+)	(+)	(+)	(+)	(+)	(+)
Scarlet tanager	FI	+	1	1.5	2	+	0.5	0.5	1		+	
Cardinal	OF	3.5	5.5	5	2.5	6	7.5	3	3	3	8	4
Indigo bunting	OF	2	1	1		1	0.5	4	6.5	6	14	4
Rufous-sided towhee	FE		1.5		1.5	+	0.5					
Totals (excluding brown-headed cowbird):												
Species		25	29	23	30	25	29	24	26	24	34	32
Pairs		57.5	88.5	52.0	61.0	70.0	92.9	72.5	78.3	51.0	110.0	73.0

Appendix 4: Yearly Breeding Bird Populations (pairs/40 ha) on Abandoned Farmland in Robert Allerton Park

Year		1946	1947	1948	1949	1950	1951	1952	1953	1954	1955
Years since cultivation		22	23	24	25	26	27	28	29	30	31
Bobwhite	FE[1]	+[2]							+		
Ring-necked pheasant	G										
American woodcock	OF	7	+	+			+				2
Mourning dove	OF	20	7	10	10	8	7	7	10	22	8
Yellow-billed cuckoo	OF	2	2		3	7	+	2	8	7	+
Black-billed cuckoo	FE	24		1	+	3		+			
Saw-whet owl	CF										
Whip-poor-will	FI	2			+					2	+
Common nighthawk	FE										
Ruby-throated hummingbird	OF	+			2	1	5	5	2	2	2
Common flicker	OF								+	+	2
Red-bellied woodpecker	CF										
Red-headed woodpecker	OF										
Hairy woodpecker	CF									2	+
Downy woodpecker	CF						+		+	1	1
Great crested flycatcher	CF	+				1	+	5	+	+	2
Eastern phoebe	FE	1	1	+	1		1	1	2	2	
Willow flycatcher	FE					1			2		
Eastern wood pewee	CF	+				1		+	1	1	
Blue jay	OF	4	+	2	5	10	1	2	3	2	4
Black-capped chickadee	OF				2	3	1	10	5	7	8
Tufted titmouse	CF					3	1	2	6	3	5
White-breasted nuthatch	CF							1			
House wren	OF		+	+			1		5	2	2
Carolina wren	CF					1					
Gray catbird	FE	2	2	2	+	3	1	2	8	+	3
Brown thrasher	FE	13	5	2	3	10	+	5	2	+	4
American robin	OF	2									
Wood thrush	CF					3		2	2		2
Eastern bluebird	FE					1					
Cedar waxwing	FE	15	10	5	2	8	8	2		2	
White-eyed vireo	FE	4	+			5	+	3	+	1	2
Bell's vireo	FE		2	2		4	4	5	3	5	5
Red-eyed vireo	CF				+	1				+	
Blue-winged warbler	FE									2	

Appendix 4 (continued)

1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1971
32	33	34	35	36	37	38	39	40	41	42	43	44	45	47
	+	+	3	2	+	+		+	3	3	8	13	8	4
			+		2				+		3	4	+	3
	+	+				2			+	1	+		1	2
8	3	10	9	13	13	7	10	14	22	14	13	23	12	9
+	+	2	5	8	7	+	7	5	3	7	8	8	12	3
1		+				+								
										1				
		+				2	2		+	3	7	5	2	6
				2		+		+	+					
1	+	2	2	3		2	2	2			+		+	
1	2	2	5	2	2	5	10	7	5	5	7	13	8	3
			+	3	2	+	2	3	3	3	3	+	+	4
				2		4	5	7	5	2	5	9	3	1
		+	+	+	+	2	3					+		
+	+	+	4	3	2	2	8	5	5	6	4	2	+	4
+	+	+	+	3	+	2	6	3	5	4	4	4	2	3
2	1	+		2										
1								+						
	2	2	3	2	3	5	5	2	3	+		+		
3	5	7	6	5	7	11	13	15	13	12	10	10	15	11
5	3	2	9	7	5	6	5	8	5	10	4	7	2	5
+	2	8	8	7	3	9	7	12	12	15	8	18	7	5
			+			+	2	+	+	2	+			
2		3	5	3	7	5	5	7	12	+	3	7		2
+			+			+			+		3	3	3	1
+	2	10	4	5	3	5	7	2	10	6	6	7	2	2
+	5	2	6	12	3	7	5	8	7	9	8	5	3	3
							+					2	+	
		2	2	+		2	+	+	+	3	+	2		1
				2		2	2	+			+			
		+		2			3							
7	3	2	2	3	2	9	7	5	8	7	8	12	2	7
3	2	+									+			
		2		+	3	+		+	+				+	
+		+			+	2	3	3	2	3	3	5	+	2

Appendix 4 (continued)

Year		1946	1947	1948	1949	1950	1951	1952	1953	1954	1955
Years since cultivation		22	23	24	25	26	27	28	29	30	31
Yellow warbler	FE				+						
Kentucky warbler	FI								+		
Common yellowthroat	FE	9	7	5	5	16	5	15	17	7	8
Yellow-breasted chat	FE	16	8	8	22	18	16	17	10	17	7
American redstart	FI	9	13	5	6	13	5	3	+	1	3
Eastern meadowlark	G					2		1	3		3
Orchard oriole	FE										
Brown-headed cowbird	–	(+)	(+)	(+)	(9)	(5)	(+)	(10)	(8)	(+)	(+)
Scarlet tanager	FI		+	+		1					2
Cardinal	OF	13	18	8	9	16	8	25	13	17	12
Rose-breasted grosbeak	OF		+	+							
Indigo bunting	OF	8	+	+	12	20	5	13	13	3	8
Dickcissel	G				3		+			+	
American goldfinch	FE	24	13	25	7	13	10	15	11	5	5
Rufous-sided towhee	FE	13	10	8	14	16	9	15	16	15	13
Henslow's sparrow	G				2	1					
Field sparrow	FE	37	54	32	45	54	38	33	40	30	28
Song sparrow	FE	2				1					
Totals (excluding the brown-headed cowbird)											
Species	G	0	0	0	2	2	1	1	1	1	1
	FE	13	11	11	11	14	11	12	12	12	9
	OF	8	8	7	7	7	9	7	9	9	10
	CF	2	0	0	1	6	3	5	5	6	5
	FI	2	2	2	2	2	1	1	2	2	3
	Total	25	21	20	23	31	25	26	29	30	28
Pairs	G	0	0	0	5	3	+	1	3	+	3
	FE	160+	112+	90+	99+	153	92+	113+	111+	86+	75
	OF	56+	27+	20+	43	65	28+	64	59+	62+	48+
	CF	+	0	0	+	10	1+	10+	9+	7+	10+
	FI	11	13+	5+	6+	14	5	3	+	3	5+
	Total	227+	152+	115+	153+	245	126+	191+	182+	158+	141+

[1] FE, forest edge; G, grassland; OF, open forest; CF, closed forest; FI, forest interior.
[2] + = present, but nesting density too low to measure.
[3] – = probably present, but not recorded.

Appendix 4 (continued)

1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1971
32	33	34	35	36	37	38	39	40	41	42	43	44	45	47
		+				+	+	5	+		1			2
3	7	2	1	2	2	4	3	3	2	3	2	2	2	2
10	8	17	9	10	8	11	15	15	8	3	3	8	5	2
+	+	+	+			2		+	+				+	
			6	+	+		2	+	+		+		+	
				2										
(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(2)	(5)	(15)	(13)	(8)
	+		2	3	2	2	2		2	2				
22	20	12	17	12	17	14	22	39	30	22	16	20	21	13
				2	2		7	5	3	5		2	5	5
15	7	12	13	15	12	14	22	22	20	11	11	19	37	9
		+												
5	3	12	4	3	$-^3$	4	+	3	7	5	2			2
18	23	28	19	13	13	9	17	15	25	17	14	20	17	14
23	27	25	35	27	23	20	30	29	42	20	8	28	17	11
0	0	1	2	1	2	0	1	1	2	0	2	1	2	1
12	11	14	9	14	10	13	11	13	11	10	12	9	9	10
10	9	10	9	11	9	11	12	11	11	11	11	11	12	11
4	4	7	8	8	7	10	8	8	12	8	7	8	7	6
1	2	3	3	1	1	4	3	2	1	2	2	1	2	2
27	26	35	31	35	29	38	35	35	37	31	34	30	32	30
0	0	+	6+	+	2+	0	2	+	+	0	3+	4	+	3
73+	81+	98+	83	87	54+	73+	92	83+	114+	76	62+	100	56+	49
57+	40+	52+	71+	72	72	70+	108+	131+	118+	89+	77+	120	116+	63
+	4+	14+	17+	18+	13+	22+	33+	30+	25+	34+	22+	29+	14+	18
+	+	+	2+	3	2	6+	4+	+	5+	5	8	5	2+	8
130+	125+	164+	179+	180+	143+	171+	239+	244+	262+	204+	172+	258+	188+	141

Literature Cited

Allison, D. G. 1947. Bird populations of forest and forest edge in central Illinois. Univ. of Illinois, MS thesis. 87 pp.

Balda, R. P. 1963. Breeding populations of birds of the upland forest and forest-edge in central Illinois. Univ. of Illinois, MS thesis. 80 pp.

Batzli, G. O. 1977. Population dynamics of the white-footed mouse in floodplain and upland forests. Amer. Midl. Nat. 97: 18–32.

Beckwith, S. L. 1954. Ecological succession on abandoned farm lands and its relation to wildlife management. Ecol. Monographs 24: 349–376.

Bell, D. T. 1974. Tree stratum composition and distribution in the streamside forest. Amer. Midl. Nat. 92: 35–46.

Berthold, Peter. 1976. Methoden der Bestandserfassung in der Ornithologie: Übersicht und kritische Betrachtung. J. f. Ornith. 117: 1–69.

Best, L. B. 1975. Interpretational errors in the "mapping method" as a census technique. Auk 92: 452–460.

Black, C. T. 1937. Ecological relations of the birds of the Champaign-Urbana region. Univ. of Illinois, MS thesis. 46 pp.

Blake, I. H. 1926. A comparison of the animal communities of coniferous and deciduous forests. Illinois Biol. Monographs 10 (4): 148 pp.

Blem, C. R., and L. B. Blem. 1975. Density, biomass, and energetics of the bird and small mammal populations of an Illinois deciduous forest. Trans. Illinois Acad. Sci. 68: 156–164.

Boggess, W. R. 1964. Trelease Woods, Champaign County, Illinois: Woody vegetation and stand composition. Trans. Illinois Acad. Sci. 57: 261–271.

Boggess, W. R., and J. W. Geis. 1966. The Funk Forest Natural Area, McLean County, Illinois: Woody vegetation and ecological trends. Trans. Illinois Acad. Sci. 59: 123–133.

Boggess, W. R., and J. W. Geis. 1967. Composition of an upland streamside forest in Piatt County, Illinois. Amer. Midl. Nat. 78: 89–97.

Bond, R. R. 1957. Ecological distribution of breeding birds in the upland forests of southern Wisconsin. Ecol. Monographs 27: 351–384.

Borst, S. S. 1967. Forest-edge breeding birds in central Illinois and northern Michigan. Univ. of Illinois, MS thesis. 56 pp.

Brewer, R. 1963. Ecological and reproductive relationships of black-capped and Carolina chickadees. Auk 80: 9–47.

Brown, W. H. 1971. Winter population trends in the red-shouldered hawk. Amer. Birds 25: 813–817.

Buckner, C. H., and W. J. Turnock. 1965. Avian predation on the larch sawfly, *Pristiphora erichsonii* (HTG), (Hymenoptera: Tenthredinidae). Ecology 46: 223–236.

Bursewicz, J. 1961. Bird studies at Robert Allerton Park, central Illinois. Univ. of Illinois, MS thesis. 69 pp.

Calef, R. T. 1953. Avian populations of the Funk Forest Natural Area in McLean County, Illinois. Trans. Illinois Acad. Sci. 46: 240–257.

Carter, J. C., and L. R. Carter. 1974. An urban epiphytotic of phloem necrosis and Dutch elm disease, 1944–1972. Illinois Nat. Hist. Surv. Bull. 31 (4): 111–143.

Case, R. M. 1964. Breeding-bird populations of a forest-edge and a floodplain in central Illinois, 1963. Univ. of Illinois, MS thesis. 90 pp.

Collier, W. H. L. 1971. The breeding avian population at Allerton Park, central Illinois, in 1969. Univ. of Illinois, MS thesis. 43 pp.

Diamond, J. M. 1969. Avifaunal equilibria and species turnover rates on the Channel Islands of California. Proc. Nat. Acad. Sci. 64: 57–63.

Diamond, J. M., J. Terborgh, R. F. Whitcomb, J. F. Lynch, P. A. Opler, C. S. Robbins, D. S. Simberloff, and L. G. Abele. 1976. Island biogeography and conservation: strategy and limitations. Science 193 (4257): 1027–1032.

Enemar, A. 1959. On the determination of the size and composition of a passerine bird population during the breeding season. A methodological study. Vår Fågelvärld, Suppl. 2: 1–114.

Enemar, A. 1962. A comparison between the bird census results of different ornithologists. Vår Fågelvärld 21: 109–120.

Evans, E. W. 1978. Nesting responses of field sparrows *(Spizella pusilla)* to plant succession on a Michigan old field. Condor 80: 34–40.

Fawver, B. J. 1947. Bird population of an Illinois floodplain forest. Trans. Illinois Acad. Sci. 40: 178–189.

Ferry, C., and B. Frochot. 1970. L'Avifaune nidificatrice d'une forêt de chênes pédonculés en Bourgogne: Étude de deux successions écologiques. La Terre et La Vie 117: 153–250.

Forman, R. T. T., A. E. Galli, and C. F. Leck. 1976. Forest size and avian diversity in New Jersey woodlots with some land use implications. Oecologia (Berl.) 26: 1–8.

Galli, A. E., C. F. Leck, and R. T. T. Forman. 1976. Avian distribution patterns in forest islands of different sizes in central New Jersey. Auk 93: 356–364.

Głowaciński, Z., and J. Weiner. 1977. Energetics of bird communities in successional series of a deciduous forest. Polish Ecol. Stud. 3: 147–175.

Graber, J. W., and R. R. Graber. 1976. Environmental evaluations using birds and their habitats. Illinois Nat. Hist. Surv., Biol. Notes 97: 1–39.

Graber, R. R., and J. S. Golden. 1960. Hawks and owls: Population trends from Illinois Christmas counts. Illinois Nat. Hist. Surv., Biol. Notes 41: 1–24.

Graber, R. R., and J. W. Graber. 1963. A comparative study of bird populations in Illinois, 1906–1909 and 1956–1958. Illinois Nat. Hist. Surv. Bull. 28 (3): 383–528.

Graber, R. R., J. W. Graber, and E. L. Kirk. 1970. Illinois birds: Mimidae. Illinois Nat. Hist. Surv., Biol. Notes 68: 1–38.

Haapanen, A. 1965. Bird fauna of the Finnish forests in relation to forest succession. I. Ann. Zool. Fenn. 2: 153–196.

Haapanen, A. 1966. Bird fauna of the Finnish forests in relation to forest succession. II. Ann. Zool. Fenn. 3: 176–200.

Hensley, M. 1948. Studies of the breeding bird population on the forest-edge in Robert W. Allerton Park, central Illinois. Univ. of Illinois, MS thesis. 76 pp.

Hespenheide, H. A. 1971. Flycatcher habitat selection in the eastern deciduous forest. Auk 88: 61–74.

Holmes, E. B. 1950. A comparison of the breeding-bird populations of floodplain forest, upland forest, and forest-edge in central Illinois. Univ. of Illinois, MS thesis. 96 pp.

Holmes, R. T., and F. W. Sturges. 1975. Bird community dynamics and energetics in a northern hardwoods ecosystem. J. Anim. Ecol. 44: 175–200.

Hudson, J. E. 1968. Breeding birds of forest edge and floodplain forest areas in central Illinois. Univ. of Illinois, MS thesis, 112 pp.

James, F. C., and H. H. Shugart, Jr. 1970. A quantitative method of habitat description. Audubon Field Notes 24: 727–736.

Johnson, F. L. 1975. Mast production in the upland streamside forest white oaks of east central Illinois. *In* D. T. Bell and F. L. Johnson's "The upper Sangamon River basin: Final report for the Springer-Sangamon environmental research program": pp. 217–220. Dept. Forestry and Illinois Agr. Exp. Sta., Univ. of Illinois, Urbana.

Johnson, F. L., and D. T. Bell. 1975. Size-class structure of three streamside forests. Amer. J. Bot. 62: 81–85.

Johnston, D. W., and E. P. Odum. 1956. Breeding bird populations in relation to plant succession on the Piedmont of Georgia. Ecology 37: 50–62.

Johnston, R. F. 1979. Woodland breeding bird communities in eastern Kansas. Trans. Kansas Acad. Sci. 82: 246–251.

Johnston, V. R. 1947. Breeding birds of the forest-edge in Illinois. Condor 49: 45–53.

Karr, J. R. 1968. Habitat and avian diversity on strip-mined land in east-central Illinois. Condor 70: 348–357.

Kendeigh, S. C. 1934. The role of environment in the life of birds. Ecol. Monographs 4: 299–417.

———. 1944. Measurement of bird populations. Ecol. Monographs 14: 67–106.

———. 1948. Bird populations and biotic communities in northern Lower Michigan. Ecology 29: 101–114.

———. 1970. The brown creeper in Illinois. Illinois Audubon Bull. 153: 19.

———. 1974. Ecology with special reference to animals and man. Prentice-Hall, Inc., Englewood Cliffs, N.J. vi+474 pp.

———. 1979. Invertebrate populations of the deciduous forest: Fluctuations and relations to weather. Illinois Biol. Monographs 50: 1–107.

Kendeigh, S. C., and B. J. Fawver. 1981. Breeding bird populations in the Great Smoky Mountains, Tennessee and North Carolina. Wilson Bull. 93: 218–242.

Kendeigh, S. C., J. W. Graber, and M. F. Campbell. 1976. A check-list of birds of east central Illinois. *In* "A birding handbook for east central Illinois," Champaign County Audubon Society: pp. 3–43.

Kilham, L. 1958. Territorial behavior of wintering red-headed woodpeckers. Wilson Bull. 70: 347–358.

Lack, D. 1969. Population changes in the land birds of a small island. J. Anim. Ecol. 38: 211–218.

Lawrence, L. de K. 1967. A comparative life-history study of four species of woodpeckers. Ornith. Monographs 5: 1–156.

Löhrl, H. 1956. Der Star als Bruthöhlonkonkurrent. Die Vogelwelt 77: 47–50.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton Univ. Press, Princeton, N.J. xi+203 pp.

Miller, R. J. 1955. Bird populations on Illinois prairie farmland. Univ. of Illinois, MS thesis. 90 pp.

Morris, R. F., W. F. Cheshire, C. A. Miller, and D. G. Mott. 1958. The numerical response of avian and mammalian predators during a gradation of the spruce budworm. Ecology 39: 487–494.

Odum, E. P. 1950. Bird populations of the Highlands (North Carolina) Plateau in relation to plant succession and avian invasion. Ecology 31: 587–605.

Oosting, H. J. 1942. An ecological analysis of the plant communities of Piedmont, North Carolina. Amer. Midl. Nat. 28: 1–126.

Palmgren, P. 1930. Quantitative Untersuchungen über die Vogelfauna in den Wäldern Südfinnlands. Acta Zool. Fenn. 7: 1–220.

Pearson, R. W. 1962. A population study of forest-edge birds in central Illinois. Univ. of Illinois, MS thesis. 60 pp.

Pielou, E. C. 1966. The measurement of diversity in different types of biological conditions. J. Theoret. Biol. 13: 131–144.

Pinowski, J., and K. Williamson. 1974. Proceedings of the fourth meeting of the International Bird Census Committee and second meeting of the European Ornithological Atlas Committee. Acta Ornith. 14: 152–461.

Preno, W. L., and R. F. Labisky. 1971. Abundance and behavior of doves, pheasants, bobwhites, squirrels, and cottontails in Illinois, 1965–1969. Illinois Dept. Conserv., Tech. Bull. 4: 1–76.

Preston, F. W. 1979. The invisible birds. Ecology 60: 451–454.

Raynor, G. S. 1975. Techniques for evaluating and analyzing Christmas bird count data. Amer. Birds 29: 626, 628–633.

Reese, R. W. 1949. Studies of vertebrate populations. I. Comparison of forest-edge bird populations in Robert Allerton Park, central Illinois, 1946, 1947, 1948. Univ. of Illinois, MS thesis. 74 pp.

Reller, A. W. 1972. Aspects of behavioral ecology of red-headed and red-bellied woodpeckers. Amer. Midl. Nat. 88: 270–290.

Robbins, C. S. 1970. Recommendations for an international standard for a mapping method in bird census work. Audubon Field Notes 24: 723–726.

———. 1978. Census techniques for forest birds. Workshop proceedings: Management of southern forests for nongame birds. USDA For. Serv. Gen. Tech. Rep't. SE-14: 142–163.

———. 1979. Effect of forest fragmentation on bird populations: Workshop proceedings: Management of North Central and Northeastern Forests for nongame birds. USDA For. Serv. Gen. Tech. Rep't. NC-51: 198–212.

Robertson, M. J. 1959. Analysis of breeding-bird populations at Allerton Park, central Illinois, 1946–1955. Univ. of Illinois, MS thesis. 121 pp.

Root, T. W., J. W. Geis, and W. R. Boggess. 1971. Woody vegetation of Hart Memorial Woods, Champaign County, Illinois. Trans. Illinois Acad. Sci. 64: 27–37.

Roth, R. R. 1967. An analysis of avian succession on upland sites in Illinois. Univ. of Illinois, MS thesis. 92 pp.

Schwager, G. M. 1961. Forest-edge breeding-bird populations at Allerton Park, central Illinois, 1946 to 1960. Univ. of Illinois, MS thesis. 57 pp.

Sheldon, A. L. 1969. Equitability indices: Dependence on the species count. Ecology 50: 466–467.

Shugart, H. H., Jr., and D. James. 1973. Ecological succession of breeding bird populations in northwestern Arkansas. Auk 90: 62–77.

Simberloff, D. S. 1978. Islands and their species. Nature Conservancy News 28 (4): 4–10.

Simberloff, D. S., and L. G. Abele. 1976. Island biogeography theory and conservation practice. Science 191: 285–286.

Sipp, S. K., and D. T. Bell. 1973. Man, land use, and tree rings. Illinois Res. 15: 3–4.

Slagsvold, T. 1973. Critical remarks on bird census work performed by means of the mapping method. Norw. J. Zool. 21: 29–31.

Smith, F. 1922. The European starling in Illinois. Trans. Illinois Acad. Sci. 15: 185.

———. 1930. Records of spring migration of birds at Urbana, Illinois, 1903–22. Illinois Nat. Hist. Surv. Bull. 19: 105–117.

Smock, L. A. 1970. The vertebrate fauna of the Vermilion River Observatory, Vermilion County, Illinois. Univ. of Illinois, MS thesis. 79 pp.

Speirs, J. M., and R. Orenstein. 1975. Bird populations in forests of Ontario County. Ontario Field Biol. 29: 1–24.

Stewart, R. E., J. B. Cope, C. S. Robbins, and J. W. Brainerd. 1952. Seasonal distribution of bird populations at the Patuxent Research Refuge. Amer. Midl. Nat. 47: 257–363.

Svensson, S. 1974. Interpersonal variation in species map evaluation in bird census work with the mapping method. Acta Ornith. 14: 179–195.

Temple, S. A., and B. L. Temple. 1976. Avian population trends in central New York State, 1935–1972. Bird-Banding 47: 238–257.

Troetschler, R. G. 1976. Acorn woodpecker breeding strategy as affected by starling nest-hole competition. Condor 78: 151–165.

Twomey, A. C. 1945. The bird population of an elm-maple forest with special reference to aspection, territorialism, and coactions. Ecol. Monographs 15: 173–205.

Udvardy, M. D. F. 1957. An evaluation of quantitative studies in birds. Cold Spring Harbor, Symposium in Quantitative Biology 22: 301–311.

Van Horn, D. H. 1952. Breeding-bird populations of floodplain and upland forests of central Illinois. Univ. of Illinois, MS thesis. 80 pp.

Walcott, C. F. 1974. Changes in bird life in Cambridge, Massachusetts, from 1860 to 1964. Auk 91: 151–160.

Webster, J. D., and D. L. Adams. 1972. Breeding bird censuses in old-growth deciduous forests. Proc. Indiana Acad. Sci. 82: 198–206.

Weise, C. M. 1951. Breeding populations and reproductive success of birds of the forest and forest-edge in central Illinois. Univ. of Illinois, MS thesis. 126 pp.

Whitcomb, R. F., J. F. Lynch, P. A. Opler, and C. S. Robbins. 1976. Island biogeography and conservation: Strategy and limitations. Science 193: 1030–1032.

Whitmore, R. C. 1980. Reclaimed surface mines as avian habitat islands in the eastern forest. Amer. Birds 34: 13–14.

Williams, A. B. 1936. The composition and dynamics of a beech-maple climax community. Ecol. Monographs 6: 317–408.

Williams, J. B. 1975. Habitat utilization by four species of woodpeckers in a central Illinois woodland. Amer. Midl. Nat. 93: 354–367.

Williams, J. B., and G. O. Batzli. 1979a. Competition among bark-foraging birds in central Illinois: Experimental evidence. Condor 81: 122–132.

Williams, J. B., and G. O. Batzli. 1979b. Interference competition and niche shifts in the bark-foraging guild in central Illinois. Wilson Bull. 91: 400–411.

Willson, M. F. 1970. Foraging behavior in some winter birds of deciduous woods. Condor 72: 169–174.

———. 1974. Avian community organization and habitat structure. Ecology 55: 1017–1029.

Yeager, L. E. 1955. Two woodpecker populations in relation to environmental change. Condor 57: 148–153.

Zar, J. H. 1974. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, N.J. 634 pp.

Zellmer, C. W. 1969. An analysis of the breeding bird populations of the forest-edge in Robert W. Allerton Park, central Illinois, 1968. Univ. of Illinois, MS thesis. 147 pp.

Index and Scientific Names of Bird Species

A Note on the Author

S. Charles Kendeigh is professor emeritus of zoology of the University of Illinois. He received an A.B. and an A.M. degree from Oberlin College and a Ph.D. from the University of Illinois. He was an assistant professor at Western Reserve University from 1930 to 1936, when he joined the Illinois faculty. The author of numerous articles and monographs and several books, Professor Kendeigh is a founder and past chairman of the Nature Conservancy, past vice-president of the American Ornithologists' Union, and past president of the Wilson Ornithological Society and the Ecological Society of America. He also received the Brewster Award of the A.O.U. in 1951 and the 1978 Eminent Ecologist award of the Ecological Society of America.

ISBN 0-252-0