HABITAT RELATIONS OF THE PARULIDAE DURING SPRING MIGRATION

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THIS study was designed to evaluate the habitat relations and habitat-niche usage of the warblers (Parulidae) in the Raleigh, North Carolina region during the spring migratory period. Although the general pattern of warbler migration has been studied extensively and the timing of first arrivals and peaks established for most species, no detailed studies have been made on habitat associations during migration. This paucity of information appears to be due primarily to the difficulty of measuring populations during migration and to the general belief that birds are much less selective of habitat during migration than in the nesting and winter seasons. Most habitat association studies have been made during the nesting season and in winter when populations are more stable.

Many warblers have been shown to have clearly defined behavioral adaptations that limit them to particular habitats or parts of habitats on the nesting grounds (MacArthur, 1958). Further it has been demonstrated that the functional anatomy of the legs of some warblers makes possible specific adaptations for particular methods of feeding (Osterhaus, 1962). As these adaptations do not change during migration, some degree of habitat selection should also operate at this time. Some lessening of the strength of selection can easily be understood, as the preferred habitats may be absent from portions of the migratory pathway. Also the internal pressures of migration may result in lessened consideration of all but the most urgent physiological needs. Most small passerine birds are nocturnal migrants and spend the daylight hours feeding. During these stopover periods each species would be expected to select those conditions most closely approximating its optimum, where it is able to feed most effectively.

Habitat is generally defined as the place where an organism lives (Odum, 1959) and is usually described at the level of the major plant community, such as deciduous forest. It has long been realized that birds are associated with particular habitats, but only recently have detailed studies been undertaken to evaluate habitat selection among birds. Many life history studies were conducted in the early 1900s, but these usually allude only briefly, if at all, to the bird's habitat. A major exception to this, concerning warblers, is Chapman's "The warblers of North America" (1907), which refers generally to the habitat of each species on the nesting grounds and in a few instances mentions the habitat frequented during migration. Stewart and Robbins (1958) also give a systematic but limited account of the habitat occurrences of warblers during migration. Recently habitat

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associations have been stressed in many papers dealing with habitat during the nesting season (Stewart, 1943; Kendeigh, 1945a, 1945b; MacArthur et al., 1962; Morse, 1967).

As researchers have developed more sophisticated ways to analyze the habitat preferences of birds they have become interested in placing the species into smaller categories than habitat. Thus the past few years have seen a renewal of interest in the niche concept as initially proposed by Grinnell (1917, 1924, 1928), and later given two different meanings by subsequent workers, either as the spatial unit as proposed by Clements and Shelford (1939) or the functional unit of Elton (1927), Hutchinson (1957), Odum (1959), and others. In this paper the niche of a species refers to its occurrence in subunits of habitat and is called the habitat-niche.

I found no complete nesting habitat-niche descriptions in the literature for any warbler species, and only very general statements for most species. A few recent studies give directly comparable information on one or more parts of the habitat-niche during the nesting period. Generally these refer to a preference for stratum and seldom indicate more precise placement except in the case of MacArthur (1958) and Morse (1967). Height of song perches is also mentioned for a few species and a preference noted for song perches above the general foraging level (Stewart, 1953).

METHODS

The study area occupied a circle about 20 miles in diameter with Raleigh, North Carolina at its center. Typical of the lower Piedmont and upper Coastal Plain, the fall line bisected it just east of Raleigh. Most of the study sites were beyond the influence of urbanization, but one was within the city limits of Raleigh.

Much farm land in North Carolina has been abandoned since the early 1900s, and all stages of old field succession (Oosting, 1942) were present within the study area. Generally the uplands consisted of pine or oak-hickory communities and the bottomlands of lowland deciduous forest communities. Most of these forest tracts were small and quite dissected, but several tracts of both upland and lowland secondary growth were rather extensive.

The field analyses were begun in March in 1962 and 1963, as daily censuses along established transects, and were continued through June to allow comparison of the habitat associations of the summer-resident warblers during migration and while nesting. The use of transects allowed coverage of most of the forest habitats in a single morning, which a series of plots, each in a different vegetative type, would not have done.

Each census consisted of a slow walk along a meandering transect, beginning at daylight and continuing through several habitats until bird activity began to lessen 3 or 4 hours later. The width of the transects varied according to the observability of the species. Observations were recorded in a coded system on a standard data sheet. Time spent in each habitat was recorded to permit the numbers of birds to be converted to birds per hour.

I censused 10 transects in 1962 and 9 in 1963, visiting each about every 10 days, with the major habitat types being repeated almost daily. The results were based on a

total of 270 hours of observation during the spring migration periods and 110 hours during the postmigratory periods.

Each warbler recorded was located when first identified as precisely as possible and its position in the vegetative substrate and height above ground were recorded. The importance placed on the detailed records of individual birds resulted in fewer observations but in more information on each than is usually obtained in "singing male" or "nest" counts where presence is often the only information presented.

The seven forest types included in the transects were: flood plain forest (14 units sampled); pine forest (10 units); oak-hickory forest (7 units); pine-hardwoods forest (6 units); dry thicket (4 units); wet thicket (3 units); and beech forest (1 unit). Within the framework of the sampling scheme (transects through several forest types) it was impossible to sample these habitats equally. Therefore the more widespread forest types were sampled on as many transects as possible and the less common types were sampled whenever it was possible to include them within transects.

Although the many variables in the sampling procedures made any sophisticated scheme of statistical analysis unfeasible, the warblers' habitat associations were tested by the standard analysis of variance test when numbers of observations were adequate and when the birds occurred regularly in samples of more than one habitat. The values tested were average numbers of birds per hour for each habitat. A habitat type was not considered adequately represented to warrant a test unless a species occurred in more than 40 per cent of the sample units of the habitat. No test to indicate selection was considered necessary if the majority of the individuals of a species occurred in a single habitat type. Evaluations of the results were made at the 5 per cent level of significance.

When the analysis of variance indicated that a difference existed in selection of habitats, Duncan's multiple range test was applied (Steele and Torrie, 1960) to compare all possible pairs of habitats and determine the actual points of difference in selection.

The placement of warblers in subunits of habitat could not be tested statistically because of the manner in which the data were taken and the low numbers in most sample units. Therefore the occurrence of species in these categories was compared by frequency of occurrence of each species. Thus only the occurrence of each species in subunits is indicated rather than actual selection.

Bird names follow the fifth edition of the American Ornithologists' Union's "Check-list of North American birds" (A.O.U., 1957).

Results

Regular daily censuses began the first week of April and continued through June. No massive waves of warblers occurred either year, but the birds passed steadily throughout the migratory period. The buildup and decline of particular species were obvious in some cases, but in others were difficult to determine. The end of the migration was signaled by the departure of the last Blackpoll Warblers during the last week of May in 1962 and the first week of June in 1963. An average of 11.1 warblers per hour was recorded in 1962 for a total of 1,460 observations. In 1963 I recorded 13.7 birds per hour with a total of 1,958 individual observations. This gave a total of 3,418 warblers for which some information on habitat association was determined.

TABLE 1
HABITAT SELECTION BY WARBLERS[1]

Warbler species	Total obs.	Average number of birds per hour in habitats where an analysis of variance was not necessary to indicate habitat preference	Average number of birds per hour in habitats where an analysis of variance was necessary to indicate habitat preference
A. SPRING MIGRATION PERIOD			
		PF PH OH DT BF FF WT	
Yellow	51	0 0 0 0 0 0.07 3.54	
		PF PH OH BF DT WT FF	
Prothonotary	64	0 0 0 0 0 0.08 0.70	
		DT PF PH WT BF OH FF	
Canada	13	0 0 0 0 0 0.04 0.13	
		DT BF PH PF OH FF WT	
N. Waterthrush	26	0 0 0 0 0.04 0.21 0.69	
		DT WT PH PF OH	FF BF
La. Waterthrush	70	0 0 0 0.01 0.09	0.67 1.63
		DT PF OH PH WT	BF FF
Black-t. Blue	60	0 0 0.03 0.07 0.08	0.27 0.54
		DT WT BF OH FF	PH PF
Pine	70	0 0 0 0.09 0.37	0.75 1.86
		BF OH PF PH	FF WT DT
Yellow-b. Chat	77	0 0 0.11 0.30	0.15 2.00 4.48
		BF OH WT PH	FF PF DT
Prairie	112	0 0.13 0.48 0.97	0.14 1.09 7.58
		DT WT	FF BF PH OH PF
Ovenbird	145	0 0	0.28 0.82 1.55 1.62 1.75
		BF PH	PF OH FF DT WT
Yellowthroat	195	0 0.08	0.19 0.19 1.55 2.00 3.28
		DT WT	PF PH OH FF BF
Parula	199	0 0	0.36 1.09 1.19 1.46 3.27
		DT WT OH PH	FF PF BF
Yellow-throated	44	0 0 0.04 0.30	0.15 0.64 0.82
		DT WT BF	PH PF FF OH
Hooded	243	0 0 0	1.42 1.54 1.60 1.98
		DT WT PF	PH FF OH BF
Kentucky	68	0 0 0.11	0.37 0.48 0.82 1.09
		DT BF PH	PF FF OH WT
Blackpoll	136	0 0 0.07	0.16 0.47 1.13 1.31
		DT PF WT	OH PH BF FF
Am. Redstart	232	0 0.14 0.56	0.66 0.77 1.63 1.73
		DT PH	PF BF FF WT OH
Black-and-white	98	0 0.60	0.26 0.54 0.60 0.60 0.78
		WT	DT PF FF PH OH BF
Myrtle	295	0.64	0.78 0.91 1.37 2.23 2.81 4.36

TABLE 1—*Continued*

Warbler species	Total obs.	Average number of birds per hour in habitats where an analysis of variance was not necessary to indicate habitat preference	Average number of birds per hour in habitats where an analysis of variance was necessary to indicate habitat preference
B. POSTMIGRATORY PERIOD			
Yellow	16	DT 0 BF 0 PF 0 PH 0 OH 0 FF 0 WT 4.08	
Prothonotary	35	DT 0 BF 0 PF 0 PH 0 OH 0 WT 0 FF 1.44	
Prairie	40	OH 0 BF 0 FF 0.21 WT 0.26 PF 0.59 PH 1.00 DT 4.55	
La. Waterthrush	18	DT 0 WT 0 PF 0 PH 0 OH 0 BF 0.70 FF 0.70	
Pine	25	DT 0 WT 0 BF 0 FF 0 OH 0	PH 0.94 PF 2.44
Am. Redstart	62	DT 0 WT 0 PF 0 OH 0.20 PH 0.43	BF 1.41 FF 1.81
Parula	27	DT 0 WT 0 PF 0.20 OH 0.79	PH 0.35 FF 0.52 BF 2.85
Ovenbird	33	DT 0 WT 0 FF 0 OH 0.34	BF 0.70 PF 1.36 PH 1.68
Yellowthroat	58	BF 0 PF 0.10 OH 0.20 PH 0.43	FF 0.54 DT 2.59 WT 2.89
Kentucky	36	DT 0 WT 0 PF 0.39	OH 0.46 PH 0.55 BF 0.70 FF 0.85
Yellow-b. Chat	41	PF 0 BF 0 OH 0.20	FF 0.37 PH 1.11 WT 2.92 DT 3.96
Hooded	89	DT 0 WT 0	OH 0.95 PF 1.37 FF 1.76 BF 2.11 PH 3.19

[1] An analysis of variance was conducted only when habitat preferences were not obvious i.e. the species occurred in more than 40 per cent of the sample units of more than one habitat type. Duncan's multiple range test was used to determine the points of difference when the analysis of variance indicated that there were differential preferences among a group of habitats. A dotted line was drawn beneath all habitats in which the species occurred in less than 40 per cent of the sample units, thus rendering an analysis of variance unnecessary. A solid line was drawn beneath all habitats tested by the analysis of variance and found to show no significant differences in preferences. Any two means tested by the analysis of variance not underlined by the same solid line are significantly different at the 5 per cent level. The order of species in this table is a qualitative effort to demonstrate the general trend from more selective to less selective. The habitat abbreviations are: PH = pine-hardwood forest, PF = pine forest, BF = beech forest, OH = oak-hickory forest, FF = floodplain forest, WT = wet thicket, DT = dry thicket.

HABITAT SELECTION

Table 1 presents the major evaluation of the habitat selection of warblers by species. This table contains several kinds of information. For each species the results of the analysis of variance between habitats are presented when such analyses were justified and needed. The total number of observations upon which the evaluations were based is also listed. This

varies considerably, and the reliability of the statements about each species probably varies with the number of birds seen as well as with the number of sample units of each habitat utilized.

In Table 1 the coded habitat designations always proceed from the habitats with the lowest numbers of warblers per hour on the left to those with the highest numbers of warblers per hour on the right. This was necessary to permit using Duncan's multiple range test. In cases where no analysis of variance was conducted, the basic data are presented in the same manner, so that comparisons between species and habitats could be made directly from the number of birds observed per hour.

During the migratory period four species of warblers (Prothonotary, Yellow, Canada, and Northern Waterthrush) were so selective that no test was necessary to demonstrate strong habitat preference (Table 1). These were usually found regularly in only one or two habitats.

All the remaining species except the Myrtle Warbler indicated some selection by their failure to occur in all habitat types. The Magnolia Warbler occurred in several habitats but did not occur in 40 per cent of the sample units of any habitat, and thus was not suitable for testing by the analysis of variance. The remaining 15 species occurred with enough frequency in more than one habitat to necessitate testing. The test showed that the Myrtle Warbler indicated no selection among the six habitats tested. The Parula Warbler, Pine Warbler, Prairie Warbler, Ovenbird, Yellowthroat, and Yellow-breasted Chat, in addition to failing to occur in some of the available habitats, demonstrated further selection among the habitats in which they occurred regularly. Duncan's multiple range test showed that the Black-and-white Warbler, Yellow-throated Warbler, Blackpoll Warbler, Kentucky Warbler, Hooded Warbler, Black-throated Blue Warbler, Louisiana Waterthrush, and American Redstart, while indicating some selection by their absence from certain habitats, made no selection for particular habitats within the groups in which they frequently occurred.

The Black-and-white Warbler, Myrtle Warbler, Yellow-throated Warbler, Blackpoll Warbler, Kentucky Warbler, and American Redstart occurred commonly in most forest habitats. The Prothonotary Warbler, Black-throated Blue Warbler, and Canada Warbler generally selected floodplain forests, while the Pine Warbler was seldom found away from pine forests. The Yellow Warbler indicated strong preference for wet thickets, while the Prairie Warbler selected dry thickets, although occurring occasionally in several other types. Northern Waterthrushes, Yellowthroats, and Yellow-breasted Chats were usually found in both wet and dry thickets. The Parula Warbler, while occurring in several habitats, showed a preference for beech forest, while the Louisiana Waterthrush

TABLE 2

RELATIONSHIPS BETWEEN OBSERVATIONS OF WARBLERS IN STRATA AND HABITAT-NICHES DURING THE SPRING MIGRATION[1]

Species	Strata and habitat-niches									
	Canopy					Low tree				
	Top of crown	Inner crown	Lower crown	Bole	Total %	Top of crown	Inner crown	Lower crown	Bole	Total %
Black-and-white	6.2	6.2	2.5	39.4	54.3	2.5	7.4	6.2	29.6	45.7
Prothonotary	2.3	11.6	4.7	–	18.6	9.3	14.0	30.2	–	53.5
Worm-eating	–	–	–	–	–	–	33.3	22.2	11.1	66.6
Blue-winged	12.5	12.5	–	–	25.0	12.5	25.0	12.5	–	50.0
Parula	24.6	19.6	7.3	–	51.5	17.4	21.7	6.5	–	45.6
Yellow	7.9	2.6	–	–	10.5	34.2	42.1	–	–	76.3
Magnolia	–	4.6	–	–	4.6	–	59.1	18.2	–	77.3
Cape May	14.3	57.1	–	–	71.4	14.3	14.3	–	–	28.6
Black-t. Blue	–	10.2	8.5	–	18.7	3.4	32.2	37.3	–	72.9
Myrtle	24.0	18.5	10.5	–	53.0	8.7	18.8	12.9	–	40.4
Yellow-throated	19.1	26.2	16.7	–	62.0	23.8	7.1	7.1	–	38.0
Chestnut-sided	–	25.0	25.0	–	50.0	–	50.0	–	–	50.0
Blackpoll	7.4	11.5	8.2	–	27.1	8.2	46.7	13.9	–	68.8
Pine	15.8	19.3	26.3	–	61.4	10.5	22.8	5.3	–	38.6
Prairie	5.9	6.9	3.0	–	15.8	21.8	22.8	9.9	–	54.5
Palm	9.1	9.1	18.2	–	36.4	9.1	–	9.1	–	18.2
Ovenbird	–	1.6	8.1	–	9.7	–	13.7	32.3	–	46.0
N. Waterthrush	–	4.2	–	–	4.2	–	4.2	16.7	–	20.9
La. Waterthrush	–	2.3	5.3	–	7.6	5.3	5.3	21.1	–	31.7
Kentucky	–	4.5	13.3	–	17.8	8.9	8.9	22.2	–	40.0
Yellowthroat	–	1.2	1.8	–	3.0	1.8	13.9	4.8	–	20.5
Yellow-b. Chat	8.8	12.3	1.8	–	22.9	7.0	19.3	10.5	–	36.8
Hooded	–	2.3	16.3	–	18.6	4.5	11.2	32.6	–	48.3
Canada	–	–	13.3	–	13.3	–	46.7	26.7	6.7	80.1
Am. Redstart	3.8	14.6	18.8	–	37.2	5.4	23.0	29.7	–	58.1
Total obs.	161	203	185	32	581	156	391	337	26	910
% of total	8.4	10.6	9.6	1.7	30.3	8.1	20.4	17.5	1.4	47.4

selected both the floodplain forest and beech forest habitats. The Hooded Warbler and Ovenbird occurred in most forest types; the Ovenbird selected pine-hardwood, pine forests, and oak-hickory, and the Hooded Warbler also occurred commonly in floodplain forests. Observations of the Magnolia Warbler were too few to indicate selection within the several habitats in which birds were found.

The 13 species of warblers that nested in the study area all showed some degree of habitat selection during the nesting period, as they failed to occur in all habitat types. An immediate separation into thicket and forest species was possible. The Yellowthroat, Yellow-breasted Chat, Prairie Warbler, and Yellow Warbler showed preferences for thickets, although the first three also occurred to some extent in forest habitats. The Yellow Warbler occurred exclusively in wet thickets. Of the nine forest warblers only the Ovenbird, Kentucky, and Hooded Warblers occurred commonly in several habitats. The other species were highly selective, being commonly found in only one or two habitats.

TABLE 2—*Continued*

	Strata and habitat-niches												
	Shrub							Ground					
	Top of crown	Inner crown	Lower crown	Dense thicket	Brush-pile	Grasses	Total %	Dense thicket	Grasses	Water's edge	Open	Total %	Total obs.
Black-and-white	–	–	–	–	–	–	–	–	–	–	–	–	81
Prothonotary	–	2.3	2.3	11.6	–	–	16.2	2.3	–	9.3	–	11.6	43
Worm-eating	–	33.3	–	–	–	–	33.3	–	–	–	–	–	9
Blue-winged	12.5	–	–	12.5	–	–	25.0	–	–	–	–	–	8
Parula	1.5	0.7	–	0.7	–	–	2.9	–	–	–	–	–	138
Yellow	2.6	10.5	–	–	–	–	13.1	–	–	–	–	–	38
Magnolia	–	13.6	4.6	–	–	–	18.2	–	–	–	–	–	22
Cape May	–	–	–	–	–	–	–	–	–	–	–	–	7
Black-t. Blue	1.7	6.8	–	–	–	–	8.5	–	–	–	–	–	59
Myrtle	1.1	1.4	2.4	1.8	–	–	6.7	–	–	–	–	–	287
Yellow-throated	–	–	–	–	–	–	–	–	–	–	–	–	42
Chestnut-sided	–	–	–	–	–	–	–	–	–	–	–	–	4
Blackpoll	0.8	2.5	–	–	–	–	3.3	–	–	–	0.8	0.8	122
Pine	–	–	–	–	–	–	–	–	–	–	–	–	57
Prairie	9.9	6.9	4.0	7.9	–	1.0	29.7	–	–	–	–	–	101
Palm	–	–	–	–	–	–	–	–	9.1	–	36.4	45.5	11
Ovenbird	3.2	7.3	0.8	7.3	4.0	–	22.6	4.0	0.8	–	16.9	21.7	124
N. Waterthrush	–	–	4.2	16.6	12.5	4.2	37.5	8.3	–	20.8	8.3	37.4	24
La. Waterthrush	2.6	–	–	13.2	–	–	15.8	–	–	23.7	21.1	44.8	38
Kentucky	2.2	4.4	4.5	6.7	4.4	2.2	24.4	6.7	–	2.2	8.9	17.8	45
Yellowthroat	8.4	10.8	2.4	51.0	6.6	3.0	72.2	1.8	–	1.2	1.2	4.2	166
Yellow-b. Chat	8.8	8.8	1.8	21.1	–	–	40.5	–	–	–	–	–	57
Hooded	3.9	10.1	4.5	10.1	2.3	–	30.9	1.1	–	–	1.1	2.2	178
Canada	–	6.7	–	–	–	–	6.7	–	–	–	–	–	15
Am. Redstart	0.4	1.7	0.4	1.3	0.8	–	4.6	–	–	–	–	–	239
Total obs.	52	87	31	142	27	8	347	16	2	21	44	83	1,921
% of total	2.7	4.5	1.6	7.4	1.4	0.4	18.0	0.8	0.1	1.1	2.3	4.3	

[1] Expressed as percentages of the total number of individuals of each species recorded.

OCCURRENCES IN STRATA AND HABITAT-NICHES

A second goal of this study was to obtain a more precise description of the actual place of occurrence of each species of warbler within the overall habitat type or types occupied. The first logical subunit of habitat was stratum: canopy, low tree, shrub, and ground. Within these strata further subdivisions were possible, placing the bird either on the bole of a tree, in the upper part of the crown (limb tips), in the shaded interior of the crown, or in the shaded lower part of the crown. This was applicable to the canopy, low tree, and shrub layers. Occurrence on the bole was recorded in the stratum of the tree as a whole, not according to height. A bird on the bole of a canopy-stratum tree was tallied in this stratum regardless of the height of the observation. Other definite places of occurrence were obvious within the within the shrub stratum. Thus thickets (tangles of brush, vine, or briers) and brushpiles were added. Warblers were also occasionally recorded in herbaceous vegetation such as grasses, sedges, and rushes. These were recorded as grasses and placed in the shrub stratum as a matter of convenience.

TABLE 3

RELATIONSHIPS BETWEEN OBSERVATIONS OF WARBLERS IN STRATA AND HABITAT-NICHES DURING THE POSTMIGRATORY PERIOD[1]

	Strata and habitat-niches									
	Canopy					Low tree				
Species	Top of crown	Inner crown	Lower crown	Bole	Total %	Top of crown	Inner crown	Lower crown	Bole	Total %
Prothonotary	4.8	4.8	9.5	–	19.1	9.5	23.8	4.8	9.5	47.6
Parula	–	23.0	30.8	–	53.8	–	7.7	38.5	–	46.2
Yellow	–	–	–	–	–	50.0	35.8	7.1	–	92.9
Yellow-throated	40.0	20.0	40.0	–	100.0	–	–	–	–	–
Pine	31.3	25.0	12.5	–	68.8	6.2	12.5	6.3	–	25.0
Prairie	2.4	9.5	4.8	–	16.7	19.0	19.0	16.7	–	54.7
Ovenbird	3.1	–	21.9	–	25.0	–	9.4	50.0	–	59.4
La. Waterthrush	–	–	–	–	–	–	–	–	–	–
Kentucky	–	5.2	15.8	–	21.0	5.3	5.3	10.5	–	21.1
Yellowthroat	3.1	–	3.1	–	6.2	12.5	3.1	6.3	–	21.9
Yellow-b. Chat	14.3	8.6	2.8	–	25.7	17.1	20.0	8.6	–	45.7
Hooded	–	6.1	18.4	–	24.5	–	16.3	34.7	–	51.0
Am. Redstart	4.2	22.9	25.0	–	52.1	2.1	20.8	20.8	–	43.7
Total obs.	18	31	45	–	94	30	51	65	2	146
% of total	5.4	9.3	13.4	–	28.1	9.0	15.2	19.5	0.6	44.3

The ground stratum was also divided into several subunits. Birds on the ground were found in brush-free areas beneath the overstory, beneath thickets and grasses, and often at the water's edge, so these categories were added.

Habitat-niche observations were separated into the spring-migratory and postmigratory periods (Tables 2 and 3). Occurrence was calculated without reference to particular habitat types, because niche appears to be independent of habitat type and, in most cases, this would reduce the numbers of observations in each category to levels too small to be meaningful. No effort was made to determine the proportions of the total habitat occupied by each of these subunits. Thus Tables 2 and 3 should be studied as records of occurrence only and not selection, except in cases of unusually high correlation between a certain species and a particular habitat-niche.

About 48 per cent of all observations during the migratory period were in the low-tree stratum; 30 per cent of the observations were from the canopy stratum, and about 18 per cent were from the shrub stratum. Only 4 per cent of the observations were of birds on the ground (Table 2). The pattern for the postmigratory period was very similar.

During the migratory period 11 of the 25 commoner species were found more than 50 per cent of the time in the low-tree stratum; 7 species reached this level of occurrence in the canopy stratum and 1 in the shrub layer. No warbler was recorded more than 50 per cent of the time on the ground. During the postmigratory period four species occurred more than 50 per

TABLE 3—*Continued*

	Strata and habitat-niches												
	Shrub							Ground					
	Top of crown	Inner crown	Lower crown	Dense thicket	Brush-pile	Grasses	Total %	Dense thicket	Grasses	Water's edge	Open	Total %	Total obs.
Prothonotary	–	9.5	9.5	–	9.5	–	28.5	4.8	–	–	–	4.8	21
Parula	–	–	–	–	–	–	–	–	–	–	–	–	13
Yellow	–	7.1	–	–	–	–	7.1	–	–	–	–	–	14
Yellow-throated	–	–	–	–	–	–	–	–	–	–	–	–	5
Pine	–	–	–	–	–	–	–	–	–	–	6.2	6.2	16
Prairie	2.4	9.5	4.8	9.5	2.4	–	28.6	–	–	–	–	–	42
Ovenbird	–	6.2	–	–	–	–	6.2	–	–	–	9.4	9.4	32
La. Waterthrush	–	–	–	25.0	37.5	–	62.5	–	–	–	37.5	37.5	8
Kentucky	–	5.3	–	26.3	5.3	–	36.9	15.8	5.2	–	–	21.0	19
Yellowthroat	12.5	3.1	–	43.8	3.1	6.3	68.8	3.1	–	–	–	3.1	32
Yellow-b. Chat	8.6	5.7	–	14.3	–	–	28.6	–	–	–	–	–	35
Hooded	–	16.3	–	6.1	2.1	–	24.5	–	–	–	–	–	49
Am. Redstart	–	4.2	–	–	–	–	4.2	–	–	–	–	–	48
Total obs.	8	23	4	33	9	2	79	5	1	–	7	13	334
% of total	2.4	6.9	1.2	9.9	2.7	0.6	23.7	1.5	0.3	–	2.1	3.9	

[1] Expressed as percentages of the total number of individuals of each species recorded.

cent of the time in the canopy stratum and the low-tree stratum, and two species were found this often in the shrub stratum.

No species was restricted in occurrence to a single stratum, but several were found in only two of the four strata present. The pattern of placement within a stratum was characteristic for many species. The Black-and-white Warbler was particularly selective, being recorded 69 per cent of the time on the bole or larger limbs of the canopy or low-tree stratum.

HEIGHT OF OCCURRENCE

The height of occurrence was estimated in 5-foot increments and recorded for each warbler seen. These heights were arranged under two categories: singing males and birds engaged in other activities. The range, mean, and standard deviation were calculated for both categories for each species (Figure 1).

For all species except the Myrtle Warbler, singing males were found at greater average heights than were birds engaged in other activities. Some of this difference may have been due the auditory conspicuousness of singing males at greater heights, but this error was minimized by careful searching of all parts of each stratum. The error was probably more pronounced in the Ovenbird and the two waterthrushes that feed on the ground. Generally most species, except for the ground feeders, sang and foraged through the same stratum. Those species that sang while feeding showed less deviation in height between activities than did those species that sang while resting. The latter species typically flew to perches above their foraging level to sing.

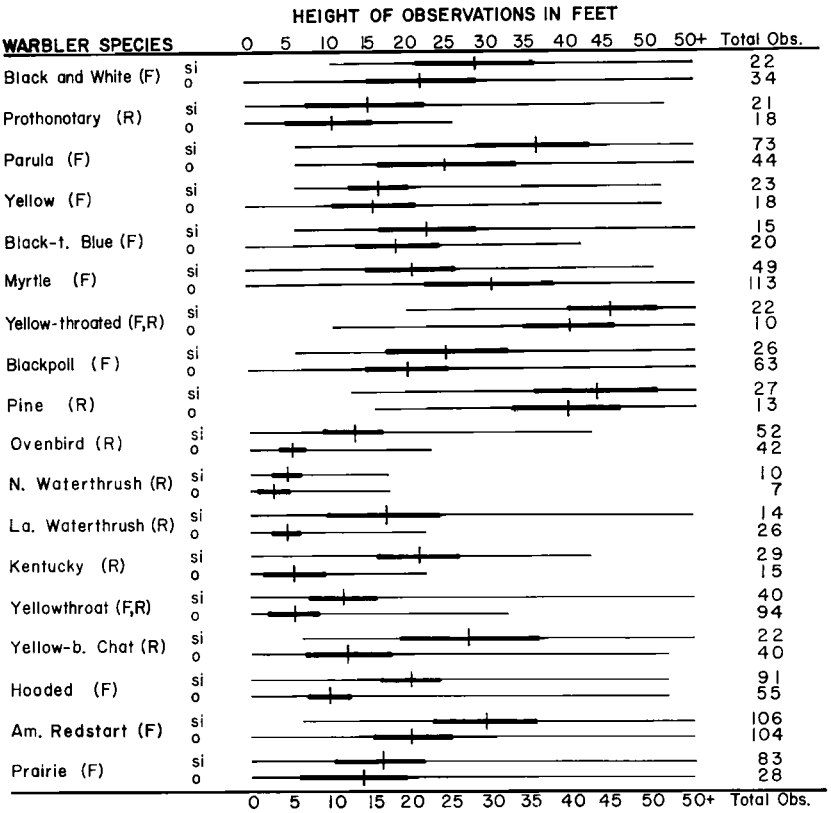

Figure 1. Recorded heights of singing males compared with heights of observation of all other birds. The long line represents the range of observations, the vertical slash the mean height, and the thick bar one standard deviation. F = warblers that sing while feeding, R = warblers that sing while resting (only data from 1963 are presented); si = singing males, o = all other birds.

The bar indicating standard deviation in Figure 1 is presented to indicate only the degree of variation from the mean. It is not to be taken as a statistical comparison indicating a significant difference when the bars do not overlap.

Warbler Groupings

Table 4 is designed to indicate the natural groupings of warblers as they occurred in the study area during the spring migration. By considering the occurrences in stratum and niche, these groupings can be broken into smaller units of more closely associated species. While this study was not designed to study relationships between species, it may provide a starting point for such analyses.

TABLE 4
WARBLER GROUPINGS BY HABITAT[1]

Habitat	Species	
Dry thicket	Prairie L, S	Yellowthroat S
	Yellow-b. Chat S, L	Myrtle L
Pine forest	Pine C, L	Yellow-throated C, L
	Ovenbird L	Parula C, L
	Hooded L, S	Black-and-white C, L
	Prairie L, S	Blackpoll L, C
	Myrtle C, S	
Oak-hickory forest	Myrtle C, L	Blackpoll L, C
	Hooded L, S	Kentucky L, S
	Ovenbird L	Black-and-white C, L
	Parula C, L	Redstart L, C
Beech forest	Myrtle C, L	Kentucky L, S
	Parula L, C	Yellow-throated C, L
	Redstart L, C	Black-and-white C, L
	La. Waterthrush G, L	Black-throated Blue L
Floodplain forest	Am. Redstart L, C	Black-throated Blue L
	Hooded L, S	Kentucky L, S
	Yellowthroat S	Blackpoll L, C
	Parula C, L	N. Waterthrush G
	Myrtle C, L	Yellowthroated C, L
	Prothonotary L	Prairie L, S
	Black-and-white C, L	Canada L
	La. Waterthrush G, L	
Wet thicket	Yellow L	Blackpoll L
	Yellowthroat S	N. Waterthrush S, G
	Yellow-b. Chat S, L	Black-and-white L

[1] Species are listed in a descending scale of relative abundance in those habitats in which they occurred regularly and frequently (see Table 1 for relative frequency values and indications of habitat preferences). Occurrence in strata is indicated for those levels containing at least 25 per cent of the total observations of a species (see Table 3 for details of stratification). Stratum abbreviations are: C = canopy, L = low tree, S = shrub, and G = ground.

DISCUSSION

The standard analysis of variance and Duncan's multiple range test were used when necessary in testing habitat selection. In dealing with a field problem of this type with many uncontrolled variables, a 10 or 15 per cent level of significance may be quite valid, but rather than deviate from a standard, widely used procedure, the preferences are indicated in Table 1 only when significant at the 5 per cent level.

The major portion of the information on subunits of habitat refer only to occurrence. The warblers were seen in these areas a given percentage of the time, and their presence becomes meaningful when correlated with the observer's and the reader's knowledge of the habitats and the species involved. The discussion of the associations of warblers with habitat-niches is based on this consideration.

Considerable diurnal migration has been postulated to occur among warblers, small flocks feeding and moving in the general direction of the

migratory movement (Chapman, 1907). In the present study this was not observed. Some flock movements were seen, but these appeared to occur in all directions and to represent random activity. The semistationary flocks usually encountered suggest that newly arriving warblers moved about until they found suitable feeding areas and then remained more or less stationary through the rest of the day.

Habitat and habitat-niche relations.—The five transient warblers present in moderate to large numbers (Black-and-white, Black-throated Blue, Myrtle, and Blackpoll Warblers, and Northern Waterthrush) showed a fairly wide distribution among habitats. Some habitat preferences were evident for all of these except the Myrtle Warbler (Table 1), although the degree of habitat selection varied, some species apparently having a wider range of ecological tolerance than others. This led to the question of whether or not a correlation existed between the nesting habitat of the transient species and the habitats selected during migration.

Of the transient warblers only the Myrtle and Blackpoll nest exclusively in coniferous forests. The others nest in both coniferous and deciduous woodlands. During migration the Blackpoll, Myrtle, and Black-and-white Warblers appeared less selective of habitat than did the Black-throated Blue Warbler and Northern Waterthrush. Less intensive selection on the part of the Myrtle Warbler and Blackpoll Warbler may indicate that these species, which are associated so closely with the northern coniferous forests during the breeding season, are unable to find similar habitats during migration and thus do not respond strongly to any of the habitats in the study area. The Black-and-white Warbler was also widespread, but it did show a tendency to increase in numbers in deciduous forests; its adaptation for feeding on the boles and large limbs of trees, which are present in all forest habitats, may have made it less restricted by forest type.

The Black-throated Blue Warbler and Northern Waterthrush showed more definite selection of habitats during their passage through central North Carolina, being found more often in forest types similar to habitats in which they nest farther north. Thus the evidence suggests that transient warblers do respond to the same habitats during migration as on the nesting grounds if such habitats are available. The occurrence of summer resident species in similar habitats both during and after migration further substantiates this observation.

A study of several species of warblers on their wintering grounds showed that most of them fed in a similar manner and at similar heights to those in the nesting regions (MacArthur, 1958). It has also been shown that during the nesting season Parula Warblers forage in a similar manner and in similar habitat-niches in the very different oak-gum forests of Louisiana and the white birch forests of Maine (Morse, 1967). Thus warblers

generally select similar habitat-niches throughout the year, even though the vegetation type occupied may vary from northern spruce-fir forests to tropical forests. Therefore habitat-niche selection may be more important to most warblers than habitat selection. A species may seek out its particular habitat-niche on the wintering grounds, during migration, and in the nesting region regardless of the composition of the forest type in which this habitat-niche occurs.

The results of this study show (Tables 2 and 3) that no warblers occurred uniformly in all subunits of habitat. Most occurred predominantly in one or two strata and often in only certain subunits of the strata. Although statistical tests were not made, obviously many species utilized only small portions of the habitats they frequented during migration. These warblers were probably selecting for some complex set of physical characteristics at the habitat-niche level rather than at the overall vegetation type level (MacArthur, 1964).

Several theories have been proposed on the factors involved in habitat and habitat-niche selection. Life form of the vegetation has been considered an important factor for many years (Odum, 1945). A recent study proposed that birds react to a density profile in habitat selection on the breeding grounds, each species selecting the habitat and subunits of habitat that represent the particular density pattern most suitable. The proportion of the total amount of vegetation in each stratum determines the density profile. For example, Yellowthroats were most common where the density profile showed the greatest proportion of the vegetation between 0 and 2 feet in height (MacArthur et al., 1962).

The floodplain forest habitat was the most mesic of the forest types studied and contained the best developed series of strata. Table 4 shows that this habitat type contained the largest group of regularly occurring warbler species. This appears to fit well with the MacArthurs' theories concerning species abundance and volume of vegetation (MacArthur and MacArthur, 1961). Apparently more habitat-niches are present in this forest type, allowing a greater number of species to occur there regularly.

Food is probably also of great importance in determining the habitat-niche of warblers at all times of year, and this may be of critical importance during migration. In the current study I found a strong correlation between warblers and blue-beech (*Carpinus caroliniana*) groves. This tree has unusually large numbers of small defoliating insects (primarily Psyllidae) present during the migration peak in early May, which was probably a major factor in its strong attraction for warblers. Most species generally fed in particular subunits of the crown.

Each species would be expected to utilize the feeding method and location most efficient for obtaining food throughout the year. Thus each species

should occur in similar habitat-niches at all times of year, as each species has specific adaptations that allow it to feed more efficiently in certain situations (Osterhaus, 1962). When the habitat-niches that particular warblers utilized during migration were compared with those inhabited on the nesting grounds (from the literature) they showed close agreement in most cases.

An approach to further study indicated by the results of the present research would be to apply a similar methodology to a group of species on the wintering grounds, sections of the migratory routes, and the central or optimal parts of the nesting ranges. A careful analysis of the conditions utilized by the warblers throughout their range would allow a much more precise and thorough determination of the factors of habitat being selected than studies carried out in one locality.

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SUMMARY

The habitat relations of the Parulidae during the spring migration were studied at Raleigh, North Carolina during the spring migratory and post-migratory nesting periods of 1962 and 1963 by the use of censuses along timed transects, each passing through several habitat types. These daily censuses provided information on the occurrence of birds in specific habitats in relative values of birds per hour. The placement of birds in subunits of habitat was recorded simultaneously and converted to percentages for comparison.

Of 31 species of warblers recorded, 20 occurred commonly; 13 of the common species nested within the study area, while 7 were entirely transient. Analysis of the associations of each species with the major habitats in the study area showed nearly all species to exhibit some degree of habitat selection during migration. Those species that found habitats available similar to their nesting habitats occurred most often in these vegetative types. Those species that nest in the northern coniferous forests (habitats not available in the study area) were less selective. Species that were summer residents in the study area tended to occur most often during migration in the same habitats that they nest in.

Statistical analysis of habitat-niche selection was not possible, but a qualitative analysis indicated that often the association between warbler and habitat-niche appeared stronger than between warbler and habitat.

The results of this study agree with the general concept, as expressed in the current literature on habitat association in warblers, that physical features of the vegetative substrate are important factors in determining the habitats and habitat-niches occupied.

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