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Organization of the Bird Community of a Michigan Oak Forest

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ORGANIZATION OF THE BIRD COMMUNITY OF A MICHIGAN OAK FOREST

by

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INTRODUCTION

Community organization is one of the central themes of ecology. Birds have recently been much used in studying community organization, but these studies have largely been limited to consideration of species and numbers during the breeding season. A community exists throughout the year. Bird populations are constantly changing as individuals enter and leave the area and as birds are hatched or die. Habitat utilization is also a changing entity. The realistic way to study an avian population is to consider both temporal and spatial occupancy of the community.

It is usually assumed that breeding bird censuses from a total season adequately represent the breeding population (Williams, 1936; Hall, 1964). The method generally used (termed the Williams spot-map method) consists of 8-10 traverses of a mapped area during the breeding season. Territorial males are plotted on maps. Groups of observations, along with other supplementary information, allow approximate delimitation of territories. Breeding bird censuses such as these tend to ignore temporal changes in the population and many important segments of the population. Unsatisfactorily dealt with are females, young, unmated and non-territorial birds, and visitors. Temporal changes in a population will not usually allow single values for numbers of species or numbers of territorial males for the total breeding season.

The spatial organization of the avian community was approached

by observing the occupancy of vegetation by the birds. Spatial occupancy for a species changes with population fluctuations, vegetational aspection and physical factors (e.g. weather).

METHODS

The canopy and understory trees of the tract were sampled using the point-centered quarter method (Cottam and Curtis, 1956). The area had been staked at 200-foot intervals and these thirty points were used in the sampling (Fig. 1). Distances from the point to the nearest tree and tree diameter at breast height (dbh) in each quarter were measured. In order to obtain data on both canopy and understory trees, the trees were divided into two categories before sampling took place. One consisted of trees 1.5-4.99 inches dbh and the other consisted of trees 5 inches or larger dbh. The following were then calculated: number of trees per acre, total basal area per acre, relative frequency, relative density, relative dominance, and importance values (equals the sum of the three preceding values) for each species.

The herbaceous vegetation and the woody vegetation which formed the lower strata were sampled using square milacre quadrats. Fifteen randomly chosen samples were taken during the summer of 1967. The plot stakes were used as points from which 60 feet was paced in predetermined directions. The nearest corner of the quadrat to the investigator was placed at the 60-foot point, keeping the quadrat edges in compass directions. The plants were divided into three size classes: 2 feet high or less, more than 2 feet to 6 feet high, and 6 feet high to 1.49 inches dbh. Densities were recorded using individual plants except for sassafras, roses, dewberry and sedges

which were recorded in clumps. Only those plants whose densities were greater than one per milacre and whose frequencies were 20 percent or greater are presented in this study.

Owing to the low density of cherry, shadbush and white pine on the tract it was thought that a total count was warranted. This count was undertaken 3, 11 and 12 May 1967. The vegetation was divided into three size classes: 2 feet high or less, more than 2 feet high to 1.49 inches dbh, and 1.5 inches and greater in dbh.

Scientific names of plants, given in the next section, follow Gleason (1958).

Leaf litter samples from the area were available (Wenger, 1969) to determine primary consumption by invertebrates (Bray, 1961) and to give a relative index of tree species cover. Hardware cloth squares (100 square inches) were placed on the forest floor near the plot stakes. They were put out in late summer and collected after most of the leaves had fallen. The leaves were collected, steamed flat and a random sample of each species was taken for measurements. The original leaf outline was estimated, and the total area and consumed area measured. The leaves were also weighed. Caloric content of the consumed plant material was calculated. The number of calories present in the lepidopteran larvae population was estimated from the consumed plant material.

The bird populations occupying the oak forest tract were determined using two methods. During the breeding season (May-August) the Williams spot map method (Williams, 1936) and variations thereof were employed. Singing males and other birds were located

and mapped from April to August, and territories were determined. Data from this method were collected for three successive years, 1966-68. The second year of study was the most intensive of the three. During this breeding season the tract was visited at least three times per week. This high frequency of visits per week gave a basis for the study of population fluctuations during the breeding season. The time of day was written beside each observation recorded on the map. A few censuses were taken using two observers simultaneously, where each person censused half of the tract. In this way males singing at the same time, but not audible to one observer, could be recorded. Several all-day censuses (17 hours) were taken, changing observers every 3 to 4 hours. This gave fresh starts several times throughout the day and allowed for greater probability of recording an individual bird. Late evening censuses were also taken to determine the nocturnal bird populations (e.g. whip-poor-wills). The number of hours spent in censusing and the number of trips were as follows: 1966--10 trips and 22 man-hours, 1967--57 trips and 219 man-hours, and 1968--19 trips and 57 man-hours.

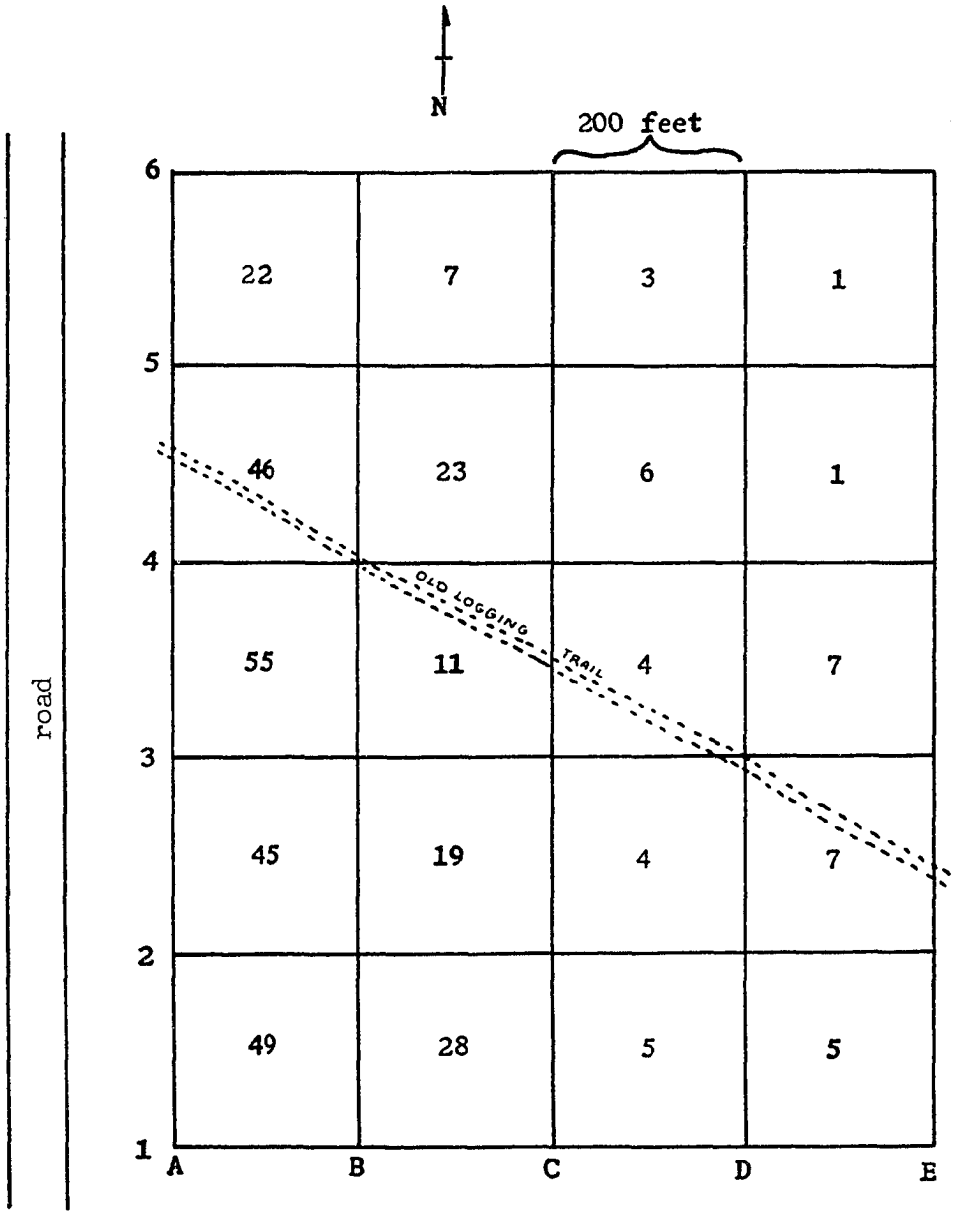
Winter populations were studied during 1966-67 and 1967-68 using a second method. The populations were determined using the birds per trip method employed in the winter bird population studies published annually in Audubon Field Notes (Kolb, 1965). The only alteration was that the observer stopped at every plot stake for 90 seconds. This standardized the time spent censusing

the tract to insure complete coverage. The total number of birds seen on the area each trip was recorded. The average number of birds per trip for each species was determined using the total number of trips taken during the winter. The time spent in censusing from November 1 to April 30 was 34 man-hours during the 1966-67 winter and 21 man-hours during the 1967-68 winter.

Standardized observations (Hartley, 1953; Gibb, 1954) were used to study various factors in habitat utilization of the oak forest species. These observations included the following items: date, time of day, species of bird plus sex and age when they could be determined, height of bird from ground, activity (singing, foraging, etc.), species of plant, area of plant ($\frac{1}{4}$ up, $\frac{1}{2}$ up, etc.), position on the plant (trunk; large branch, over 3/4 inch diameter; small branch, 1/4-3/4 inch diameter; twig, under 1/4 inch diameter; and foliage), the slant of the branch in relation to horizontal, and whether the branch was dead or alive. Height was estimated to the nearest foot or five feet. Lines painted on a few trees at ten feet and a knowledge of the general canopy height (determined at several points using an Abney level) aided in estimations. For analysis, 10-foot height intervals were used. The general weather conditions were also recorded for each census. Only one observation for a given activity per individual was taken within at least a fifteen-minute period. The first sighting was the standard observation for that individual. It was thought that this method of collecting data provided statistically independent

observations. The main drawback of the method was the difficulty of obtaining an adequate sample size. The maximum number of standardized observations obtained during a single census was nine per hour. There was a total of 1,156 observations made.

Fig. 1. Map of the study tract showing the plotting pattern and giving the density of Pinus strobus for each 40,000 square foot block.



STUDY AREA

The study area consisted of 18.4 acres of oak forest located in the Allegan State Game Area. The tract was essentially flat with slight rises in the extreme NE and SE corners. It was located west of the city of Allegan, Michigan, in Valley Township, Allegan County. Located by the Congressional Land Survey System, the area was in the $W\frac{1}{2}$ of the $NW\frac{1}{4}$ of Sect. 30, R14W, T2N.

The forest was homogeneous, the canopy consisting primarily of black oak (Quercus velutina) with a few scattered white oak (Q. alba). The understory trees were mainly white oak and flowering dogwood (Cornus florida). Because many of the white oaks were taller than the dogwoods, the tree strata had a complex, three-layered nature. The density of the understory and canopy trees combined was 364 trees per acre. The canopy trees, 5 inches dbh and over, had a density of 123 trees per acre. The understory trees, 1.5-4.99 inches dbh, had a density of 241 trees per acre (Tables 1, 2 and 3).

The densities of the low density species from the total count were as follows: wild black cherry (Prunus serotina) 0.9 per acre, shadbush (Amelanchier canadensis) 0.4 per acre, and white pine (Pinus strobus) 2.1 per acre. These densities represent trees 1.5 inches dbh and over. Most of the white pines occurred on the western edge of the tract near the road (Fig. 1). Some of the pines were probably planted, although some may have seeded from a small

group of white pines across the road or from the two large (canopy) pines on the area.

The shrubby and herbaceous vegetation (less than 2 feet high) consisted primarily of Carex pennsylvanica, Sassafras albidum and Vaccinium spp. (Table 4). Smilax rotundifolia, greenbrier, was found in patches, particularly near the road and along an old logging trail (Fig. 1). A patch of witch-hazel (Hamamelis virginiana) was located near B-4. Another low density plant scattered through the forest was New Jersey tea (Ceanothus americana). Tick tree-foil (Desmodium nudiflorum and other species) was also found in patches on the tract.

Aspection in the oak forest was radically different from that of more mesic forests. Spring flowers which are abundant in mesic forests were absent in the xeric oak forest. This is in agreement with the findings of Curtis (1959) for Wisconsin oak forests. Most of the flowers blooming in the oak forest were summer flowering and seem to have prairie or open country affinities. Such plants were Antennaria plantaginifolia, Euphorbia corollata, Lupinus perennis Rubus hispida, Potentilla recta, Ceanothus americana, and Helianthus divaricatus. These species are probably able to live in these forests because of the lateness of leafing of the trees and the relatively open canopy.

Most oak forest plants bloomed about the same time each year. The exceptions were early bloomers like the sedge which seemed to fluctuate according to the weather. After the middle of May the

fluctuations in yearly flowering times diminished. A species flowering after June first tended to bloom within a week of the date of the previous year (Table 5).

The time of appearance of leaves seemed more variable than time of flowering. Early-leafing trees such as cherry, dogwood and shadbush fluctuated according to the weather during the early spring. However, after mid-May each plant species leafed out about the same date each year (varying less than a week). This included the two oak species. New Jersey tea leafed out just before the oaks but kept its leaves long after the oaks had lost most of their leaves in the autumn (Fig. 2).

The canopy trees started leafing in mid-May but the canopy was not complete until early June. In 1968, the black oak leaves were being eaten by lepidopteran larvae before these leaves were completely grown, leaving openings in the canopy. The understory trees were fully leafed by mid June. Bracken fern fiddleheads appeared in mid-May and were fully grown by mid-June.

Through much of June the lepidopteran larvae were so abundant that their droppings sounded like rain striking the forest floor. Leaf rollers were already present in the witch-hazel in early June just after the leaves were fully developed. Tent caterpillars were present on the cherries before they had fully leafed. Carabid beetles were very common in mid-June.

White oak acorns fell from the trees in early September. Desmodium fruits appeared mature by mid-August and by late August

the dogwood fruits were turning red. Blueberries were ripe and disappeared rapidly in early July.

Sassafras and dogwood leaves changed color in early October and by mid-October these species plus cherry, shadbush and maple had lost their leaves. The oak leaves started turning brown in early October and by late October the trees had lost two thirds of their leaves. By mid-November the oaks had lost most of their leaves.

The pH of the soil (determined colorimetrically) in the oak forest was acidic and ranged from 4.5 to 5.0. The soil was sand with about one inch of A horizon. The parent material was deposited during a glacial highwater stage of Lake Michigan (Martin, 1955).

Table 1. Characteristics of both canopy and understory trees of the oak forest.

Characteristics	Quercus velutina	Q. alba	Cornus	Pinus	Sassafras	Acer	Prunus
Density in trees per acre	106.9	214.6	24.1	10.1	1.9	4.1	1.9
Basal area in ft^2/acre	70.9	22.2	0.7	0.4	+	0.1	+
Percent frequency	70.0	90.0	16.7	6.7	1.8	+	+
Relative density	29.4	57.0	6.6	2.8	0.5	1.1	0.5
Relative dominance	75.0	23.7	0.7	0.4	+	0.1	+
Relative frequency	37.5	48.2	8.9	3.6	1.8	+	+
Importance values	141.9	130.9	16.2	6.8	2.3	1.2	0.5

+ was less than 0.1

Table 2. Characteristics of the canopy trees of an oak forest using the point-centered quarter method.

Characteristics	*Quercus velutina*	*Q. alba*
Density in trees per acre	88.8	33.7
Basal area in feet^2/acre	69.3	15.5
Percent frequency	96.7	66.7
Relative density	72.5	27.5
Relative dominance	81.7	18.3
Relative frequency	59.2	40.8
Importance values	213.4	86.6
Average dbh in inches	12.0	9.2

Table 3. Characteristics of the understory trees of an oak forest.

Characteristics	Quercus velutina	Q. alba	Cornus	Pinus	Sassafras	Acer	Prunus
Density in trees per acre	18.1	180.9	24.1	10.1	1.9	4.1	1.9
Basal area in ft^2/acre	0.9	6.7	0.7	0.4	+	0.1	+
Percent frequency	13.3	99.7	26.7	10.0	3.3	6.7	3.3
Relative density	7.5	75.0	10.0	4.2	0.8	1.7	0.8
Relative dominance	10.2	76.1	8.0	4.5	+	1.1	+
Relative frequency	8.2	61.2	16.4	6.1	2.0	4.1	2.0
Importance values	25.9	212.3	34.4	14.8	2.8	6.9	2.8
Average dbh in inches	3.0	2.6	2.3	2.6	1.6	2.1	1.9

+ was less than 0.1

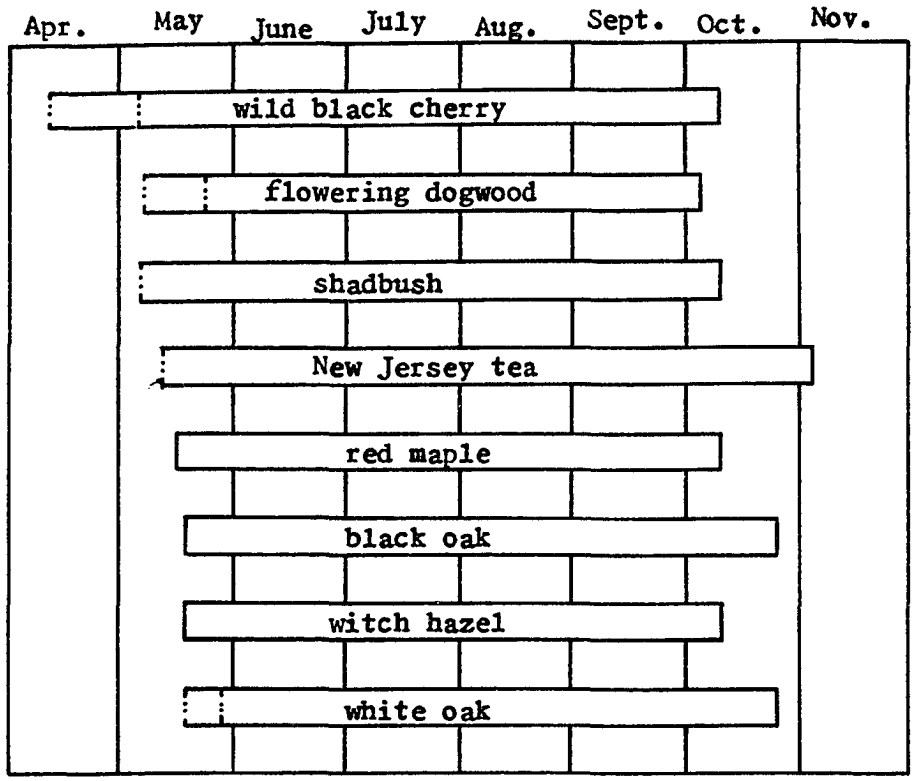
Table 4. The shrubby and herbaceous vegetation in the oak forest tract. Only vegetation less than two feet high is included. The sample consisted of 15 one-milacre quadrats.

Species	Percent Frequency	Density ind./milacre	Density relative
Carex pennsylvanica	93.3	47.7	49.9
Sassafras albidum	86.7	10.3	10.8
Vaccinium spp.	80.0	8.0	8.4
Quercus velutina	73.3	2.5	2.6
Smilacina stellata	66.7	1.8	1.9
Desmodium nudiflorum	53.3	13.9	14.5
Rubus hispida	53.3	1.3	1.3
Quercus alba	46.7	1.4	1.5
Rosa spp.	40.0	1.3	1.3
Cornus florida	26.7	2.6	2.7
Gaultheria procumbens	20.0	2.2	2.3

Table 5. Initial flowering times for various plant species in the oak forest. The months are divided into 3 parts; early, mid and late.

Period	Plant species
Early April	Carex pennsylvanica
Mid-April	Acer rubrum
Late April	Amelanchier canadensis
Early May	Vaccinium spp.
	Antennaria plantaginifolia
	Viola fimbriatula
	Quercus velutina
Mid-May	Cornus florida
	Pedicularia canadensis
Late May	Lupinus perennis
	Comandra umbellata
Early June	Prunus serotina
	Rubus hispida
	Viburnum acerifolium
	Potentilla recta
	Stipa avenacea
	Smilicina stellata
Late June	Asclepias exaltata
	Rosa spp.
Early July	Ceanothus americana
	Chimaphila umbellata
Mid-July	Pyrola sp.
	Euphorbia corollata
Late July	Desmodium nudiflora
	Gaultheria procumbens
Mid-August	Helianthus divaricatus
	Solidago caesia
Late August	Monotropa uniflora
	Monotropa hypopithys
Early November	Hamamelis virginiana

Fig. 2. Oak forest leaf aspection showing the time and extent of leaf coverage. Dotted lines indicate variability in leafing times.



BREEDING POPULATIONS

In general, the population estimates were obtained by summing the number of territories and fractions of territories on the tract. Sixteen species were included in this method. Populations of species which had no definite territorial song were estimated in an analogous fashion by establishing the area over which the male habitually ranged. Included were great crested flycatcher (weep song); brown-headed cowbird (concentrations of birds); hairy and downy woodpeckers (presence of male and especially female in an area); blue jay (nests).

Densities from the 1967 breeding season as given in Table 6 are the peak populations for species which displayed fluctuations in population size. The maximum population for a two-week period (Table 7) was used for the whole breeding season. Densities from 1966 and 1968 reflect seasonal populations disregarding any territorial fluctuations.

A large drop in breeding populations occurred in black-capped chickadees from 1967 to 1968 (Table 6). There was no apparent reason for this drop. Another phenomenon noticed was fluctuations in the sizes of chickadee territories during the breeding season (Stefanski, 1967 and personal observations during the extensive censusing in 1967). Territories were apparent during April and May. Later during nesting, the males were silent and secretive. In July, when there were family groups foraging together, activity

increased and semblances of territories could once again be determined.

Ovenbird territories shifted tremendously during the early part of the breeding season (Stenger and Falls, 1959, and personal observations). One difficulty encountered was ovenbirds following the census taker and singing from perches that were considered outside its territory.

Stenger (1958) stated that ovenbird territories become larger with increasing density of the canopy. The oak forest is open compared to more mesic forests (e.g. maple), but the territories appeared to be nearly as large. Territory size in maple forest, calculated by Stenger, was 3.2 acres. Most of the territories in the oak forest were at least that large. Food availability is also a factor and could have been influencing territory size more than canopy cover.

The red-eyed vireos appeared to select the south half of the tract for their breeding territories. Early in the season there were red-eyed vireo males singing on the north half of the tract, but they vacated that area within a few weeks. Bond (1957) stated that the red-eyed vireos increased in abundance and in importance with a more mesic seral stage and that they preferred more mesic stands within a forest. Nothing in this southern part of the tract appeared to make it more mesic than the northern part. Southern (1958) listed some niche requirements for the vireos. They prefer an open deciduous woods with several tall trees, scattered clusters

of saplings, small openings within the woods, loose fibrous bark for nests, and a supply of larvae for food. To human eyes, all of these requirements were available in either part of the tract; therefore, no conclusions were drawn for the observed distribution.

Bond (1957) found that downy woodpeckers were five times more numerous in xeric stands than were hairy woodpeckers. Our data failed to show such a relationship. Downy woodpeckers were less than twice as numerous as hairy woodpeckers (Table 6).

According to Bond (1957); scarlet tanagers, rose-breasted grosbeaks, black-capped chickadees, blue jays, downy woodpeckers and yellow-billed cuckoos were species living in xeric forests of Wisconsin. His xeric communities ranged from 500 to 1000 on the continuum scale developed by Curtis and McIntosh (1951) in their study of Wisconsin forests. The Allegan forest tract would have an index value of 790 on the Wisconsin continuum. Scarlet tanagers and rose-breasted grosbeaks were the most abundant species on the tract. There were at least 11 territorial male grosbeaks with territories or parts thereof on the tract in 1967. In 1968 there were 7 males present.

Those species for which oak forest was marginal breeding habitat exhibited large yearly population fluctuations. Blue-gray gnatcatchers and yellow-throated vireos are intermediate forest birds (Bond, 1957) which nested on the oak forest tract. Probably the habitat was not optimal for breeding, but could be utilized with some measure of success. In the 1968 breeding season the gnat-

catchers successfully raised young. The yellow-throated vireos raised a cowbird in 1967 and they were not seen often enough to determine breeding success in the 1968 season. It appeared that large oaks were not suitable for whip-poor-will breeding either. In 1968 a nest was found across the road in an old field near some trees. In 1967 some fringes of whip-poor-will territories were present on the tract. Tufted titmice populations also fluctuate possibly because they are at the northern limit of their present range.

Visitors are a segment of the population including late migrants; residents of nearby areas; unmated, surplus males; birds wandering about before or after nesting or after nest failure; and wandering young birds of that breeding season. Included as visitors were Swainson's thrush (late migrant), cedar waxwing (late migrant feeding on wintergreen berries), red-headed woodpecker (early spring visitor), chipping sparrow, field sparrow, catbird, cardinal (species found around the edge of the forest and occasionally wandering into the woods), red-winged blackbird (inhabits small bog off NE corner of plot), and American redstart, warbling vireo, Acadian flycatcher, least flycatcher (nest in nearby mesic forests). We also recorded wood ducks on the tract in June of 1967 and 1968. As far as could be determined, they did not nest in the area. The wood ducks could have been attracted by standing water in a pond (which later dried up) off the NE corner of the tract. Wood thrushes were found on the area each year for

a few weeks in July. They probably did not nest or have territories on the tract during 1966 and 1968. During 1967, four fledglings were seen being fed by an adult on August 4. Prior to this a male had been heard singing on several censuses since July 5. This indicated a probable territory on the tract during 1967.

Population fluctuations during the breeding season were not very extreme (Table 7). Populations began declining after the initial peak at the beginning of the breeding season. Eastern wood pewee and scarlet tanager populations were the most constant of any bird populations through the spring and summer. The red-eyed vireo population drop during mid-June and early July was probably caused by vireo males leaving the northern half of the tract as discussed earlier. The departure of the oak forest species (e.g. ovenbird) early in the season may indicate nest failure and no renesting. The male seemed to vacate their territories.

After breeding was over, most of the summer residents seemed to disappear, with a few late nesting or renesting birds remaining. It was thought that many leave the oak forest before they molt. The forest is devoid of bird songs by August except for the occasional call of a wood pewee. However, upon visiting a nearby lake surrounded by more mesic oak forest, a different situation was apparent. The same bird species which had departed from or were silent in the upland forest were singing as if it were earlier in the breeding season.

Ovenbirds were the first species to leave the oak forest after

breeding. Examination of skins at the University of Michigan Museum of Zoology indicated that ovenbirds molt in late July. By late July no ovenbirds were seen or heard on the tract. Some ovenbirds were seen later in September, but they were probably migrants from farther north. Stoddard and Norris (1967) found dead ovenbirds around a TV tower during August in Florida, although the peak kill was in early October. This probably indicates that migration was taking place as early as August, inasmuch as ovenbirds are not known to breed further south than northern Georgia.

The last summer residents to leave the oak forest were the eastern wood pewees. They were present until the last part of September.

Densities of bird populations are remarkably different between open forests (oak) and dense forests (fir-spruce). The number of territorial males at Allegan per 100 acres was 178 in 1966, 266 in 1967, and 153 in 1968. According to Udvardy (1957), densities of about 200 pairs per 100 acres can be expected in deciduous forests having 21 breeding species. Stewart and Aldrich (1952) found from 323 to 370 bird pairs per 100 acres in a fir-spruce forest. This is over one bird per acre more than in oak forests. In Warren Woods, a beech-maple forest, there were about 45 red-eyed vireo singing males per 100 acres (personal communication from Ray Adams) as compared to 15 males per 100 acres in the oak forest.

Understory stratum and canopy are very thick in both fir-spruce and beech-maple forests. The oak forest understory stratum is quite

sparse and the canopy open. Perhaps visual distance is a factor in regulating population densities of birds. Birds in dense forests may rely more on sound to locate other individuals and less on sight when defending a territory. This might permit higher densities and smaller territories in dense forests where vision is limited.

Another factor affecting density estimates was the censusing technique. The 1967 estimates (the year the tract was the most intensively censused) were almost 20 birds higher than either 1966 or 1968 estimates for 18.4 acres. In order to obtain an equatable population estimate based on a lower number of censuses, one census per week was extracted out of the 1967 breeding season data and this reworked data, for rose-breasted grosbeaks and scarlet tanagers, was presented to another observer experienced in the methods used. His estimates from these data were lower than the peak numbers based on the more intensive censusing and comparable to the figures obtained in 1966 and 1968. It appears that more censuses improve the probability of finding birds otherwise missed or lumped with other bird territories. Therefore, our population estimates based on a small number of censuses tended to be low.

There was a fluctuation in many of the forest species populations from year to year. Brewer (1963b) stated that populations seem to be least variable in vegetation which is most nearly optimum for each species. High density bird species in the oak forest such as tanagers and grosbeaks had smaller unutilized area within their territories and between their territories

(see Odum and Kuenzler, 1955, on utilized area of territories). This may show that bird species of xeric forests living in optimum habitat can utilize more completely the area and energy available than can mesic or intermediate forest species. Low density birds, such as yellow-throated vireos and ovenbirds, have large areas of unutilized space between their territories.

Table 6. The number of territorial males in the Allegan oak forest tract of 18.4 acres during breeding season.

Species	Year 1966	1967	1968
Wood duck	0	+	+
Yellow-billed cuckoo	1.5	2.1	1.4
Whip-poor-will	nc	0.2	0
Yellow-shafted flicker	0.7	0.8	1.0
Downy woodpecker	+	1.4	1.0
Hairy woodpecker	0.8	1.0	0.7
Red-bellied woodpecker	0.8	0.5	+
Great crested flycatcher	1.9	2.0	1.1
Eastern wood pewee	2.8	3.8	2.8
Blue jay	1.8	1.0	1.0
Black-capped chickadee	4.0	4.0	0.8
Tufted titmouse	1.2	2.0	0.6
White-breasted nuthatch	2.1	2.4	1.8
Robin	+	1.5	0.7
Wood thrush	+	0.4	+
Blue-gray gnatcatcher	0	0	0.7
Yellow-throated vireo	0	1.0	0.1
Red-eyed vireo	2.7	4.6	3.5
Ovenbird	1.4	2.5	0.9
Brown-headed cowbird	1.3	1.0	1.0
Baltimore oriole	1.7	2.2	1.0
Scarlet tanager	4.6	7.4	3.8
Rose-breasted grosbeak	4.1	7.5	4.4
Totals	32.7	49.3	28.3

nc--not censused
+--present on tract

Table 7. Population fluctuations for various oak forest species during the breeding season of 1967.

Species	Two week periods starting May 15, 1967								
	1	2	3	4	5	6	7	8	9
Great crested flycatcher	2.0	1.8	1.6	1.1	1.2	0.9[1]	0	0	0
Eastern wood pewee	1.4	3.7	3.8	3.7	3.6	3.1[2]	2.6	(1.8)	(1.0)
Yellow-throated vireo	1.6[3]	1.0	0.8	0.4	0.4	0.1	0	0	0
Red-eyed vireo	0.5	4.6	(1.8)	(1.0)	3.1	2.0	3.1	1.0	0
Ovenbird	2.5	2.3	2.3	1.4	1.0	0	0	0	0
Scarlet tanager	6.6	4.4[4]	7.0	6.5	7.4	7.1	4.7	(2.0)	(0.5)
Rose-breasted grosbeak	7.5	6.9	6.6	5.4	4.1	3.9	0	0	0
Total for all species on tract	39	42	38	34	33	27	16	11	8

()--scanty data, populations roughly estimated
1---territory boundaries breaking down
2---beginning to wander, one seems to have left
3---several apparent transient birds
4---quiet period in singing

ENERGY AVAILABILITY

Most of the oak forest bird population feeds on lepidopteran larvae for a large part of the nesting season. Therefore, an index to consumption by these larvae of the forest foliage should give an indication of the available energy for the population (McAtee, 1926).

Black oaks made up the greatest portion of the leaf mass (Table 8). The individual leaf area as well as the total number of leaves were largest in black oaks. The percent consumption by larvae was also the highest in black oaks (Table 8). This higher consumption rate may result from the greater number of black oaks in the canopy or because the larvae may be more abundant in the canopy.

It was calculated that 1,433 kilograms per acre of material was available to the primary consumers (dry weight). Using conversion factors given by Ovington and Heitkamp (1960), one can estimate the energy content in kilocalories. The conversion factor used for Quercus spp. was 4,781 calories per gram (oven dried) of leaf material. For other tree species, the conversion factor used was an average of Ovington's values. The consumption from the leaves was 212.7 kilograms per acre. This yielded 1,095,900 kilocalories per acre which was eaten by primary consumers (Tables 8 and 9).

Since most of the consumers are lepidopteran larvae, a production-consumption ratio was used representing this order.

The ratio given by Gere (1956) for Hyphantria cunea appears to be the best available in the literature at this time. He has found that these larvae are rather wasteful feeders with an intermediate level of assimilation/consumption effeciency (29 percent) and a very high production/assimilation effeciency (57 percent). Using the production/consumption ratio of 17 percent, the energy available to secondary consumers was 186,300 kilocalories per acre (Table 9).

Comparing the secondary production of lepidopteran larvae with other insects showed a high productivity among these larvae. The oak forest lepidopteran larvae produced 46 kilocalories per square meter per year. Golley (1968) found that planthoppers yielded 70 kilocalories per square meter per year. The only other insect demonstrated by Golley to be a high producer was the grasshopper with 11 kilocalories per square meter per year.

During the breeding season, energy theoretically required per acre by the avian community was estimated using the following criteria. Maintenance or existence energy was calculated from formulae given by Zar (1968); non-passerine birds, $EE=76.7\ W^{0.74}$, and passerine birds, $EE=113\ W^{0.63}$. The maintenance energy (Table 10) was doubled to allow for extra energy required for flight, nesting, egg laying, growth, etc. during the breeding season (Karr, 1968). Population fluctuations during the breeding season were taken into account where data were available. Breeding season

energy requirements for year-around residents were calculated on the basis of 20 weeks (April through August). The average number of birds per nest for each species was used for determining young bird population requirements (values were taken from Kendeigh, 1952 and the Bend series of life histories published as bulletins of the U.S. National Museum). From census data taken during this study, it appeared that young birds were present three-fourths of the breeding season. It was assumed that the young stayed in the forest as long as the parents did. Since full nesting success was assumed, the theoretical energy requirements are near maximum for the population. The seasonal energy requirement was calculated as 23,947 kilocalories per acre. This was 13 percent of the available energy.

It appeared, consequently, that food was not a limiting factor for the population in 1967. There was still over 162,000 kilocalories per acre of available food for the bird population. Even insect predation, pupation and unavailable larvae probably could not diminish the energy level significantly to where it would become an important population limiting factor during the breeding season. The 1967 breeding population was the largest from three years of censusing. Therefore, a large population's energy requirements did not come close to the available energy in the oak forest.

Before leafing, energy is available to birds in the form of early insects, acorns, buds, and pupae. Some early insects which were noticed were flies and a few hibernating butterflies. Spiders

were also common early in May and could be used as a source of food. The early morning temperatures were probably low enough to make insects sluggish and easy to capture. This may possibly be one reason for the large amount of bird activity during the early morning. Old bunches of leaves and squirrel nests were visited by Baltimore orioles during the early spring while foraging. Blue jays eat acorns which could be found on the forest floor after the snow melted. The grosbeaks and perhaps a few other species will eat flower and leaf buds of plants (personal observations). Woodpeckers would be expected to eat more coleopteran larvae than lepidopteran larvae, especially during early spring. Most species have other sources of energy during the peak of lepidopteran production, but the abundance of the larvae probably causes food switching. This is especially important while adult birds are feeding nestlings.

Table 8. The percent consumption and the mass consumed in various species of tree leaves of an oak forest.

Species	Percent consumption	Kg./acre before consumption	Kg./acre consumed
Black oak	16.99	1,144.3	194.4
White oak	13.13	230.6	30.3
Fl. dogwood	4.72	47.5	2.2
Misc. spp.	8.58	27.4	2.4
Total	14.84	1.433.2	212.7

Table 9. The energy available for the bird population, given in kilocalories per acre. Consumed, assimilated and produced energy is given for the lepidopteran population.

Species	Kcal/acre of leaf material consumed	Kcal/acre assimilated by larvae	Energy produced in body tissue in Kcal/acre
Black oak	929,500	269,600	158,000
White oak	144,700	42,000	24,600
Fl. dogwood	10,600	3,100	1,800
Misc. spp.	11,100	3,200	1,900
Totals	1,095,900	317,900	186,300

Table 10. The maintenance energy levels for some oak forest birds. The bird weights were taken from a variety of sources in the literature. Required energy for the population was calculated from existence energy (see text).

Species	Average mass (grams)	Maintenance energy (Kcal/day/bird)	Required energy (Kcal/acre/ season/pop.)
Yellow-billed cuckoo	57.6	15.4	449.4
Yellow-shafted flicker	127.9	27.8	2,185.8
Downy woodpecker	26.6	8.7	920.8
Hairy woodpecker	63.6	16.6	1,256.6
Red-bellied woodpecker	81.0	19.8	748.4
Robin ----	80.4	18.1	2,050.2
Great crested flycatcher	33.8	10.4	679.4
Eastern wood pewee	13.4	5.8	922.6
Black-capped chickadee	11.2	5.2	2,044.1
Tufted titmouse	21.8	7.9	1,380.2
White-breasted nuthatch	20.4	7.6	1,792.6
Blue jay	84.0	18.6	1,124.9
Baltimore oriole	34.0	10.5	698.6
Ovenbird ----	19.5	7.4	531.5
Yellow-throated vireo	20.3	7.6	245.6
Red-eyed vireo	18.4	7.1	780.2
Scarlet tanager	28.5	9.4	3,439.6
Rose-breasted grosbeak	43.2	12.2	2,696.8

WINTER POPULATIONS

Winter bird populations in the oak forest were very low compared to breeding populations. There were only nine wintering species (Table 11). The winter population per 100 acres for 1966-67 was 21 and for 1967-68 it was 45 birds. Webster (1966) in his analysis of winter bird-population studies showed that 45 birds per 100 acres was a reasonable expectation for nine species in eastern forests. He showed that the number of wintering species decreased with increasing latitudes. For the latitude of Allegan (43 N) his regression curve showed an expected 12 species and about 70 birds per 100 acres. Our values may have been lower because of the starkness of the winter forest. Cover was very scarce and the underbrush and understory trees were not very dense compared to more mesic forests.

White-breasted nuthatches and black-capped chickadees were the most abundant and stable portion of the avian population in the forest during the winter (Table 11). Nuthatches were the most abundant species and chickadees the second most abundant. The populations of each were similar during the two winters.

Tufted titmice were abundant during the 1967-68 winter and relatively scarce during the 1966-67 winter. Relating the winter population fluctuations to breeding population changes, an increase in numbers occurred in 1967 (Table 6). But this breeding population increase does not seem to account for the tremendous increase in

the winter population. Gillespie (1930) thought that titmice population levels showed four-year cycles. Winter population data for 1968-69 (personal communication with Ray Adams) showed no titmice present. Perhaps there are four-year cycles, but snow cover may also be important. During the winters of 1966-67 and 1968-69 the ground snow cover was deeper and longer than in 1967-68 (U.S. Dept. of Commerce Climatological Data for Michigan, 1966-69). Tufted titmice are often found feeding on the ground, frequently eating acorns. Therefore, snow cover would be an important factor in winter population regulation of titmice at their northern limit of their range.

Another species which fluctuated radically was the blue jay. Snow cover is probably important with this species also. The jays are largely acorn eaters and a heavy and long snow cover would limit their food supply. Another factor may be alteration of residence status from year to year. According to Nunnely (1964) winter resident jays can become migrants the next year. She also found that blue jays may exhibit great changes in population numbers in an area from month to month. Her work, however, must be regarded with some reservations due to banding activity as explained by Bergstram (1964). It was possible that snow cover may have caused the monthly and yearly fluctuations in her blue jay populations.

Normally only December through February are included in the Audubon Field Notes winter censuses (Kolb, 1965). But in this study, November and March were included because of two factors.

One was the early evacuation of summer residents from the forest. The other was the lateness of arrival of the summer residents.

The month of April was an intermediate season between winter with interspecific flocks and the breeding season. Some year-around residents such as downy woodpeckers had already begun to excavate nest holes (Kilham, 1962, and personal observations). Nuthatches were heard singing during April. By late April, chickadees were observed examining possible nesting sites. But during this period spells of cold weather seemed to arrest the breeding activities and initiate a reactivation of wintering habits.

It was observed that robins were not true winter residents in the oak forest. They stayed in the woods until the first snow and were back in the forest as soon as the snow melted in the spring. Being forest floor feeders, the snow cover must prevent them from finding insects and other food in the litter.

Some of the winter residents in the oak forest form foraging flocks. During the fall, warblers in migration joined this foraging flock. Later during the winter, the flock was usually composed of 2-3 chickadees, 2 nuthatches and from 1-4 tufted titmice. Occasionally the flock was joined by brown creepers. The flock usually followed a northwest-southeast path through the tract.

Table 11. The winter populations of birds on the Allegan oak forest tract. The area is 18.4 acres.

Species	Nov. 1-Mar. 31		April		Combined	
	66-67	67-68	66-67	67-68	66-67	67-68
Red-bellied woodpecker	0.2	0.5	0	0	0.1	0.4
Hairy and downy woodpeckers	0.3	0.1	0.6	0.5	0.5	0.2
Black-capped chickadee	1.1	1.3	1.0	0	1.0	1.1
Tufted titmouse	0	2.1	0.2	0	0.1	1.8
White-breasted nuthatch	1.8	2.3	1.2	2.0	1.5	2.3
Brown creeper	0.2	0.2	0	0	0.1	0.2
Blue jay	0	1.4	0.1	1.0	0.1	1.2
Robin	0.2	0.5	0.6	1.0	0.4	0.6
Number of trips	9	12	8	2	17	14
Birds/100 acres	21	45	20	24	21	42

SPATIAL OCCUPANCY

Analysis of utilization of plant species took as its premise that if a given bird species showed no preferences among the various plants, utilization would correspond with availability. There is, however, no one measure of availability that is obviously most appropriate. In the following consideration, two measures were generally used.

In the first, importance values derived from the point-centered quarter method were used as an index to the available foraging and singing perches in the various tree species during the winter and early spring before full foliage was present. These percentages were black oak 47 percent, white oak 44 percent, and other species 9 percent. It must be realized that only those trees over one and one half inches dbh were recorded; therefore, smaller trees in the understory are not represented. They are, however, represented in the second method, used for late spring and summer. The percentages after full foliage was achieved were derived from leaf area taken in the autumn while studying energy availability. These percentages were black oak 68 percent, white oak 19 percent and other species 13 percent. It was apparent that the miscellaneous species, particularly flowering dogwood, provided a substantial block of foliage in the oak forest during this time of year.

The rationale for the second method was, first the leaf area gave an index to forest structure. Leaves could be what the birds

were responding to. Secondly, weight of the leaves would indicate the amount of leaf material available to primary consumers which are eaten by the birds (the weight ratios do not differ much from the leaf area ratios; they were black oak 74 percent, white oak 16 percent and other species 10 percent). The first method utilized density and percent frequency. These parameters can be equated with the numbers of leaves utilized in the second method. The basal area gives an estimate of the number of small and large branches as well as the size of the trunk for utilization of some bird species.

The year was divided into three periods in relation to the state of foliation and weather. Winter was from November 1 until March 31. Early spring was from April 1 until May 31. After June 1 the foliage was fully developed and this represented the late spring-summer period. This period continued until October 31. No autumn period was used.

Woodpeckers

The foraging utilization of the woodpeckers roughly corresponded to the ratio of the importance values of canopy trees (Tables 2 and 12). The greatest deviation was the hairy woodpecker which seemed to prefer black oaks (Fig. 3). The woodpeckers did not use miscellaneous woody species of trees. The birds were probably responding to tree trunks and large branches, and these tree species were too small in diameter and height. The preferred height appeared to be between 40 and 50 feet from the forest floor (Table 13). The

yellow-shafted flicker, of course, is primarily a ground feeder and flies out of the forest for part of its foraging periods. The hairy woodpecker used tree trunks more extensively than did any of the other woodpeckers (Fig. 5).

Eastern Wood Pewee

The wood pewee arrived in mid-May after the black oaks had started leafing. It appeared that the pewees responded to the vegetation about the same before June 1 as after. Perhaps this was due to the black oaks already having begun leafing. The tree species utilization appeared to remain the same for both periods (using the second method values). This species utilized dead branches for its flycatching perches. The slight downward shift in height utilization may be because of the decreased amount of open space in the canopy for flycatching. The shift was not because of decreased visibility in the canopy of the observer since the pewees sat on dead branches. The shift could also be correlated with the increased insect activity at lower levels owing to the new white oak foliage and warmer weather.

The pewees used small branches about half of the time for flycatching perches during the summer. These birds also used the tops of dead white oak stubs for perches which explains the usage of trunks in Table 14. The foraging and perching height preference during the summer was about 30 feet and was probably correlated with the large number of suitable perches in this height interval.

Great Crested Flycatcher

The great crested flycatchers arrived in early May before the black oaks had leaves. The flycatchers utilized black oaks when they were flycatching. They used perches of 30 feet above the ground more extensively than other heights during early spring (Fig. 4). Later, after full foliation, there was a shift so that the 50 and 60 foot intervals were used as extensively as those perches at 30 feet. Corresponding to the upward shift in perches, black oaks were used more after June 1 (Fig. 3). Perches used for singing "weep" songs were more predominant in black oaks than in other tree species. Usage of small branches early in the spring decreased as the season progressed, while large branch utilization increased (Fig. 5).

Black-capped Chickadee

Species utilization stayed relatively constant throughout the year, the main trend being a consistent increase in the use of black oaks corresponding to a decreased usage of white oaks from winter to late summer. During the winter the ratio of utilization corresponded very closely with the forest tree ratio obtained by method one. Later as spring progressed, the black-capped chickadees continued to feed in the black and white oaks as in the winter, but seemed to abandon other species of trees as foraging habitats. After June 1, the birds again utilized the miscellaneous species (Fig. 3). The

black oak preference rose during the late spring-summer period. This could have been caused by sight response to the leaves or to the increased amount of food in the canopy.

Height preference shifted from about 20 feet upward as spring approached. After the trees were fully leafed, the chickadees appeared to use all heights from 20 to 50 feet equally (Fig. 4). These observations corresponded with the findings by Brewer (1963a) except that the shift in the oak forest was probably greater than in mesic or wet-mesic vegetation.

During the winter months the black-capped chickadees seemed to use all parts of the trees while searching for insect eggs, pupae, and hibernating adults. Later in the early part of spring when the leaves were just appearing, the chickadees were found foraging on twigs 67 percent of the time (Fig. 5). This shift may have been in response to the spiders and newly hatched larvae found near the ends of twigs. Later when the lepidopteran larvae were larger, the usage of small branches would correspond to more of the larvae using the branches while crawling around.

Tufted Titmouse

Tufted titmice used black oaks for foraging 60 percent of the time throughout the year (Table 12). During the leafless periods of the year the titmice did not use the miscellaneous trees; however, during the late spring-summer period usage of this group was 10 percent.

Height preference remained fairly constant throughout the year except during the early spring when the upper canopy was also used (Gillespie, 1930, and personal observations). Most of the foraging was done from 20 to 30 feet from the ground (Fig. 4). The titmice primarily used large branches while foraging during the winter. As the season progressed from spring to summer the large branches were used less and smaller branches and twigs were used with greater frequency (Fig. 5).

White-breasted Nuthatch

The nuthatches had a slight preference for black oaks during the winter. This was probably based on the position preference for tree trunks while foraging. During the foliage period there was no preference for black oaks in relation to foliage ratios derived from the second method. White oaks were also used but less extensively. Other miscellaneous tree species were rarely used (Fig. 3). Height preference appeared to remain about the same throughout the year, averaging 30 feet (Table 13). Although the position preference was for tree trunks, during the early spring period there was an increased utilization of large branches until finally in the summer large branches were used more than the tree trunks (Fig. 5). This was probably due to the increased number of insects crawling on large branches.

Blue Jay

The blue jays showed a preference for black oaks during the

winter and early spring if they were responding to those parameters measured in method one. During the late spring-summer period there were no preferences but utilization closely correlated with that of ratios derived from method two. Miscellaneous tree species were used by blue jays during foraging and perching while hunting for acorns on the forest floor. The blue jays utilized all levels of the forest strata except the 30-foot interval which they seemed to avoid during the spring and summer. They may have to compete with summer residents (e.g. wood pewee, rose-breasted grosbeak) during these periods. The utilization of lower levels of the forest strata correspond to the usage of miscellaneous species such as dogwood. Blue jays preferred foraging and perching on large branches (Fig. 5). This preference for large branches may be related to the size of the bird. During the summer the utilization of small branches increased indicating that the jays were probably eating lepidopteran larvae.

Vireos

Both the red-eyed and the yellow-throated vireos were found on the tract. The red-eyed vireo was the more common of the two species. The vireos were inconspicuous, making observations hard to obtain. They seemed to be high in the black oaks before the forest was foliated while foraging. After the leaves were present, there was a downward shift in height preferences and these birds started utilizing white oaks (Table 12). Singing in the early summer was

still primarily done from black oaks. The average singing perch height shifted down about 10 feet after June first. Southern (1958) found that red-eyed vireos in mixed deciduous forests did most of their singing from the tree tops. He also found that feeding was confined to foliage and twigs from the tree tops to the lower fringe of the upper canopy. In the oak forest the same pattern was present except that the vireos appeared to feed lower at times, possibly because of a lower canopy. Both the red-eyed and the yellow-throated vireos preferred small branches when they were foraging or perching (Fig. 5). The yellow-throated vireo arrived in the forest about mid-May and the red-eyed vireos usually arrived a week later.

Ovenbird

The ovenbird arrived in early May and was one of the first birds to leave the oak forest during the summer after nesting and molting. All birds observed foraging were feeding on the ground. According to Stenger (1958) most of the food taken from the leaf litter on the forest floor is made up of adult Coleoptera (mostly Carabidae) and gastropods. She also states that the nestlings are fed lepidopteran larvae. Since the ovenbirds were only seen foraging on the forest floor perhaps they were catching crawling and pupating larvae which had left the trees.

If the ovenbirds were disturbed or if they were descending from singing perches, they would utilize small white oaks, white pines and dogwoods for perching. Singing was primarily done from

perches in black oaks about 30 to 40 feet from the ground. The singing is done from large branches upon which the male ovenbird walks up and down. This agrees with Stenger and Falls (1959) who found that ovenbirds sang from the lower branches of the canopy. Swinebroad (1960) found ovenbirds using dogwood perches 71 percent of the time for singing, but during this study ovenbirds were never seen singing from flowering dogwood.

Scarlet Tanager

Male scarlet tanagers arrived in the early part of May and began setting up territories before the leaves appeared on the trees. During this time, black oaks were highly preferred trees for both foraging and singing. The utilization of white oaks for foraging increased after foliation (Fig. 3). However, the use of white oaks while singing decreased. The tanagers seemed to use a substantial number of leafless branches for singing perches. Prescott (1965) recorded that the male tanagers sing less frequently when the female arrived in the territory. This same behavior pattern was also noted in this study. During the nest building period the males resumed loud, conspicuous singing again.

During May the scarlet tanagers chose heights ranging from 30 to 50 feet while foraging. After June first, the preference for specific heights seemed to diminish and the birds utilized most all of the strata except the top of the canopy (Fig. 4). Tanagers used both small and large branches extensively while foraging. A

slight shift toward greater usage of small branches was evident after June 1 when the white oaks were fully leafed (Fig. 5).

Rose-breasted Grosbeak

The grosbeak males arrived in the oak forest in early May and immediately began actively setting up territories. It was not uncommon to see two males engaged in a chasing fight usually ending with both birds on the ground.

Foraging in the early spring essentially took place in the black oaks. Later when full foliage was achieved, utilization of white oaks increased (Fig. 3). A shift in strata utilization also corresponded strongly with this tree preference shift. In the early spring the 60 foot interval was in common usage but by summer the preference had shifted down to 20 feet (Fig. 4). Dunham (1966) found that rose-breasted grosbeaks in New York do most of their foraging at the periphery of the tree canopy at all levels. He also found that trees were used more than vines or the ground. This is in agreement with this study except more small trees were utilized than large trees in the summer.

Foraging position preference changed very little with the onset of foliation except for twig usage (Fig. 5). The utilization of twigs declined after the forest had leafed out, and perhaps this is because of the movement of larvae onto larger branches. Dunham (1966) states that the grosbeaks glean insects from the foliage and also, less commonly, catch insects in the air. Seeds, buds, fleshy

fruits and young leaves comprise the bulk of vegetable matter that is eaten. In the early spring during the leafing period of black oaks the grosbeaks were frequently seen eating buds or small leaves.

The male grosbeaks preferred black oaks for singing perches. During May they used perches high in the canopy. Later during the late spring, the males utilized a wide range of heights in the black oaks for singing.

Table 12. The tree preference percentages during three seasons of some oak forest birds while perching and/or foraging.

Species	Season	Number of observations	Preference percentages Black oak	White oak	Others
Hairy woodpecker	1-3*	19	94.7	5.3	00.0
Downy woodpecker	1-3	19	73.7	26.3	00.0
Red-bellied woodpecker	1-3	17	82.4	17.6	00.0
Great crested flycatcher	2	23	78.3	21.7	00.0
	3	15	86.7	13.3	00.0
Eastern wood pewee	2	6	83.3	16.7	00.0
	3	77	75.3	24.7	00.0
Blue jay	1	7	85.7	14.3	00.0
	2	36	75.0	16.7	8.3
	3	29	69.0	20.7	10.3
Black-capped chickadee	1	22	54.6	40.8	4.6
	2	24	62.5	37.5	00.0
	3	48	72.9	20.8	6.3
Tufted titmouse	1	15	60.0	40.0	00.0
	2	10	60.0	40.0	00.0
	3	20	60.0	30.0	10.0
White-breasted nuthatch	1	20	65.0	35.0	00.0
	2	39	59.0	41.0	00.0
	3	60	71.6	28.4	00.0
Robin	1-3	29	64.9**	31.0	4.1
Yellow-throated vireo	2,3	10	90.0	10.0	00.0
Red-eyed vireo	2,3	15	46.7	46.7	6.7
Ovenbird	2	7	28.6**	28.6	42.8
	3	7	00.0	57.2	42.8
Scarlet tanager	2	38	84.2	13.2	2.6
	3	53	67.9	30.2	1.9
Rose-breasted grosbeak	2	58	82.7	12.1	5.2
	3	40	52.5	42.5	5.0

* 1-winter, 2-early spring, 3-late spring-summer

** these birds are primarily ground foragers and these data were for perching only

Table 13. The mean and median height at which the birds were found during different seasons of the year. Those numbers in parenthesis are the median. Heights are given in feet. The numbers of observations are the same as in Table 12.

Species	Winter	Early spring	Late spring-summer
Hairy woodpecker	40(40)	46(50)	42(40)
Downy woodpecker	40(40)	43(45)	37(40)
Red-bellied woodpecker	43(40)	-	44(40)
Great crested flycatcher	-	35(30)	40(40)
Eastern wood pewee	-	44(45)	31(30)
Blue jay	44(50)	39(45)	43(50)
Black-capped chickadee	28(25)	31(30)	34(40)
Tufted titmouse	28(30)	30(30)	30(30)
White-breasted nuthatch	27(30)	31(30)	30(40)
Robin	28(30)	18(25)	18(10)
Yellow-throated vireo	-	35(30)	38(40)
Red-eyed vireo	-	50(50)	30(35)
Ovenbird	-	6(Gr)*	14(10)
Scarlet tanager	-	38(40)	37(40)
Rose-breasted grosbeak	-	45(50)	29(20)

- stands for no data
* Gr stands for ground

Table 14. The position preference of various species of birds while foraging and/or perching in the oak forest. Seasonal symbolism and numbers of observations are the same as in Table 12.

Species	Season	Position percentages trunk	large br.	small br.	twig	fol.
Yellow-billed cuckoo	2,3	0	38.5	61.5	0	0
Hairy woodpecker	1-3	36.8	63.2	0	0	0
Downy woodpecker	1-3	15.8	63.2	21.0	0	0
Red-bellied woodpecker	1-3	17.6	76.5	5.9	0	0
Great crested flycatcher	2	4.3	34.8	47.8	13.0	0
	3	0	60.0	33.3	6.7	0
Eastern wood pewee	2	0	83.3	16.7	0	0
	3	2.6	26.3	47.4	17.1	0
Blue jay	1	0	57.1	42.8	0	0
	2	0	65.0	30.0	0	0
	3	3.6	35.7	57.1	3.6	0
Black-capped chickadee	1	8.3	25.0	20.8	20.8	20.8
	2	0	4.2	29.2	66.7	0
	3	2.2	15.2	58.7	23.9	0
Tufted titmouse	1	12.5	50.0	25.0	6.2	0
	2	0	36.4	45.4	9.1	0
	3	5.0	25.0	45.0	25.0	0
White-breasted nuthatch	1	60.0	35.0	5.0	0	0
	2	47.5	37.5	12.5	2.5	0
	3	40.0	50.0	6.7	3.3	0
Robin	1-3	13.8*	44.8	41.4	0	0
Yellow-throated vireo	2,3	0	10.0	70.0	20.0	0
Red-eyed vireo	2,3	0	0	66.7	33.3	0
Ovenbird	2,3	13.8*	44.8	41.4	0	0
Scarlet tanager	2	0	47.4	34.2	18.4	0
	3	0	38.5	42.3	19.2	0
Rose-breasted grosbeak	2	5.0	20.0	46.7	25.0	0
	3	2.6	33.3	53.8	10.2	0

* these species are ground feeders most of the time; these data are for perching

Fig. 3. Tree species utilization of some oak forest birds when foraging and/or perching. Seasonal symbols are as follows: 1-winter, 2-early spring, 3-late spring/summer. Key on next page.

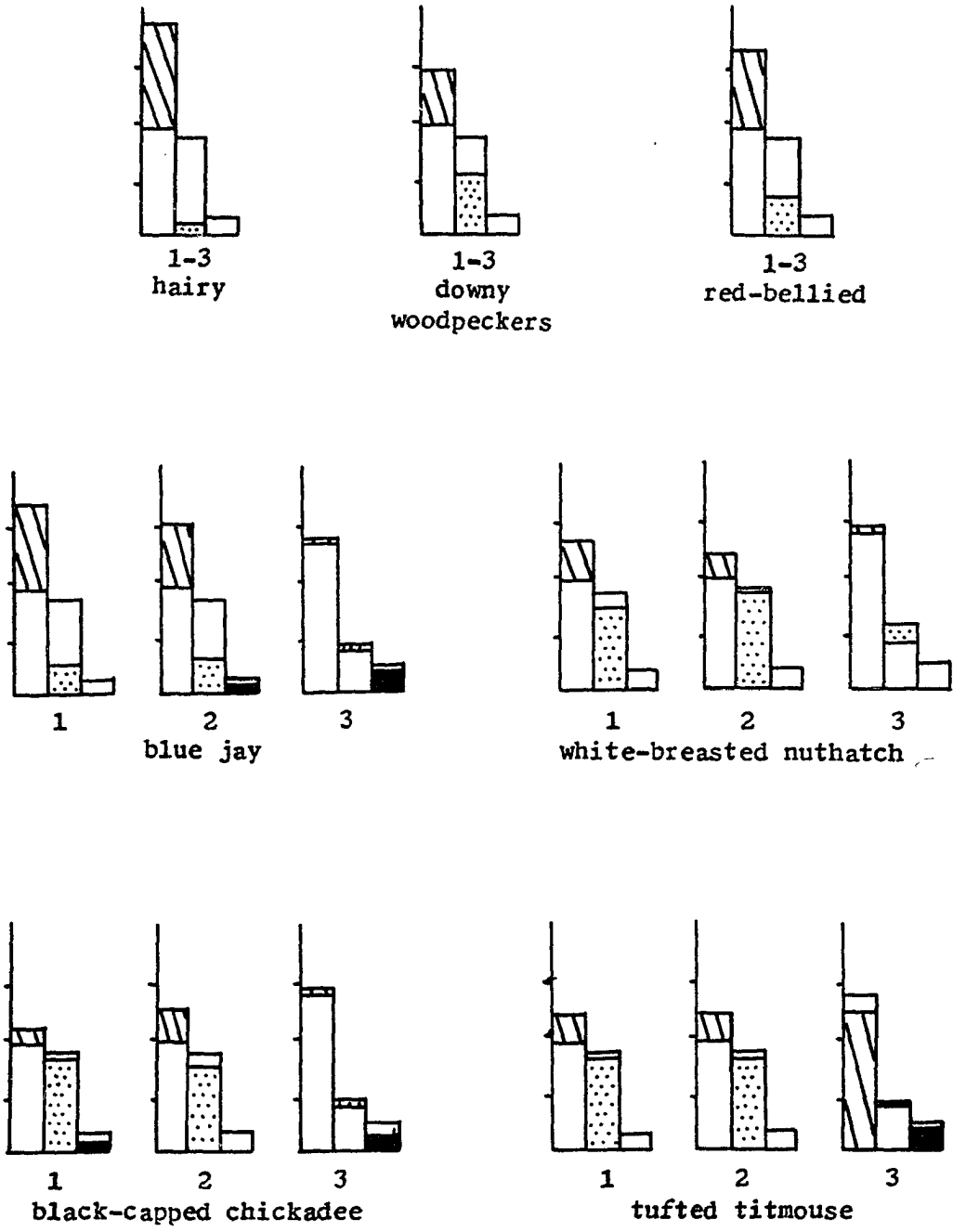


Fig. 3. Tree species utilization of some oak forest birds when foraging and/or perching. Seasonal symbols are as follows: 1-winter, 2-early spring, 3-late spring/summer. Key at bottom of this page.

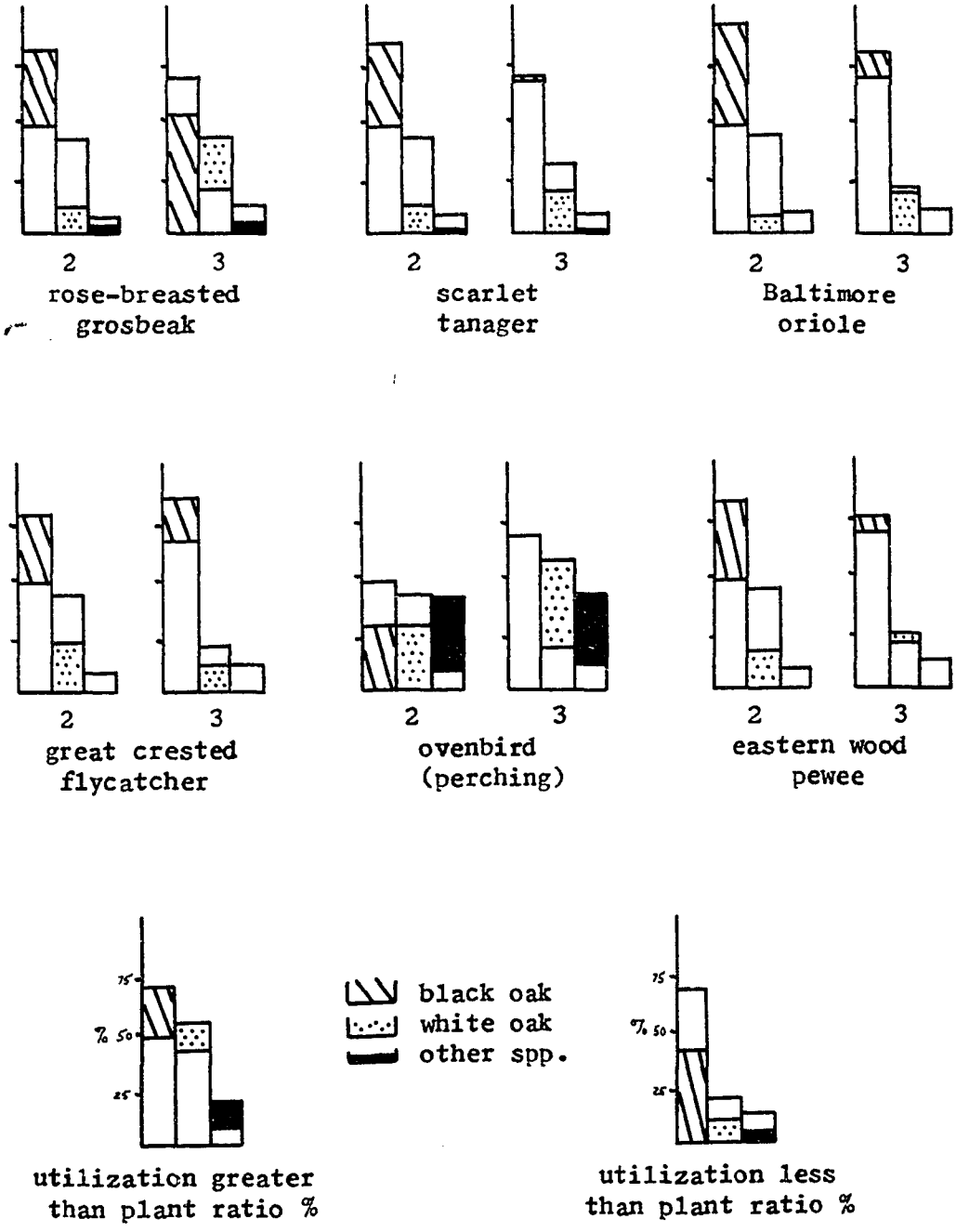


Fig. 4. Percent utilization of foraging and perching heights of several oak forest birds.

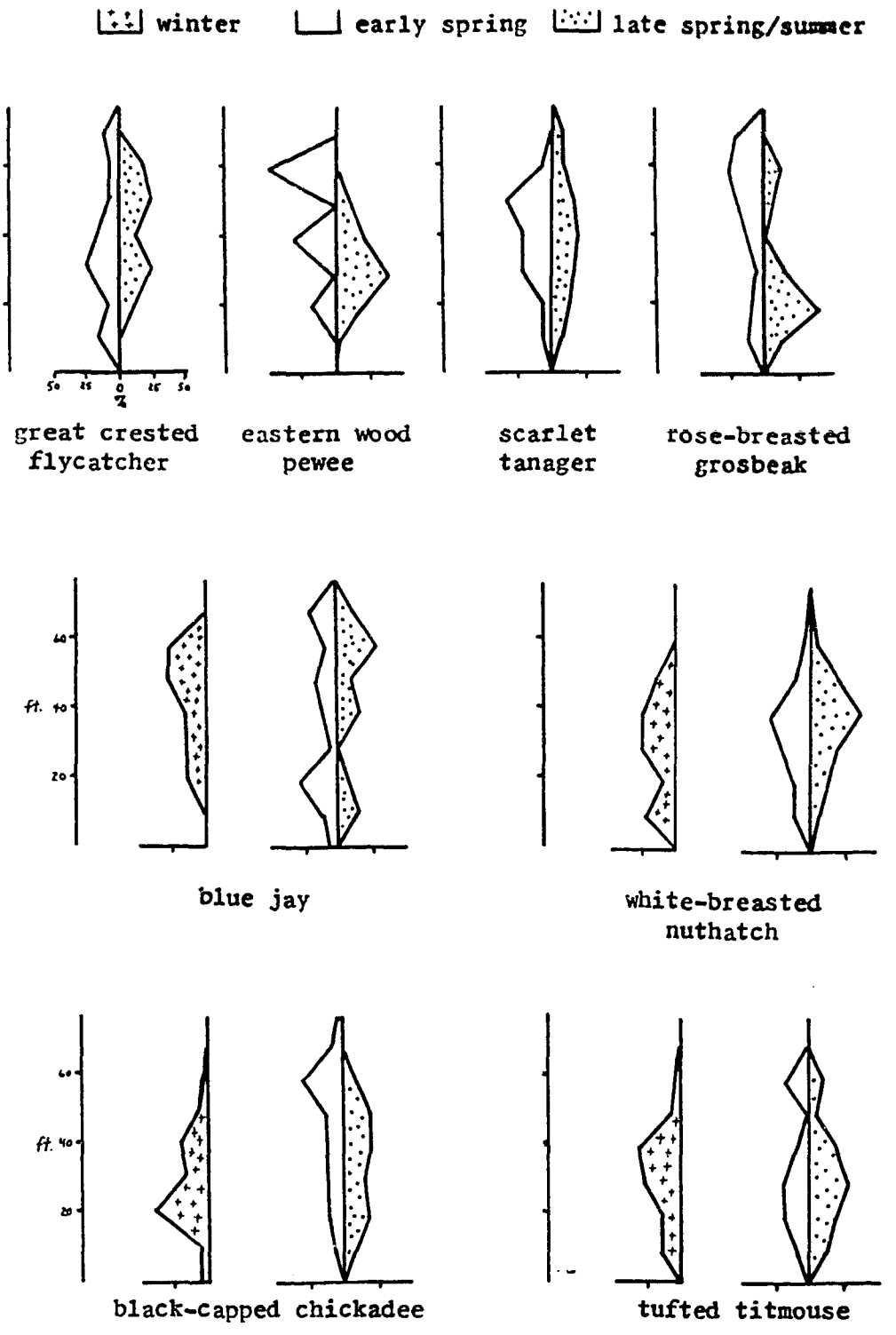


Fig. 5. Position preferences of oak forest birds while foraging and/or perching. Seasonal symbols are as follows: 1-winter, 2-early spring, 3-late spring/summer.

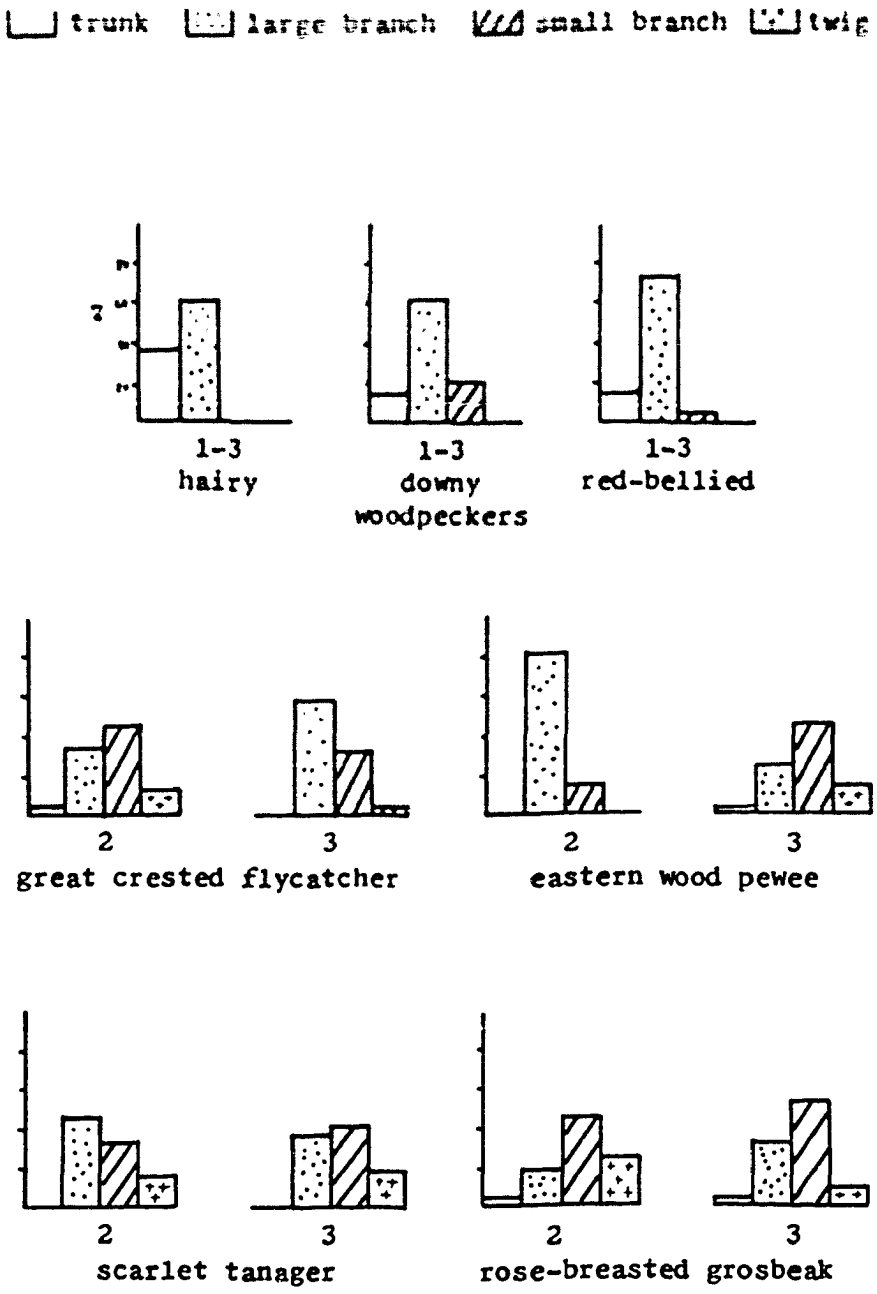
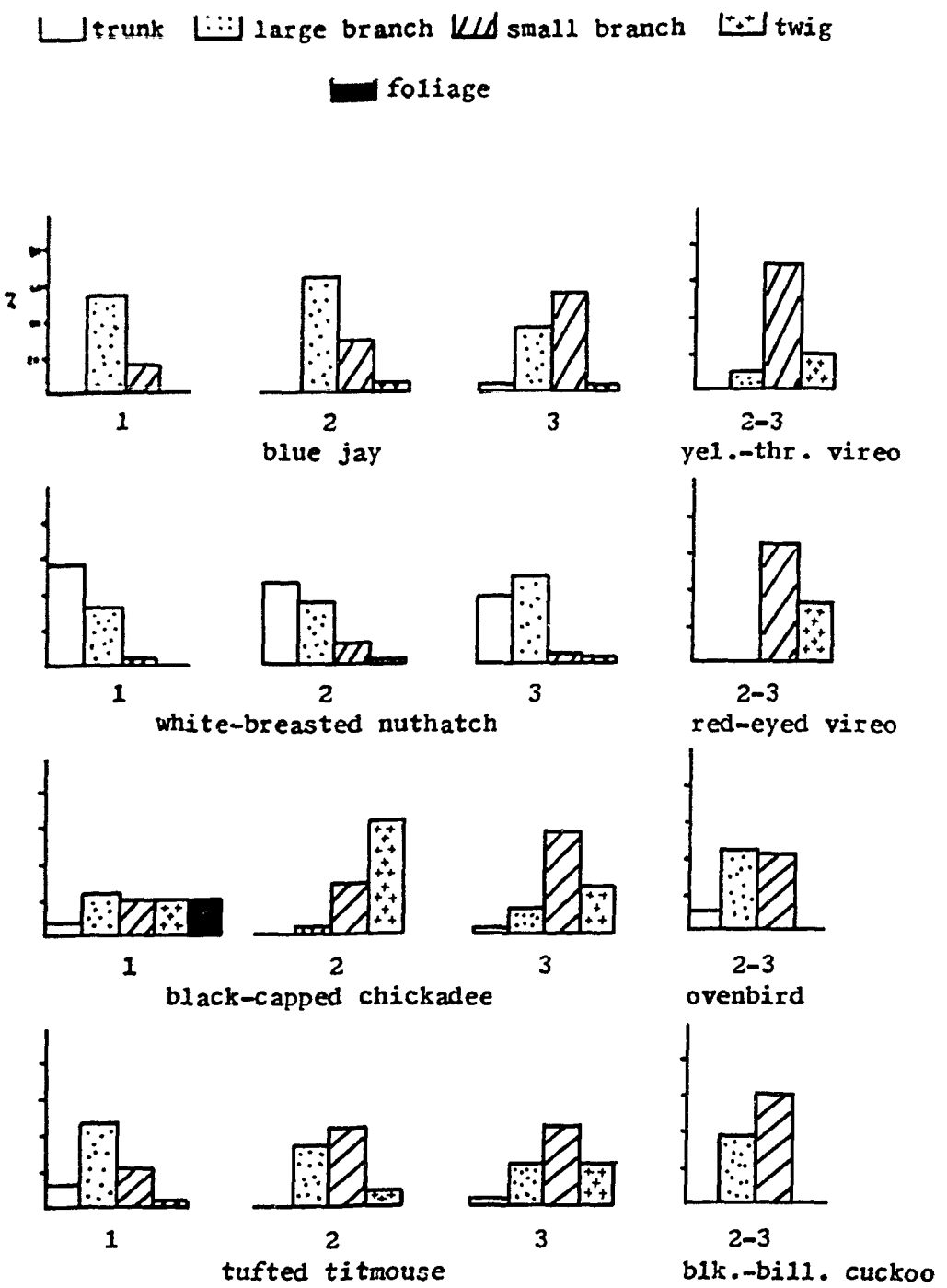


Fig. 5. Position preferences of oak forest birds while foraging and/or perching. Seasonal symbols are as follows: 1-winter, 2-early spring, 3-late spring/summer.



GENERAL DISCUSSION

The period of occupancy for breeding in the oak forest seems brief compared with many other communities. Over 50 percent of the breeding population left the forest by mid-August. Lepidopteran larvae are pupating during August. Food, as an ultimate factor (Hilden, 1965), does not appear to be a limiting factor during the height of the breeding season, but later could become limiting. Historically a shortage of food in late summer owing to pupation may have led to the development of a behavioral pattern causing early migrating or shifting to other habitats. The presence of wood pewees late in the season is possible because they do not, as flycatchers, rely on lepidopteran larvae as a major source of food. Small flying insects were still abundant into September.

Aside from instances of territorial abandonment and an occasional new territory appearing, possibly resulting from nest failure elsewhere and the pair moving onto the area, shifting and changes in numbers were slighter than had been expected. Nothing resembled the shifting pattern found by Robins (1967) for Henslow's sparrows (a grassland species). The closest approach was perhaps the ovenbird, but here, although shifting occurred, there was little evidence of the real change of numbers of birds that Robins found (and that is suspected to occur in many grassland species).

The segregation of habitat utilization was generally lacking. The observations indicated much overlapping in foraging utilization

of most forest characters by two or more species. Height preferences for singing and foraging were largely lower canopy and subcanopy. The high number of dead branches for perches and the relative openness of this stratum in the forest probably caused this behavior. During the summer the superabundance of energy (food) may reduce interspecific competition. Evacuation of the forest in August allows the species to escape competing for foraging characters and perhaps eliminating the need for segregation.

When studies of this sort are available from other kinds of forests and also non-forest communities more can be said about paterns of community organization and their evolution.

SUMMARY

The avian community was studied by observing temporal and spatial occupancy of the populations. The study area consisted of 18.4 acres of black and white oak forest located in Allegan County, Michigan. The vegetation was sampled using several methods: point-centered quarter method, square milacre quadrats, total counts, and leaf area and weight samples. Bird populations were determined by variations of the Williams spot map method during the breeding season, and a slight variation of the Audubon Field Notes winter-bird censuses for the non-breeding season. Standardized observations were used to study various factors in habitat utilization of the oak forest birds.

Analysis of utilization of plant species took as its premise that if a given bird species showed no preferences among the various plants, utilization would correspond with availability. Two methods were employed. In method one (used for winter and early spring observations) availability ratios were derived from the point-centered quarter method. In the second method (used during the late spring and summer) ratios were derived from leaf area samples. Most bird species utilized black oaks more than the availability ratios, but during the late spring-summer period black oak utilization diminished (availability derived by method two). Many birds utilized the 30-40 foot intervals, probably because of the large number of perches and openness in this stratum.

Generally the larger the bird, the larger the branches utilized. Woodpeckers and nuthatches generally preferred foraging on tree trunks.

Breeding populations (territorial males) for the oak forest were: 1966, 178 per 100 acres; 1967, 266 per 100 acres; and 1968, 153 per 100 acres. It was found that temporal changes in the populations were greatest near the end of the breeding season. Summer residents seemed to disappear, even before molting. Ovenbirds were the first summer residents to vacate the oak forest and eastern wood pewees, the last. Good visibility in the oak forest may be a factor in causing less dense populations than in a low visibility forest (e.g. spruce-fir). It was also found that a high number of censuses produced larger population estimates because of the greater probability of separating adjacent territories and of detecting the presence of inconspicuous birds.

Energy availability in the form of lepidopteran larvae was determined since they are a major source of food. Leaf area consumed was used for the estimate. There were 186,300 kilocalories per acre theoretically available to the birds. The seasonal energy requirement for the bird populations was estimated as 23,947 kilocalories per acre, or only 13 percent of the available energy. Other sources of energy were discussed.

APPENDIX OF BIRD NAMES[1]

Wood duck	Aix sponsa
Yellow-billed cuckoo	Coccyzus americanus
Whip-poor-will	Caprimulgus vociferus
Yellow-shafted flicker	Colaptes auratus
Red-bellied woodpecker	Centurus carolinus
Red-headed woodpecker	Melanerpes erythrocephalus
Hairy woodpecker	Dendrocopos villosus
Downy woodpecker	Dendrocopos pubescens
Great crested flycatcher	Myiarchus crinitus
Acadian flycatcher	Empidonax virescens
Least flycatcher	Empidonax minimus
Eastern wood pewee	Contopus virens
Blue jay	Cyanocitta cristata
Black-capped chickadee	Parus atricapillus
Tufted titmouse	Parus bicolor
White-breasted nuthatch	Sitta carolinensis
Brown creeper	Certhia familiaris
Catbird	Dumetella carolinensis
Robin	Turdus migratorius
Wood thrush	Hylocichla mustelina
Swainson's thrush	Hylocichla ustulata
Blue-gray gnatcatcher	Polioptila caerulea
Cedar waxwing	Bombycilla cedrorum
Yellow-throated vireo	Vireo flavifrons
Red-eyed vireo	Vireo olivaceus
Ovenbird	Seiurus aurocapillus
American redstart	Setophaga ruticilla
Red-winged blackbird	Agelaius phoeniceus
Brown-headed cowbird	Molothrus ater
Baltimore oriole	Icterus galbula
Scarlet tanager	Piranga olivacea
Cardinal	Richmondena cardinalis
Rose-breasted grosbeak	Pheucticus ludovicianus
Chipping sparrow	Spizella passerina
Field sparrow	Spizella pusilla

[1] names taken from the A.O.U. Check-list of N. Am. birds, 1957.

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