FORAGING ECOLOGY OF THE COMMON YELLOWTHROAT, THE PRAIRIE WARBLER AND THE WHITE-EYED VIREO

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ABSTRACT

Aspects of the foraging ecologies of the Common Yellowthroat *Geothlypis trichas*, the Prairie Warbler *Dendroica discolor* and the White-eyed Vireo *Vireo griseus* are quantified and compared.

Interspecific differences were found in foraging behavior, in foraging areas, in habitat preferences and in feeding structures. These differences help effect ecological isolation in these species and facilitate coexistence. Correlations between feeding behavior and morphology are discussed.

Niche breadth and niche overlap values were calculated. Niches of all three species are fairly broad (values range from 0.70 to 0.79) and are thought to be adaptations to the rapidly changing successional environment which these species inhabit.

FORAGING ECOLOGY OF THE COMMON YELLOWTHROAT,

THE PRAIRIE WARBLER AND THE WHITE-EYED VIREO

INTRODUCTION

Ecological theorists have postulated that coexisting species cannot exploit a common limiting resource in the same way, but that ecological differences between them allow interspecific subdivision of the resource and coexistence (Darwin 1859; Grinnell 1917, in Gaffney 1975; Gause 1934). Each species of a community must have a set of morphological, behavioral or habitat characteristics which effect ecological isolation. This species-specific set of attributes assures the species a unique means of life. A species' manner of exploitation of vital resources is usually termed the ecological niche.

Although many studies have been devoted to the niche, the student of ecology often has misconceptions of what the term represents. The ecological niche is usually described as either the space in which an organism feeds, or as the "role" or function of a species in the community. The first idea is incomplete and the other is confusing and anthropomorphic.

Fortunately, ecologists have begun to consider the niche as a phenotype that is inseparable from any part of the ecology of a species (Colwell and Fuentes 1975). Colwell and Futuyma (1971) have suggested that "phene pool" may be a more appropriate term. As a phenotype, the niche has a genetic basis, is a population phenomenon and is therefore subject to change by evolution. It is important to view the concept in this manner because it emphasizes the dynamic quality of the niche.

The niche phenotype consists of innumerable parts, so it is highly unlikely that the niche of any species will ever be completely defined. However, specific ecological parameters can be investigated and quantified to determine how potentially competing species may coexist.

Competition cannot occur unless a vital resource is in short supply. The most important limiting resource is usually food (Lack 1954, Orians and Horn 1969). Therefore, differences in feeding ecology (i.e., the portion of the species niche involved with feeding) should exist between all syntopic species which share the same food resource. Lawlor and Smith (1976) suggest a model by which species could have evolved ecological distinction through specialized use of resources and character displacement. The result would be interspecific differences in structural, morphological or behavioral components of feeding ecology (Newton 1967, Ellis and Travis 1975).

A group of species in the same community which possess similar resource exploitation patterns comprise a foraging guild (Root 1967). Investigators have studied guilds of species from diverse groups of animals, including bees (Johnson and Hubbell 1975), fish (Mendelson 1975), reptiles (Schoener 1967, 1975), and mammals (Ellis and Travis 1975). However, a great deal of evidence for divergent feeding ecologies has come from studies of birds.

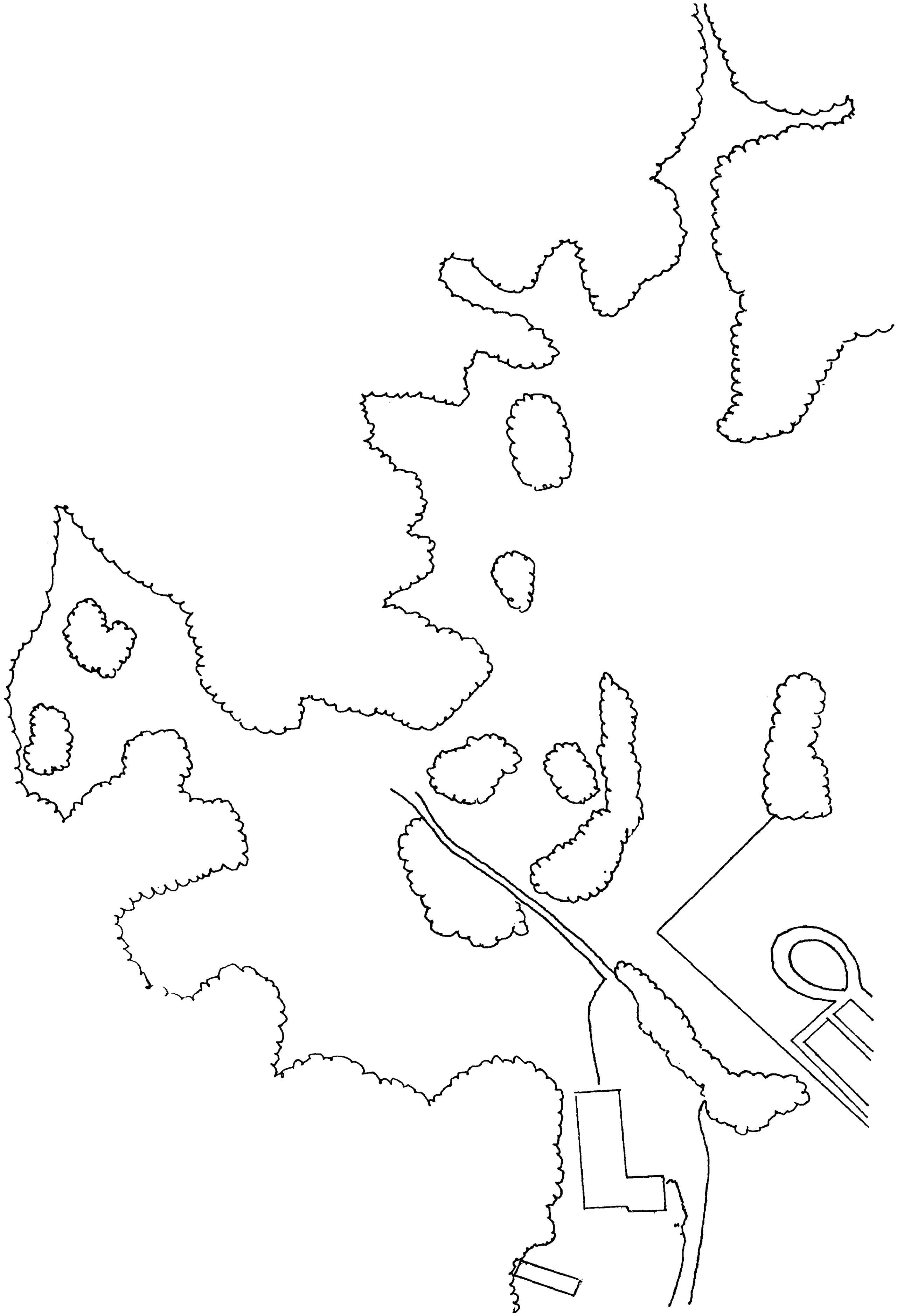
Ecologists have approached the problem by examining three major aspects of avian foraging ecology: morphological specializations, habitat preferences and behavior. Interspecific differences which would allow coexistence have usually been found within one or more of these categories.

Hartley (1953) and Gibb (1954, 1960) have studied relationships in guilds of British titmice (Parus, Family Paridae) and found interspecific differences in foraging heights, foliage preference and plant species in which birds fed. Johnston (1971), Hespenheide (1971) and Verbeek (1975) investigated feeding strategies of species assemblages of flycatchers (Family Tyrannidae). Different species fed from different heights, and their basically similar flycatching behaviors differed. Morse (1967) studied feeding patterns and interactions between the Pine Warbler Dendroica pinus (Family Parulidae) and the Brown-headed Nuthatch Sitta pusilla (Family Sittidae) and found that when they feed together they utilize different portions of limbs and substrates of different character.

In addition to interspecific differences in exploitation strategies, there may also be intraspecific differences between the sexes. Selander (1966) suggests that sexual dimorphism in foraging morphology and strategies would both decrease intersexual competition and increase the proportion of the resource available to the species as a whole. Physically dimorphic species should exhibit greater sexual differences in feeding. He surveyed woodpeckers of the genus Centurus (Family Picidae), and found that the sexes differed in feeding structures and in behavior. Morse (1968), in a study of Dendroica (Family Parulidae) warblers, has shown that behavioral differences exist between males and females in both monomorphic and dimorphic birds. Williamson (1971) investigated foraging habits of the monomorphic Red-eyed Vireo Vireo olivaceus (Family Vireonidae), and found that the males possessed behavioral patterns which kept them higher in the foliage than females, a difference probably correlated with singing by males and incubation by females. Selander (1966) found a similar situation in the dimorphic Indigo Bunting *Passerina cyanea* (Family Fringillidae).

The purpose of this study was to investigate and compare foraging strategies and structures of the Common Yellowthroat *Geothlypis trichas* (Family Parulidae), the Prairie Warbler *Dendroica discolor* (Family Parulidae) and the White-eyed Vireo *Vireo griseus* (Family Vireonidae), three insectivorous species which commonly coexist in grass-shrub communities (Bent 1950, 1953; Johnston and Odum 1956). Because of underlying similarities in habits, the three are potential competitors.

Figure 1. Sketch of the study area.



STUDY AREA

The primary study area was an overgrown field of about 5 ha located adjacent to the Laboratory of Population Ecology and Endocrinology of the College of William and Mary, approximately one-half mile southeast of the main campus of the college in Williamsburg, Virginia. Additional observations were made in an adjoining 6.6 ha field. The Williamsburg area receives an average of about 117 cm of rain annually, about half of which falls between March and September. Temperatures range from -19.4°C to 40°C with a yearly average of 14.7°C (Giles 1974).

The study took place in an open field and in the more overgrown areas which bordered it. The vegetation of open areas was primarily herbaceous, and included mainly goldenrods (*Solidago* spp.), daisy fleabane (*Erigeron annuus* (L.) Pers.), orchard grass (*Dactylis glomerata* L.), Johnson grass (*Sorghum halapense* (L.) Pers.), and vetch (*Vicia* spp.). Poison ivy (*Rhus radicans* L.), grape (*Vitis* spp.), Japanese honeysuckle (*Lonicera japonica* Thunb.), and blackberry (*Rubus* spp.) are patchily distributed in fields and in denser border areas. The study area is divided into several smaller fields by hedgerows of black cherry (*Prunus serotina* Ehrh.), tree of heaven (*Ailanthus altissima* (Mill.) Swingle), black locust (*Robinia pseudoacacia* L.) and hackberry (*Celtis occidentalis* L.). Woods of tulip trees (*Liriodendron tulipifera* L.), hickory (*Carya* spp.) and oak (*Quercus* spp.) occur on the eastern and southern borders of the study area. Young thickets of trees of heaven are common in field borders, where trees are frequently overgrown with honeysuckle, poison ivy and grape.

METHODS AND MATERIALS

Banding and Measurements

Field work was conducted on the Yellowthroat alone from 28 March 1974 through 1 August 1974, and on all three species from 31 March through 18 August 1975. Birds were captured from banding and measurement by mist-netting an average of 3 mornings a week. During migration, banding was conducted as often as 6 times a week. Nets were opened just before dawn, and remained open from four to six hours, depending on the season. Twenty-nine English mist nets, measuring 2.6 m by 12.2 m, were placed throughout the study area, encompassing a variety of habitats. Each bird captured was banded with four bands: three colored plastic bands and a serially numbered aluminum band provided by the U. S. Fish and Wildlife Service. Each bird received a unique color combination obtained from a master list generated by computer; these combinations permitted identification of individuals in the wild. Six colors were used. Records were kept of color combinations and band numbers.

When a bird was first netted, a number of measurements were made and recorded on special forms. Data were cataloged by band number and color combination. Sex was determined in Prairie Warblers and Yellowthroats through plumage characteristics, but since the White-eyed Vireo is not sexually dimorphic, sex determination was not feasible. A bird's age was determined by examination of plumage, fleshy parts and eye color, and by skulling. Skulling consists of examination of the skull bones with a monocular lens for the presence of white dots, which are evidence of areas of completed ossification. Juveniles lack the dots, or have them distributed in a non-uniform pattern (Wood 1969, after Miller 1946).

Structures which might have been specially adapted to feeding were measured for comparison between the three species. Wing chord lengths were measured to the nearest 0.01 cm with a Mitotoyu dial caliper as the distance from the shoulder of the right wing to the tip of the longest primary feather. For weighing, birds were placed in a plastic mesh onion bag, which was attached to a Pesola spring scale.

All leg and bill measurements were made with an architect's divider and a millimeter ruler as described by Baldwin (1931). The tibiotarsus was measured from the feathered joint at the femur to the joint with the tarsometatarsus. The tarsometatarsus was measured from the elbow to the last undivided scale of the foot. Culmen length was measured from the tip of the bill to the proximal unfeathered base. Bill height and width were measured at that proximal point. The gape-tip length was the distance from the commisural point (the gape) to the end of the upper mandible.

Because relatively few White-eyed Vireos and Prairie Warblers were captured, I measured a number of study skins of those species in the Museum of Natural History at the Smithsonian Institution. All specimens were collected in Virginia with the exception of a few from the District of Columbia and North Carolina. Data on weight were not available, and tibiotarsi of the study skins were not measured for fear of damaging the skins.

Feeding observations

Observations of feeding birds were made 4 to 5 days a week between 0500 h and 1200 h, the period of greatest avian activity.

Field technique was similar to that of Root (1967). Whenever I encountered a foraging bird, I measured the duration of the act with a stopwatch and noted the following: date, time of day, sex, age and color combination when possible, foraging method, perch plant, plant on which the bird was feeding, perch size, height of the bird in the vegetation and height of the plant. Trees were divided into three vertical zones (upper, middle and lower) and three horizontal zones (core, middle and outer), and each feeding individual was assigned to a vertical and a horizontal position. The general character of the feeding substrate was described. Any unusual behavior, agression, vocalization or movement was recorded. Also, the habitat and types of vegetation were briefly described for each observation. In 1974 heights were estimated. In 1975, heights of birds feeding in trees were measured using a Spiegel Relaskop; heights in herbaceous plants were estimated.

Statistics

Feeding and tree heights for the Yellowthroat for 1974 and 1975 (estimated, and measured, respectively) were pooled after Student's t-test showed that they were not significantly different ($P>0.05$).

Simple descriptive statistics for numeric variables were computed using the Statistical Analysis System, a computer package prepared at the North Carolina State University (Barr and Goodnight

1972). Information computed by the system was used for further tests. Males and females of each species were first compared for each parameter using Student's t-test. If no intersexual differences were revealed, data were combined. Variances were tested for homogeneity. If variances were homogeneous, an analysis of variance was run. If not, an approximate test of equality of means was used. If anovas and approximate tests indicated that differences might exist, means were compared using the Student-Newman-Keuls test.

Non-numeric data were compared interspecifically using the chi-square test of independence.

In all tests, differences were considered significant at the 0.05 level. Procedures for statistical tests were taken from Sokal and Rohlf (1969).

RESULTS

Foraging Tactics

Yellowthroats, Prairie Warblers and White-eyed Vireos all fed while perched more often than they fed aerially (see Table 1). When species pairs were compared for frequency of aerial foraging, only the comparison between the Yellowthroat and the White-eyed Vireo was significant (see Appendix A). The vireo fed aerially in 62.5% of the observations, a frequency about 7 times greater than in Yellowthroats ($P<0.005$). Subtler differences underly basic foraging tactics which are impossible to analyze statistically; these will be described in the section on feeding behavior.

Perch Size

Perches were classified into 5 categories according to size and character: herbaceous stems, twigs, branches, limbs and trunks. The difference between Yellowthroats and Prairies in choice of perch size was highly significant ($P<0.005$, see Appendix A). Yellowthroats concentrated foraging on herbaceous stems and on twigs. Prairies also use these perches, but prefer slightly larger ones (see Figure 2).

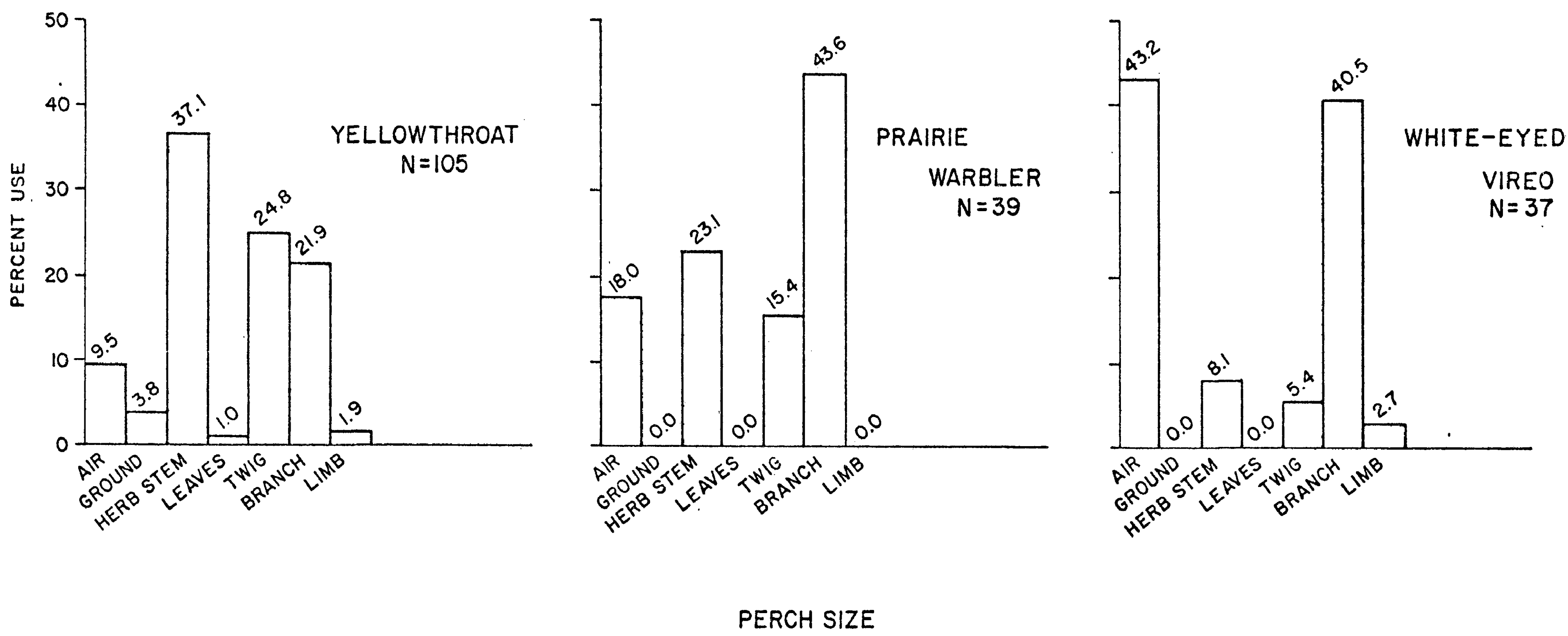
White-eyed Vireos differed significantly in perch size from both the Yellowthroat ($P<0.05$) and the Prairie Warbler ($0.005<P<0.05$). The vireo foraged on larger limbs than did the Yellowthroat. The White-eyed Vireo never used herbaceous stems, although it did perch on viny stems. Most perching occurred on branches.

TABLE 1

FREQUENCIES OF FORAGING IN AIR VS. FROM PERCH BY COMMON YELLOWTHROATS (YT), PRAIRIE WARBLERS (PW) AND WHITE-EYED VIREOS (WEV).

	Perched	Aerial	N	% Aerial
YT	114	10	124	8.1
PW	32	8	40	20.0
WEV	24	15	39	38.5

Figure 2. Per cent use of different sized perches by Yellowthroats, Prairie Warblers and White-eyed Vireos.


PERCENT USE
0
10
20
30
40
50
YELLOWTHROAT
N=105
9.5
3.8
37.1
1.0
24.8
21.9
1.9
PRAIRIE
WARBLER
N=39
18.0
0.0
23.1
0.0
15.4
43.6
0.0
WHITE-EYED
VIREO
N=37
43.2
0.0
8.1
0.0
5.4
40.5
2.7
AIR
GROUND
HERB STEM
LEAVES
TWIG
BRANCH
LIMB
PERCH SIZE

Feeding Zone

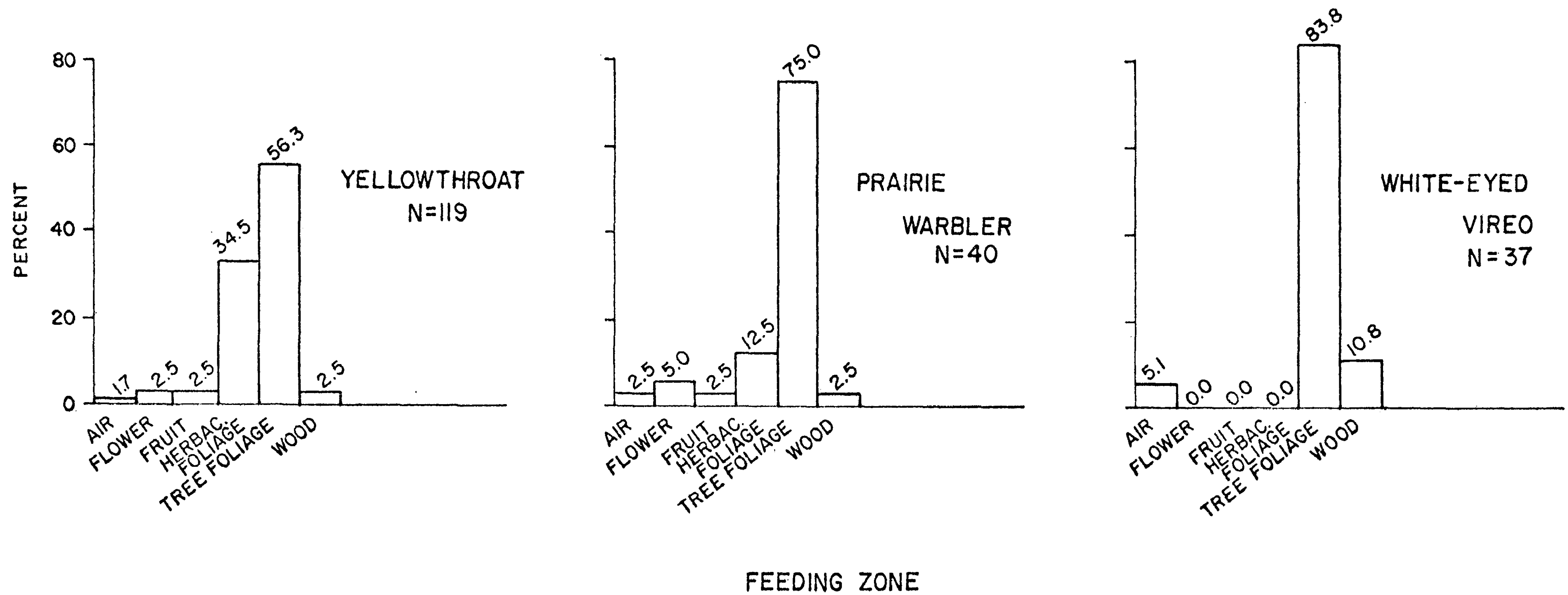
Differences in choice of foraging substrate were significant in two of the three comparisons (see Appendix A). All three species forage while perched most of the time. (Although 62.5% of the White-eyed Vireo feedings were aerial, most food-searching involved peering among the leaves from a perch. See Figure 3.) Marked similarity exists between the foraging substrates chosen by Yellowthroats and Prairies ($P>0.05$). The Yellowthroat used herbaceous plants more than twice as often as the Prairie; the White-eyed was never seen foraging in herbaceous vegetation. Differences between the White-eyed and both Prairies and Yellowthroats were significant ($0.01<P<0.025$, $P<0.005$, respectively).

Vertical Position

Using the chi-square test of independence, each species differed significantly from each of the others in preference of vertical zone (see Appendix A). Prairies and Yellowthroats foraged primarily in herbaceous plants and in the upper portions of trees (see Figure 4). Prairies used herbs less than Yellowthroats and fed nearly twice as often in the upper third of trees. Yellowthroats also foraged in the lower branches of trees. These differences were significant ($P<0.05$).

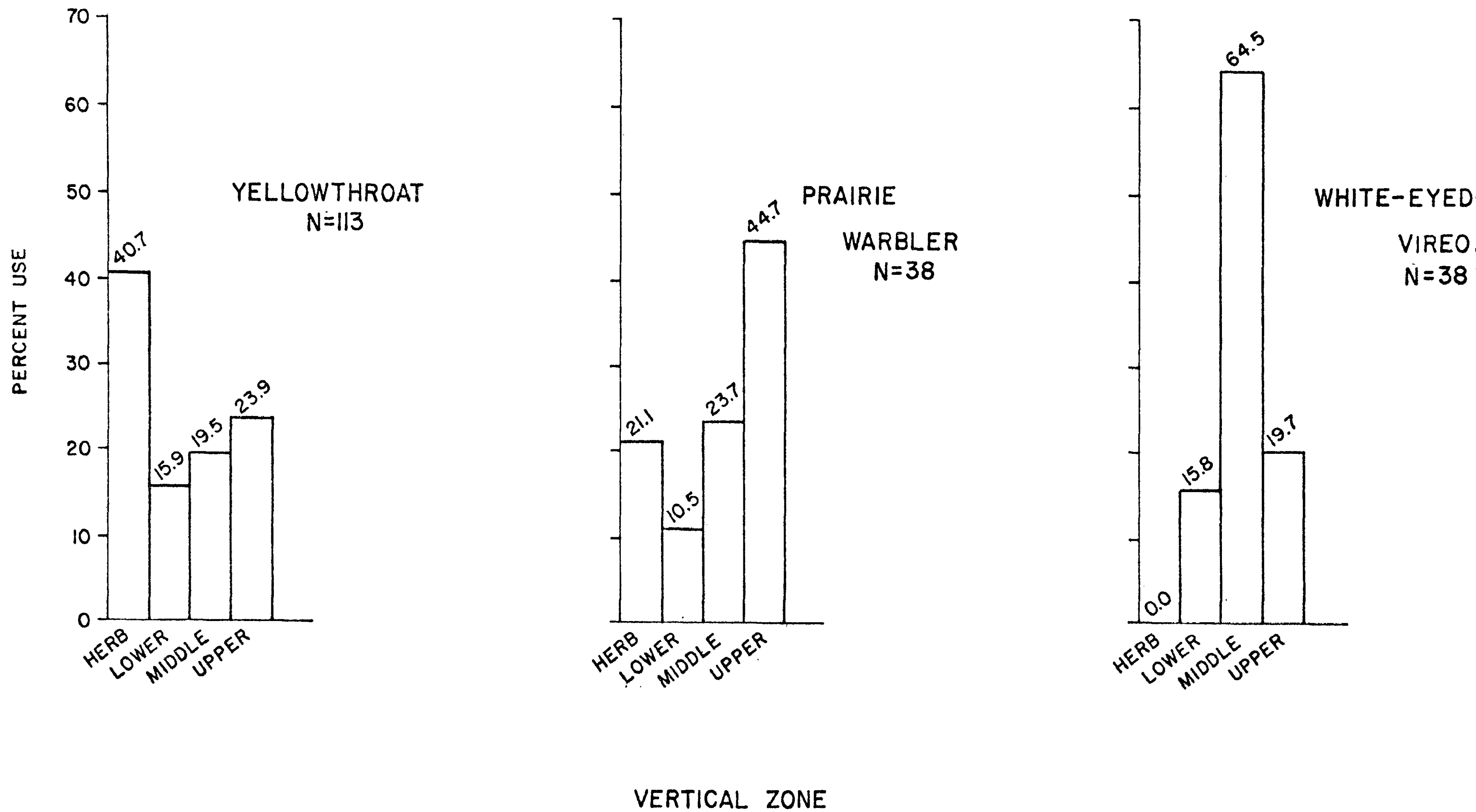
Comparisons of both warblers to the vireo were significant at the 0.005 level. Vireos never fed in herbs. They concentrated feeding upon the middle third of the trees, and used other portions of trees much less often.

Figure 3. Per cent use of different feeding zones by Yellowthroats, Prairie Warblers and White-eyed Vireos.



80
60
40
20
0
PERCENT
YELLOWTHROAT
N=119
1.7
2.5
2.5
34.5
56.3
2.5
AIR
FLOWER
FRUIT
HERBAC. FOLIAGE
TREE FOLIAGE
WOOD
PRAIRIE
WARBLER
N=40
2.5
5.0
2.5
12.5
75.0
2.5
AIR
FLOWER
FRUIT
HERBAC. FOLIAGE
TREE FOLIAGE
WOOD
WHITE-EYED
VIREO
N=37
5.1
0.0
0.0
0.0
83.8
10.8
AIR
FLOWER
FRUIT
HERBAC. FOLIAGE
TREE FOLIAGE
WOOD
FEEDING ZONE

Figure 4. Per cent use of different vertical zones by Yellowthroats, Prairie Warblers and White-eyed Vireos.


PERCENT USE
0
10
20
30
40
50
60
70
YELLOWTHROAT
N=113
40.7
15.9
19.5
23.9
PRAIRIE
WARBLER
N=38
21.1
10.5
23.7
44.7
WHITE-EYED
VIREO
N=38
0.0
15.8
64.5
19.7
HERB
LOWER
MIDDLE
UPPER
VERTICAL ZONE

Horizontal Position

Choices of horizontal zone were not significantly different in any comparison ($P>0.05$, see Appendix A and Figure 5).

Heights of Feeding Birds

The comparison between the Yellowthroat and the White-eyed Vireo for feeding height was the only one that was significant ($P<0.005$, see Appendix A). Yellowthroats foraged more frequently in the 0-1.2 m level (see Figure 6). White-eyed Vireos fed more often in the 3.0-6.1 m zone; two thirds of all feedings occurred in this zone. Prairies used all 3 zones frequently.

Tree Height

Table 2 lists the mean of heights of trees in which foraging occurred for the three species. The White-eyed Vireo fed in taller trees than either other species ($P<0.05$ in each case). The difference between the Yellowthroat and the Prairie was not significant ($P>0.05$).

Niche Breadth and Overlap

Various indices of niche breadth and overlap have been devised to wuantify ecological specialization and interspecific similarity, respectively. Values of niche breadth and overlap were calculated, for all niche dimensions studied, using the Shannon-Weiner formula (Colwell and Futuyma 1971).

The formula is $H' = -\Sigma p_i \log p_i$, where H' is the niche breadth of a species and p_i is the proportion of total foraging which occurred in the i^{th} category of the niche dimension. The value obtained was then converted to a proportion of H_{max}, the maximum diversity possible

Figure 5. Per cent use of different horizontal zones by Yellow-throats, Prairie Warblers and White-eyed Vireos.

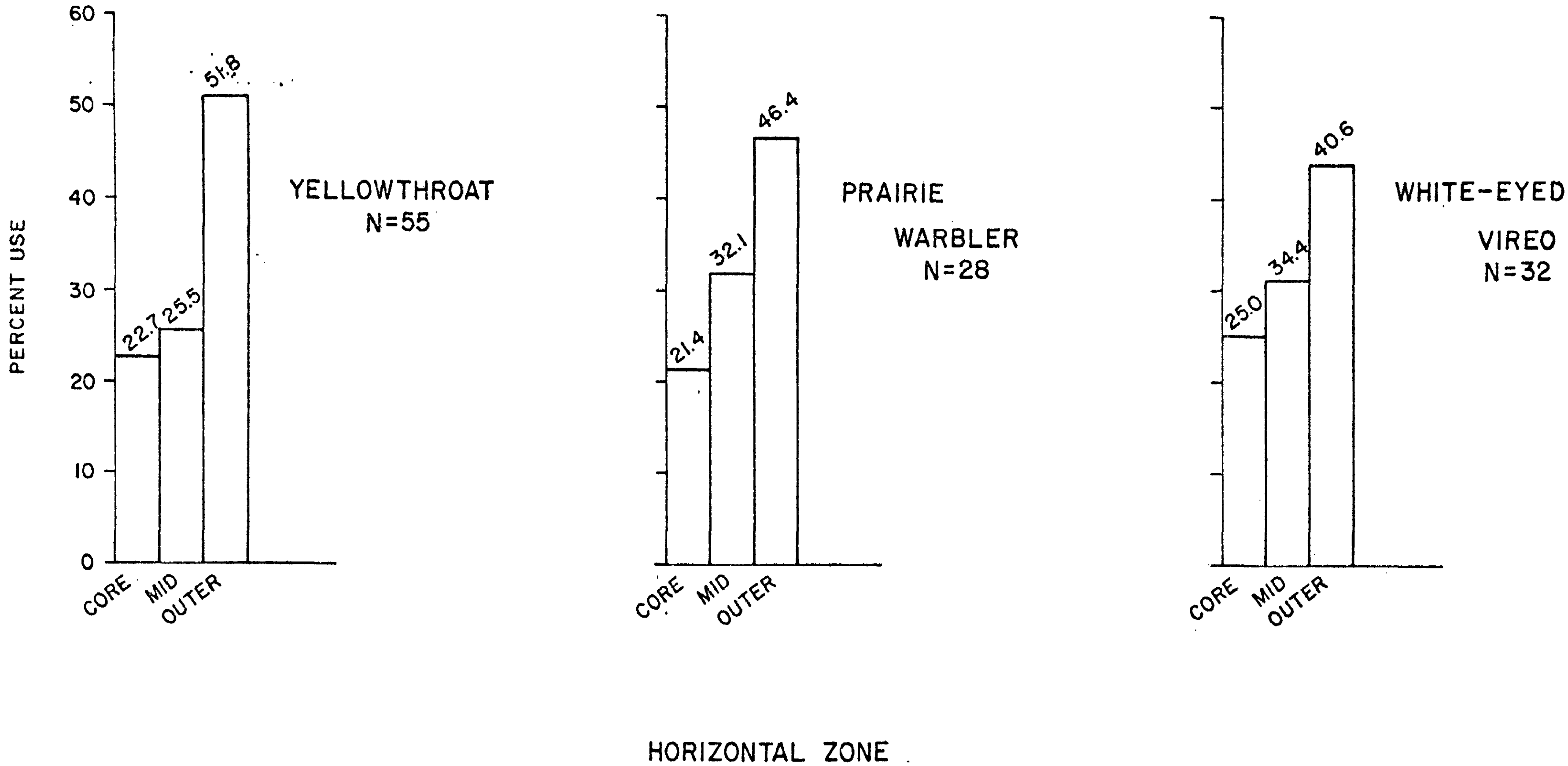

PERCENT USE
0
10
20
30
40
50
60
22.7
25.5
51.8
CORE
MID
OUTER
YELLOWTHROAT
N=55
21.4
32.1
46.4
CORE
MID
OUTER
PRAIRIE
WARBLER
N=28
25.0
34.4
40.6
CORE
MID
OUTER
WHITE-EYED
VIREO
N=32
HORIZONTAL ZONE

Figure 6. Per cent use of different height intervals by Yellowthroats, Prairie Warblers and White-eyed Vireos. Heights in m.

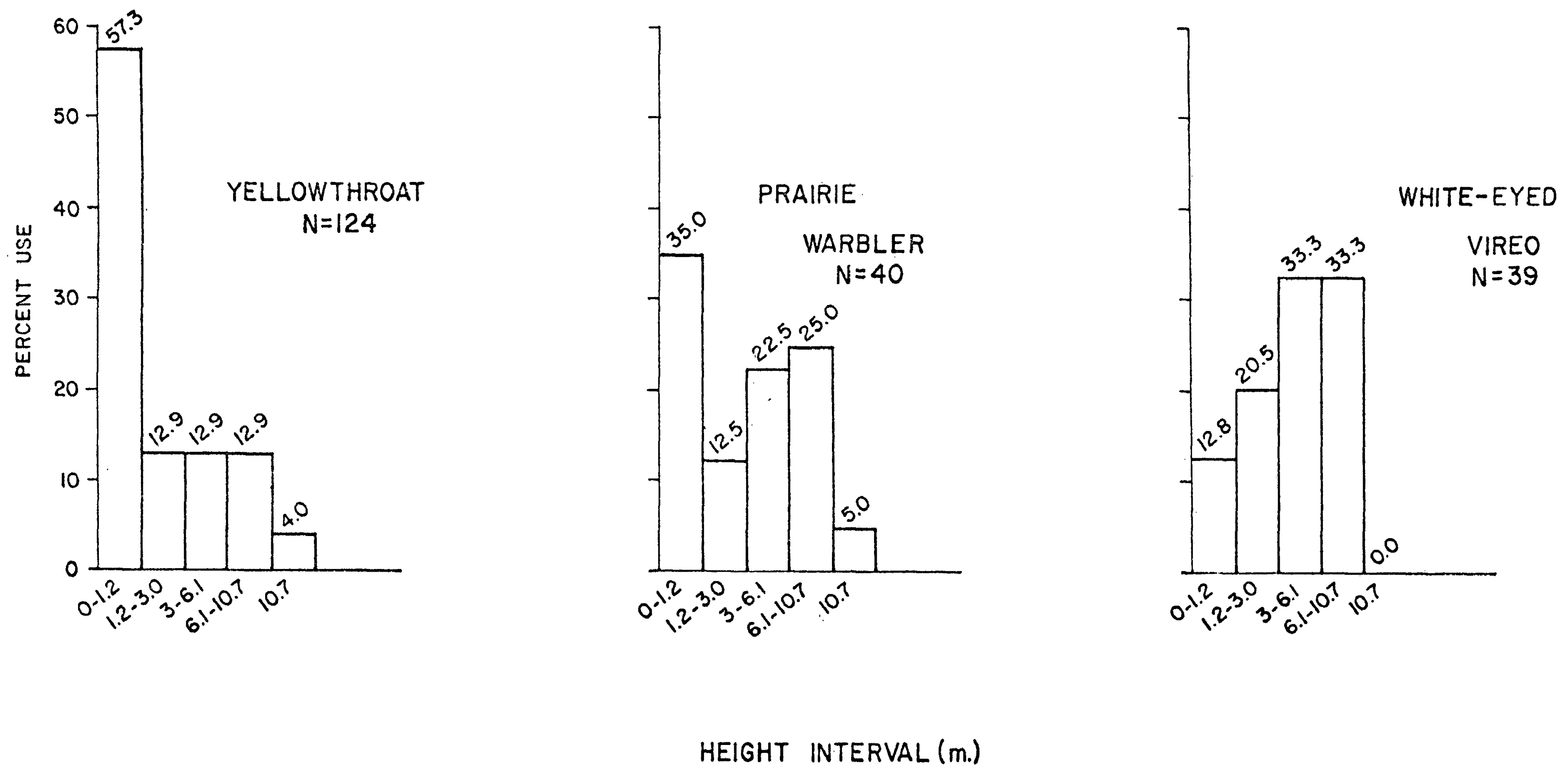

PERCENT USE
60
50
40
30
20
10
0
YELLOWTHROAT
N=124
57.3
12.9
12.9
12.9
4.0
PRAIRIE
WARBLER
N=40
35.0
12.5
22.5
25.0
5.0
WHITE-EYED
VIREO
N=39
12.8
20.5
33.3
33.3
0.0
0-1.2
1.2-3.0
3-6.1
6.1-10.7
10.7
HEIGHT INTERVAL (m.)

TABLE 2

MEAN HEIGHTS (IN M.) OF TREES IN WHICH BIRDS FORAGED.*

Species	Mean	s^2	N
Yellowthroat	7.0	184.90	64
Prairie Warbler	8.0	139.73	29
White-eyed Vireo	10.0	130.92	35

*Comparisons using the Student-Newman-Keuls test showed significant differences between each warbler and the vireo but not between the warblers.

TABLE 3

NICHE BREADTH VALUES FOR EACH SPECIES AND FORAGING DIMENSION, AND AVERAGE VALUE FOR EACH SPECIES.

Niche dimension	YT	PW	WEV
Foraging tactic	0.41	0.72	0.96
Perch size	0.78	0.94	0.74
Feeding zone	0.58	0.36	0.49
Vertical pos.	0.84	0.90	0.80
Horizontal pos.	0.81	0.83	0.95
Height interval	0.77	0.91	0.95
Tree height	0.83	0.90	0.80
Average	0.72	0.79	0.81

TABLE 4

FORAGING OVERLAP VALUES FOR SPECIES PAIRS.

Niche dimension	YT-PW	YT-WEV	PW-WEV
Foraging tactic	0.88	0.70	0.82
Perch size	0.70	0.47	0.72
Feeding zone	0.78	0.61	0.80
Vertical pos.	0.71	0.49	0.50
Horizontal pos.	0.72	0.87	0.69
Height interval	0.79	0.52	0.73
Tree height	0.66	0.46	0.76
Average	0.75	0.59	0.72

if use of each category were equitable. The niche breadth B, then, equals H'/H_{max}, and ranges between 0 and 1, with values representing specialized through generalized, respectively. Table 2 lists niche breadth values for each species and niche dimension, and gives the average niche breadth for each species.

Foraging overlap between pairs of species was calculated by ahe formula $C_{ab} = 1-\frac{1}{2}\Sigma|p_{ia}-p_{ib}|$ (Colwell and Futuyma 1971), where C_{ab} is the overlap between species A and B for use of a niche dimension, and p_{ia} and p_{ib} are proportions of foraging which occurred in category i of a niche dimension by species A and B, respectively. Overlap indices may range between 0 and 1, with 1 representing complete overlap between the two species in use of a particular niche dimension. Table 3 shows foraging overlap values for each pair of species and average overlap values for each niche dimension considered.

Foraging Behavior

Insectivorous passerine birds use a variety of foraging maneuvers which may be classified into several gross categories based on activity of the bird and on the positions of both bird and prey. Flycatchers (Family Tyrannidae) are named for their habit of feeding by flycatching (also called hawking), in which both predator and prey are in flight. Many of our more actively feeding warblers (e.g., the American Redstart and the Yellow Warbler) frequently forage by hovering like a hummingbird among leaves; those species also flycatch (Morse 1973). Vireos also hover (Williamson 1971). Gleaning, a more deliberate tactic, involves a search among leaves by a perched bird. Root (1967) describes another type, rushing, in the Blue-gray Gnatcatcher

Polioptila caerulea (Family Sylviidae), during which the birds attack stationary prey during a flight to another perch. The Yellowthroat, Prairie Warbler and White-eyed Vireo are all considered foliage gleaners, but upon closer observation subtler differences are noticed.

A study of Table 1 shows that the White-eyed feeds aerially to a significantly greater degree than the Yellowthroat. The categories "aerial" and "non-aerial" feeding could have been called "hovering" and "gleaning" except that differences in both aerial and non-aerial feeding existed between species such that the terms hovering and gleaning were not always appropriate. These differences were not amenable to statistical testing, but I feel that they are real and worthy of discussion.

Differences in non-aerial foraging behavior involved the degree of deliberateness of feeding, randomness of movements, the existence between the bird and the area searched for prey, and relatively inconspicuous movements of the body parts. It was possible to delineate the immediate foraging area of a feeding bird. Distinctions exist both in the size of this area and in the means by which birds searched it for food.

Prairie Warbler

The Prairie changes perches rapidly and often. While gleaning, birds may cover many twigs or branches by hopping in a pivoting motion from one to another, during which the bird's body oscillates from side to side. Prairies often search most of the smaller branches of a limb by pivoting, using branches and twigs as a ladder. In addition, they often flew, or used flight to aid in a non-pivot hop. When they did not use smaller limbs or twigs to complete searching the immediate area, they generally worked by sideways shifts along the limb. While gleaning Prairies usually flicked the tail such that the white tail spots were conspicuous. This behavior was often accompanied by vibration of the wings and high-pitched vocalizations.

The Prairie Warbler also used a less thorough method involving a descent which allowed incomplete coverage of a number of limbs.

In gleaning, the Prairie generally probed among leaves, although they were also seen peering into leaves that were out of reach. They usually maneuvered themselves as described so that they could glean with aminimum of complex body movements. Hard to reach prey were reached by hovering, or by more difficult contortions without leaving the perch. They generally accomplished the latter by stretching the neck and/or by bending the legs to reach leaves with the head and bill. On one occasion a bird leaned at right angle to the ground to forage in a spike of wild cherries (it was not eating cherries, however). Another bird fed once by hanging completely upside-down from a limb in the manner of titmice and chickadees. Another used its wings for non-flight elevation to reach leaves above it without leaving its perch.

Prairies foraged aerially 25% of the time. Aerial maneuvers were hovers and rushes. Hovers were active movements in which birds foraged among leaves, held aloft by rapid wing beats. Usually, the number of pecks at each hover ranged from one or two to five, but one fem ale hovered in herbaceous plants for about half an hour, gleaning intermittently. Hovers usually occurred in herbs or at the tips of twigs; occasionally Prairies were seen hovering inside margins of trees.

Rushes were usually preceded by a type of searching that can best be described as peering, during which the bird surveyed foliage from a distance well beyond its reach. After rushing, birds perched on a different limb. Rushing was rarer in the Prairie than hovering.

I noted no overall tendency in directionality in foraging Prairie Warblers. Many feeding maneuvers were aerial and thus unclassifiable in this regard. Gleaning seemed to occur in all directions. Birds were seen both ascending and descending. Some birds progressed proximally as they foraged, others moved distally. Prairies sometimes spiraled upwards on vertical limbs while feeding.

Yellowthroat

The Yellowthroat is a deliberate and thorough forager, with characteristic peculiarities in gleaning and aerial foraging. Differences in gleaning include greater use of herbaceous plants, systematic searching methods and directionality of gleaning. Yellowthroats also hover in a chracteristic manner.

Gleaning Yellowthroats introduced the bill into the foliage, whereas the other species peered more frequently. They rarely hover, but reach difficult prey by stretching the neck and body, and by extending the legs. Careful examination of most of the foliage along a limb allowed for a very systematic technique.

In the herbaceous zone, Yellowthroats often perched on a different plant species or type of perch than the area they were searching. This was especially evident in early spring when birds perched on the stem of the previous year's goldenrod to feed from a live goldenrod plant or from vetch. In later summer they perched on long stems of Johnson grass, which would bend under their weight, giving them access to another plant or to the ground.

Movement while gleaning was accomplished by short flights and deliberate hops and pivots, similar in character, but slower, than those of Prairies. Birds moved usually in a direction away from trunks of trees while feeding, and usually ascended. When in herbs, Yellowthroats ascended to a taller stem (where males would often sing), then descend, probably to feed, obscured by the foliage.

Hovering in Yellowthroats was quite different in nature from that in the other two species. They are less delicate and more deliberate than the Prairie, and less thorough, aiming for a target but once, hovering, then returning to a perch.

White-eyed Vireo

The White-eyed Vireo is usually called a foliage gleaner, probably because most of its searching time is spent at a perch, but it peers more than it gleans. In peering, birds scanned a large volume of foliage from a fair distance. They kept the body quite still, rotating or swiveling the head in a variety of planes to search a large area of foliage. Yellowthroats and Prairies used more finely-tuned tactics to examine a smaller area in detail. Peering usually preceded in-flight attacks, and about the only movements other than rotation of the head were changes of perch and the rush itself. Rushes occurred in two directions. White-eyeds often flew through a tree in a chord-like path across the perimeter of a tree. Smaller distances were travelled by pivoting or zig-zagging between branches, and often involved a vertical descent. During a rush, perch changes were often along an arc which included the site of attack.

Habitat Preferences

Ecological distinction between species may be determined in part by choice of habitat (Cody 1974). Kiester, Gorman and Arroyo (1975, after Rand 1964) use the term "structural niche" to describe a species' preference for a particular vegetational structure in its habitat. James (1971) and Whitmore (1975) used sophisticated statistical techniques to quantify and ordinate habitat preferences of various birds. Although habitats of the Yellowthroat, Prairie Warbler and White-eyed Vireo were not compared statistically in this study, it was possible to compare them qualitatively. For each feeding observation, the habitat was briefly described with regard to density of trees, density of underbrush, viny character, plant species and the like.

The most obvious difference was in the density of the vegetation of the area in which the three species usually fed. The White-eyed Vireo fed in the densest vegetation. Field observations contain numerous references to the White-eyed feeding in thickets of trees of heaven. Almost 80% off all vireo observations describe thick undergrowths of honeysuckle, grape and/or poison ivy. All three vines are common climbers throughout the sparsely wooded borders of the study area.

Yellowthroats fed in open areas with mainly herbaceous plants about 80% of the time. They perched on and fed in various composites (including daisy fleabane and various goldenrods), in grasses (including orchard grass and Johnson grass), and from vetch.

They also fed in vine-covered trees in edge areas, but were fairly restricted to open and sparsely wooded areas. Trees occurred within the open areas, and Yellowthroats fed from them, but they are rarer there, and vines are less dense on trees and the ground.

In general, the Prairie was intermediate between the White-eyed Vireo and the Yellowthroat in choice of habitat. They fed a third of the time in dense areas similar to the White-eyed, but overlapped more with the Yellowthroat, feeding twice as often in more open areas than in the denser habitats.

Measurements of Feeding Structures

The mean measurements of structures possibly related to foraging are given in Tables 5, 6 and 7 with their standard errors and sample sizes. All comparisons of means were significant ($P = 0.05$) except for two: culmen length between Yellowthroat females and White-eyed Vireos, and bill width between Prairie males and Yellowthroats.

Diets

Information from this study concerning the diets of the study species is very scarce. Data in the literature comes mainly from Bent's (1950, 1953) life history studies. This information is given in Appendix B.

TABLE 5

LENGTHS OF TIBIOTARSI AND TARSOMETATARSI OF YELLOWTHROATS, PRAIRIE WARBLERS AND WHITE-EYED VIREOS.* MEASUREMENTS IN MM.

	Tibiotarsus			Tarsometatarsus		
	Mean	S. E.	N	Mean	S. E.	N
YT	28.54	0.090	140	21.28	0.091	141
WEV	27.77	0.243	28	20.84	0.135	69
PW	25.68	0.288	15	18.29	0.156	58

*All differences significant (P=0.05 in Student-Newman-Keuls test)

TABLE 6

CULMEN LENGTHS, GAPE-TIP LENGTHS, BILL WIDTHS AND BILL HEIGHTS OF YELLOWTHROATS, PRAIRIE WARBLERS AND WHITE-EYED VIREOS.* MEASUREMENTS IN MM.

	Culmen length			Gape-tip length			Bill width			Bill height		
	Mean	S. E.	N	Mean	S. E.	N	Mean	S. E.	N	Mean	S. E.	N
YT	____	____	__	14.41	0.069	141	4.72	0.046	139	4.43	0.040	140
YT	11.76	0.169	76	____	____	__	____	____	__	____	____	__
YT	11.33	0.086	62	____	____	__	____	____	__	____	____	__
PW	10.06	0.078	58	12.58	0.117	58	____	____	__	4.17	0.055	56
PW	____	____	__	____	____	__	4.62	0.085	36	____	____	__
PW	____	____	__	____	____	__	5.03	0.095	22	____	____	__
WEV	11.30	0.098	70	15.87	0.121	69	6.30	0.052	70	5.19	0.049	66

*All comparisons revealed significant differences (P=0.05 in Student-Newman-Keuls test) except YT -WEV for culmen length and YT-PW for bill width.

TABLE 7

WEIGHTS, WING CHORD LENGTHS AND WING-TO-WEIGHT RATIOS OF YELLOWTHROATS, PRAIRIE WARBLERS AND WHITE-EYED VIREOS.*
WEIGHTS IN G: WING CHORDS IN CM.

	Weight			Wing chord			
	Mean	S. E.	N	Mean	S. E.	N	Wing/Wt.
YT	10.15	0.092	83	5.38	0.024	84	0.53
YT	9.58	0.116	70	5.07	0.026	72	0.53
PW	7.31	0.120	16	5.57	0.056	16	0.76
WEV	11.74	0.117	27	5.99	0.046	28	0.51

*all comparisons revealed significant differences (P=0.05 in Student-Newman-Keuls test).

DISCUSSION

The results of this study are in accord with current ecological theory. Differences in feeding strategies and morphologies exist between the study species which would lessen interspecific competition for food and allow coexistence.

In this study, ecological distinction between species is expressed mainly by differential foraging tactics, unequal use of herbaceous plants for foraging, different perch size preferences and choice of different feeding zones. Greatest divergence was observed between the Yellowthroat and the White-eyed Vireo; greatest similarity existed betwwen the Yellowthroat and the Prairie Warbler.

No difference was noted in choice of horizontal zones, an important mechanism of ecological segregation in other guilds (Morse 1967, 1968, 1973; MacArthur 1958). This may be related to the growth form of many trees in the study area. Morse (1968) and MacArthur studied congeneric warblers which inhabit coniferous forests, whose structures exhibit the most noticeable diversity along a horizontal plane. Generally, non-coniferous trees of early successional stages lack distinct horizontal zonation. The study area represented such a situation. Since foliage configurations do not exhibit well-defined horizontal zones, it would be more likely that birds of such environments would differ ecologically in other respects.

Various biologists have correlated morphologies of feeding structures with both foraging behavior and diet in birds. The measurements of structures important in foraging in the Yellowthroat, Prairie Warbler and White-eyed Vireo reveal adaptations which would partition the habitat and the food supply.

The bill is the structure most obviously related to food. Four measurements of the bill were made: culmen length, gape-tip length, bill height and bill width. The bill with the largest area uncovered by feathers (i.e., the culmen) would seem better suited for probing among leaves. Of the 3 species, the Yellowthroat has the longest culmen, which may be a specialization for gleaning in herbs where leaves are closely spaced.

When the gape-tip length is considered, however, the bill of the White-eyed Vireo is the longest. Because the gape-tip length approaches the length of the complete skeletal structure of the bill more closely than does culmen length, it is probably a better index of bill size. The gape-tip length may be larger in the vireo as a function of total body size. In addition, differences may be related to the maximum size of food items (Newton 1967), since bill size would partially determine upper limits of prey size. Allaire and Fisher (1975) found positive correlation between bill size and seed size in syntopic Bachman's Sparrow (*Aimophila aestivalis*), Field Sparrow (*Spizella pusilla*) and Chipping Sparrow (*Spizella passerina*). In addition to the larger gape-tip length in the White-eyed Vireo, greater bill height and width would tend to admit larger insects.

Williamson (1971) feels that flattening of avian bills is an adaptation to the aerial mode of foraging. A wide bill would help funnel insects into the mouth when they are caught on the wing. The bill of the White-eyed Vireo is obviously flattened dorsoventrally, and bill height and width data from Prairie Warblers also reveal some flattening. Both species have been shown to feed aerially often, and their bills seem to be adapted to this method of feeding. The Yellowthroat bill, however, is slimmer, with no flattening.

Adaptation to aerial foraging is exhibited in the wing-to-weight ratio of the Prairie Warbler. Wing-to-weight ratios (Table 6) show that much of the differences in wing chord lengths probably relate to body size, but the Prairie, the smallest of the three species studied, has the largest wing-to-weight ratio. This suggests that selection has increased wing size in this species as an adaptation to sustained hovering (Williamson 1971). However, this does not explain the small ratio of the White-eyed Vireo. One would expect this species, which often feeds by rushing or hovering, to have a larger wing-to-weight ratio than the more sedentary Yellowthroat, but it does not. Perhaps a measure of wing area, rather than of length, would be more informative.

Hespenheide (1971) reported a direct relationship between body weight and prey size. The White-eyed Vireo was among the species he studied. Based on his results prey size should increase in the following order in the species examined here: Prairie Warbler, Yellowthroat, White-eyed Vireo.

Osterhaus (1962) suggests that the longer legs of the Ovenbird relative to those of other warblers, are probably an adaptation for movement through the debris of the forest floor, where the species characteristically forages. The longer legs of the Yellowthroats could serve a similar function, since this is the only species in the present study which regularly fed on the ground. The leg bones of the White-eyed Vireo, longer than the Prairie Warbler's, might permit freedom of movement when feeding in dense epiphytic vines. Longer legs would provide leverage for gleaning in hard to reach areas, as on a vertical stem, which the Yellowthroat does frequently.

THE NICHE: VARIABILITY AND BREADTH

When one views the niche as a phenotype, one admits that ecology has a genetic basis, and is therefore subject to evolution. A species population possesses a set of ecological requisities which could be placed on a continuum between the extremes of complete generalism on one hand, and complete specialization on the other. A species in a hypothetical constant environment, one with unchanging vegetational structure, fixed species composition and invariable physical conditions, would evolve an "optimal" niche. However, no environment approaches this degree of stability. Because of evolution and the inherent variability of the niche (as of all genetic characters), the optimum shifts as the environment changes.

Smith and Sweatman (1974) add that the optimum niche will never be realized in a natural situation because evolution is a result of a number of "selective compromises" between optimization of both ecological and non-ecological characteristics. MacArthur and MacArthur (1961) suggest that a species will become specialized only to the extent that the energy gained in feeding is greater than the energy spent. Royama (1971) also emphasizes energy expenditure as a limiting factor to the degree of specialization a species can afford to attain.

For example, MacArthur and MacArthur (1961) have found bird species diversity to be correlated with foliage height diversity, but not with plant species diversity. They explained that specialization to a particular plant species in an environment with highly diverse vegetation would be a disadvantage, since much energy would be wasted in the search for a plant of the proper species. Extreme specialization to a specific habitat is partially responsible for the plights of such birds as the Ivory-billed Woodpecker and the Kirtland's Warbler at the present time.

The environment of the study area is patchy and heterogenous with regard to plant species. Because the field is of young successional age, it is unstable, and organisms that inhabit such communities generally have broad ecological capabilities, that is, are relatively unspecialized (Odum 1971). Niche breadth values for the Yellowthroat, Prairie Warbler and White-eyed Vireo are large (averaging 0.70, 0.79 and 0.79, respectively; see Table 3), which means that they are foraging generalists. One problem that individuals of these species must cope with is a rapidly changing environment. Birds of each of the three study species regularly return to the same breeding ground for 3 to 4 years in a row, a period in which their habitat can undergo extensive modification by succession. For a species to survive, it must retain enough ecological variability to be able to continue to utilize the changing habitat. A broad niche is an advantage to a species living in a changing environment (Levins 1968).

It is impossible for two coexisting species to survive if their ecologies are identical. Something, then, must act to place upper limits on the degree of generalism, and this is probably competition. Food is more often limiting than not. Therefore, when food is limiting, ecological requirements of coexisting species must be different. Ecological divergence is a result of competition, probably more severe in the past, but still a factor at present. Any ecological difference which would allow division of a limiting resource would ease interspecific competition.

There is indirect evidence to support the idea that competition and a limiting food supply result in ecological specialization. Kendeigh (1947) and Zach and Falls (1975) studied bird communities during outbreaks of the spruce budworm (*Choritoneura fumiferana*) in Canadian coniferous forests. Zach and Falls dealt with the Ovenbird's (*Seiurus aurocapillus*) response to the oversupply, and found that during such periods, feeding habits changed considerably. Normally the birds feed almost entirely on the ground, but when outbreaks of the budworm occur, they expand their feeding area throughout the forest, to take advantage of the abundant food.

Morse (1967) showed that ecological distinctions between the Brown-headed Nuthatch (*Sitta pusilla*) and the Pine Warbler (*Dendroica pinus*) may break down when pine seeds are above average in abundance. In addition, both species fed in different areas when feeding separately than they did when in mixed flocks.

It would be informative to study the foraging of the Yellowthroat, Prairie Warbler and White-eyed Vireo over a longer period of use of the same area, in relation to food supply and in situations where all three species are not present to learn how much variability exists in their ecology. The present study indicates that each species is fairly broad in foraging ecology, and that considerable overlap exists between them. But each species is sufficiently specialized in morphology, habitat and behavior that their ecologies diverge enough to relieve some competition and allow coexistence.

APPENDIX A

RESULTS OF CHI-SQUARE TESTS OF INDEPENDENCE BETWEEN SPECIES PAIRS FOR FREQUENCY USE OF VARIOUS CATEGORIES OF SIX NICHE DIMENSIONS. (*SIGNIFIES P>0.05, NOT SIGNIFICANTLY DIFFERENT)

	SPECIES PAIR		
Niche Dimension	YT-PW	YT-WEV	PW-WEV
Tactic			
χ^2	3.841	3.841	3.841
G	3.934	18.202	3.299
P	P<0.05	P<0.005	0.05<P<0.10
Perch			
χ^2	18.548	18.548	11.143
G	54.562	37.443	10.308
P	P<0.005	P<0.005	0.005<P<0.05
Feeding Zone			
χ^2	11.070	16.750	15.086
G	8.202	33.494	13.258
P	*P<0.5	P<0.005	0.01<P<0.025
Vertical Zone			
χ^2	11.070	16.750	16.750
G	12.390	45.708	26.810
P	P<0.05	P<0.005	P<0.005
Horizontal Zone			
χ^2	9.488	9.488	9.488
G	9.156	1.781	6.548
P	*P<0.1	*P<0.9	*P<0.5
Height Intervals			
χ^2	9.488	9.488	9.488
G	7.415	32.163	9.022
P	*P<0.5	P<0.005	*P<0.1

APPENDIX B

DIETS

Bent (1953) reports that the Yellowthroat eats beetles, grubs, lepidopteran adults and larvae, ants, spiders, plant lice and leafhoppers. He cites other references which mention diets. Forbush (1907, in Bent 1953) stated that the Yellowthroat was one of the gipsy moth's main predators in areas where the insect is common. One bird was seen to eat 52 larvae of that species. Forbes (1883, in Bent 1953) examined 3 Yellowthroat guts and found that 80% of all food items were cankerworms and other types of larvae. Beetles made up 8%, and gnats 4%, of the diet. Henderson (1934, in Bent 1953) found 8 locusts in one stomach. King (from Butler 1898, in Bent 1953) found that one bird had eaten 16 caterpillars, 6 dragonflies, 3 each of moths, flies, wasps, beetles and spiders, 2 each of grasshoppers, hemipterans and insect eggs, and one leaf hopper. Chapman (1907) cites Forbush (1900) who saw a Yellowthroat eat 89 aphids in one minute.

In the present study, birds were observed carrying or swallowing food items of various kinds. I saw Yellowthroats with the following items during the study: 7 green larvae (probably lepidopteran), one white larva (possibly a beetle larva), one lacewing, 2 grasshoppers, 3 leafhoppers (at the same time) and a wild cherry. Foliage in which birds had fed revealed a small beetle, lepidopteran larvae, aphids and leafhoppers. After a male fed on a cracked limb of a peach tree, I found ants feeding on the exuding sap.

Even less information is available concerning the Prairie Warbler's diet than that of the Yellowthroat; again it is necessary to rely on Bent's life history. He cites a study by Wetmore, who analyzed contents of 15 stomachs, and found the food to be completely animal matter (Bent 1953). The food was about 44% hemipterans, 16% beetles, 4% hymenopterans, less than one percent flies, 20% spiders and 4% miscellaneous. Forbush (1929, in Bent 1953) analyzed an undetermined number of stomachs and found that they contained mainly plant lice, grasshoppers and locusts. I was able to determine only one food item which a Prairie Warbler ate, a slender larva.

Bent (1950) summarizes information on the diet of the White-eyed Vireo. Chapin (1925, in Bent 1950) studied the food in 221 stomachs and determined that the diet was about 90% arthropods. The vireo feeds regularly on hemipterans, beetles (about 13%), hymenopterans and dipterans (12%), grasshoppers (13%) and spiders (4%). Lepidopteran adults and larvae comprise about a third of the diet. One stomach contained bones of a chameleon. The amount of vegetable food eaten varies with the time of the year. More plant matter is used in late summer and in winter. Martin _et als_. (1951) list caterpillars, moths, hemipterans, beetles, ants, wasps, bees, flies and spiders as main animal foods of the White-eyed Vireo. Its vegetable foods include mainly berries of the following plants: wax myrtle, blackberry, holly, Virginia creeper, poison ivy, elderberry and sassafras.

I saw a White-eyed Vireo swallow a one-inch green larva lengthwise, in stages. Birds were seen carrying one brown larva, 3 green larvae and one lacewing. After a bird rushed the end of a limb, two large leafhoppers flew from the plant.

LITERATURE CITED

Allaire, P. N. and C. D. Fisher. 1975. Feeding ecology of three resident sympatric sparrows in eastern Texas. Auk. 92: 260-269.

Baldwin, S. P., H. C. Oberholser and L. G. Worley. 1931. Measurements of birds. Sci. Publ. Cleveland Mus. Natur. Hist. 2: 1-165.

Barr, A. J. and J. H. Goodnight. 1972. Statistical analysis system. Student Supply Store, North Carolina State University, Raleigh.

Bent, A. C. 1950. Life histories of North American wagtails, shrikes, vireos, and their allies. U. S. Natl. Mus. Bull. 197.

Bent, A. C. 1953. Life histories of North American wood warblers. U. S. Natl. Mus. Bull. 203.

Chapman, F. M. 1907. The warblers of North America. D. Appleton, New York, 386 p.

Cody, M. L. 1974. Competition and the structure of bird communities. Princeton University Press, Princeton, 318 p.

Colwell, R. K. and E. R. Fuentes. 1975. Experimental studies of the niche. Ann. Rev. Ecol. Syst. 6: 281-310.

Colwell, R. K. and D. J. Futuyma. 1971. On the measurement of niche breadth and overlap. Ecology 52: 567-576.

Darwin, C. 1859. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London, 488 p.

Ellis, J. E. and M. Travis. 1975. Comparative aspects of foraging behaviour of pronghorn antelope and cattle. J. Appl. Ecol. 12: 411-420.

Gaffney, P. M. 1975. Roots of the niche concept. Am. Nat. 109: 490.

Gause, G. F. 1934. The struggle for existence. Williams & Wilkins, Baltimore.

Gibb, J. A. 1954. Feeding ecology of tits, with notes on Treecreeper and Goldcrest. Ibis 96: 513-543.

Gibb, J. A. 1960. Populations of tits and Goldcrests and their food supply in pine plantations. Ibis 102: 163-208.

Giles, R. H., Jr. 1974. The Williamsburg environmental system. Richmond. 63 p.

Hartley, P. H. T. 1953. An ecological study of the feeding habits of the English titmice. J. Anim. Ecol. 22: 261-288.

Hespenheide, H. A. 1971. Food preference and the extent of overlap in some insectivorous birds, with special reference to the Tyrannidae. Ibis 113: 59-72.

Hogstad, Olav. 1976. Sexual dimorphism and divergence in winter foraging behavior of Three-toed Woodpeckers Picoides tridactylus. Ibis 118: 41-50.

James, F. C. 1971. Ordinations of habitat relationships among breeding birds. Wilson Bull. 83: 215-236.

Johnson, L. K. and S. P. Hubbell. 1975. Contrasting foraging strategies and coexistance of two bee species on a single resource. Ecology 56: 1398-1406.

Johnston, D. W. 1971. Niche relationships among some deciduous forest flycatchers. Auk 88: 796-804.

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.

Kendeigh, S. C. 1947. Bird population studies in the coniferous forest biome during a spruce budworm outbreak. Ont. Dep. Lands For., Div. Res., Biol. Bull. 1.

Kiester, A. R., G. C. Gorman and D. C. Arroyo. 1975. Habitat selection behavior of three species of Anolis lizards. Ecology 56: 220-225.

Lack, D. 1954. The natural regulation of animal numbers. Oxford University Press, New York.

Lawlor, R. and J. M. Smith. 1976. The coevolution and stability of competing species. Amer. Nat. 110: 79-99.

Levins, R. 1968. Evolution in changing environments: some theoretical explorations. Princeton University Press, Princeton, 120 p.

MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39: 599-619.

MacArthur, R. H. and J. W. MacArthur. 1961. On bird species diversity. Ecology 42: 594-598.

Martin, A. C., H. S. Zim and A. L. Nelson. 1951. American wildlife and plants: A guide to wildlife food habits. Dover Publications, Inc., New York, 500 p.

Mendelson, J. 1975. Feeding relations among species of Notropis (Pisces: Cyprinidae) in a Wisconsin stream. Ecol. Monogr. 45: 199-230.

Morse, D. H. 1967. Foraging relationships of Brown-headed Nuthatches and Pine Warblers. Ecology 48: 94-103.

Morse, D. H. 1968. A quantitative study of foraging of male and female spruce-woods warblers. Ecology 49: 779-784.

Morse, D. H. 1973. The foraging of small populations of Yellow Warblers and American Redstarts. Ecology 54: 346-355.

Newton, I. 1967. The adaptive radiation and feeding ecology of some British finches. Ibis 109: 33-98.

Odum, E. P. 1971. Fundamentals of ecology, 3d ed. W. B. Saunders Co., Philadelphia, 574 p.

Orians, G. H. and H. S. Horn. 1969. Overlap in foods and foraging of four species of blackbirds in the potholes of central Washington. Ecology 50: 930-938.

Osterhaus, M. B. 1962. Adaptive modifications in leg structure of some North American warblers. Am. Midl. Nat. 68: 474-486.

Pulliam, H. R. and F. Enders. 1971. The feeding ecology of five sympatric finch species. Ecology 52: 557-566.

Root, R. B. 1967. The niche exploitation pattern of the Blue-gray Gnatcatcher. Ecol. Monogr. 37: 317-348.

Royama, T. 1966. Factors governing feeding rate, food requirement and brood size of nestling Great Tits Parus major. Ibis 108: 313-347.

Schoener, T. W. 1967. The ecological significance of sexual dimorphism in size in the lizard Anolis conspersus. Science 155: 474-477.

Schoener, T. W. 1975. Presence and absence of habitat shift in some widespread lizard species. Ecol. Monogr. 45: 233-258.

Selander, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. Condor 68: 113-115.

Sokal, R. R. and F. J. Rohlf. 1969. Biometry: the principles and practice of statistics in biological research. W. H. Freeman, San Francisco, 776 p.

Smith, J. N. M. and H. P. A. Sweatman. 1974. Food-searching behavior of titmice in patchy environments. Ecology 55: 1216-1232.

Verbeek, N. A. M. 1975. Comparative feeding behavior of three coexist-in Tyrannid flycatchers. Wilson Bull. 87: 231-240.

Whitmore, R. C. 1975. Habitat ordination of passerine birds of the Virgin River valley, southwestern Utah. Wilson Bull. 87: 65-74.

Williamson, P. 1971. Feeding ecology of the Red-eyed Vireo (Vireo olivaceus) and associated foliage-gleaning birds. Ecol. Monogr. 41: 131-152.

Wood, Merrill. 1969. A bird-bander's guide to determination of age and sex of selected species. College of Agriculture, the Pennsylvania State University, University Park. 181 p.

Zach, R. and J. B. Falls. 1975. Response of the ovenbird (Aves: Parulidae) to an outbreak of the spruce budworm. Can. J. Zool. 53: 1669-1672.

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