SEASONAL VARIATION IN THE FORAGING BEHAVIOR OF SOME MIGRATORY WESTERN WOOD WARBLERS

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ABSTRACT.—I observed the foraging behavior of four warbler species (*Dendroica petechia, Oporornis tolmiei, Geothlypis trichas,* and *Wilsonia pusilla*) in the summer in Wyoming and in the winter in Nayarit, México. Of six variables (absolute foraging height, relative foraging height, vegetation density, horizontal foraging position, feeding method, and foraging substrate) believed to be potentially important in distinguishing the warbler species ecologically, the two foraging-height variables provided the greatest separation of the four species in both summer and winter. An analysis of the behavioral similarity of each species from summer to winter revealed that feeding method was the least changed behavior and that absolute foraging height involved the greatest behavioral flexibility. The behaviors that are most flexible are possibly the least well tied to the birds' morphology and are also the ones that have been shown by other workers to reveal the effects of competitors through "niche shifts." Therefore, ecological relationships among co-existing species (in terms of overlaps or positions in niche space) may never be fully derivable from morphological information alone. *Received 6 March 1980, accepted 24 March 1981.*

ECOLOGICAL studies of Nearctic migrants on their breeding grounds are relatively common, but such studies on their wintering grounds are less common (but see Eaton 1953, Schwartz 1964, Willis 1966, Lack and Lack 1972, Leck 1972, Tramer 1974, Rappole 1975, Chipley 1976, Karr 1976, Mills 1976, Post 1978, Wilz and Giampa 1978, or some of the more recent studies included in Keast and Morton 1980). Comparative studies that deal with the ecology of migratory species on both their breeding and wintering grounds are rarer still (but see Root 1967, Baker and Baker 1973, Lack 1976, Bennett 1980, Rabenold 1980). Only through such comparative studies will we begin to understand the extent to which the morphology of a species represents a compromise among behaviors that vary seasonally (Fretwell 1972).

In this paper I quantify the foraging behavior of four species of migratory wood warblers (Yellow Warbler, *Dendroica petechia*; MacGillivray's Warbler, *Oporornis tolmiei*; Common Yellowthroat, *Geothlypis trichas*; and Wilson's Warbler, *Wilsonia pusilla*) that can be found syntopically during both the breeding and nonbreeding seasons in western North America to determine (1) whether several potential mechanisms of ecological isolation change seasonally, and (2) which aspect of foraging behavior shows the grestest seasonal flexibility.

STUDY SITES AND METHODS

I collected foraging data on the four warbler species from 20 May–20 June 1975 within 4 ha of willow (*Salix*) habitat adjacent to the Jackson Hole Biological Research Station, Grand Teton National Park Wyoming (43°52′N, 110°34′W). Willows were the only large plants growing in the study area, and the open areas between them were filled with grasses and sedges. A foliage-height profile, which depicts the porportion of vegetation at different heights, is given in Fig. 1.

Winter foraging data were collected from 15 January to 15 February 1975 and 1976 in second growth
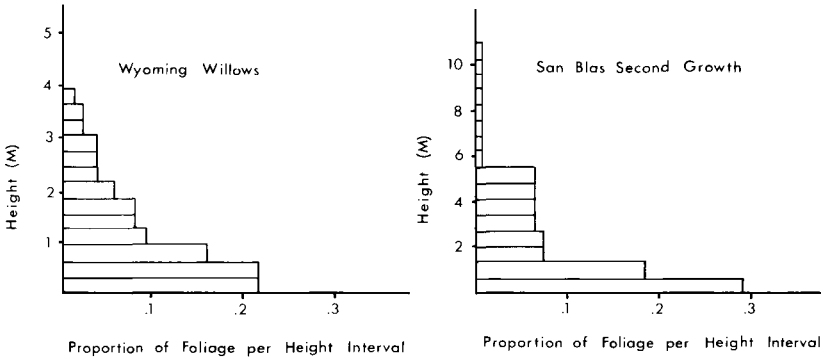

Fig. 1.　Foliage-height profiles of the principal summer (Wyoming willows) and winter (San Blas second growth) study sites.

habitats around San Blas, Nayarit, México (21°32′N, 105°12′W). All four warbler species were common in these habitats, which supported growth of plantation, mangrove, and forest elements, including the genera *Cocos, Avicennia, Randia, Ficus, Ceiba, Acacia,* and many others. The average vegetation height was around 5 m, but ranged from herbaceous ground cover to 15 m. A foliage-height profile for the principal study area (located 1 km southeast of San Blas) is given in Fig. 1.

　　Additional foraging data were obtained from the following sites during the time intervals shown: Alamo Canyon, Organ Pipe Cactus National Monument, Arizona (32°04′N, 112°44′W), 1–11 April 1974; Wolverton, Sequoia National Park, California (36°30′N, 118°44′W), 9–20 July 1974; Wyoming Willows (same site as described above), 7–20 August 1974, 15 August–7 September 1975; Mangroves, Tropical Evergreen Forest Edge, and Coconut Plantation (all located around San Blas, as described above), 15 January–15 February 1975, 1976; Rio Cuchujaqui, Alamos, Sonora, México (27°01′N, 108°58′W), 1–10 April 1975; Christian Bridge slough and Lodgepole Pine Forest (both within 1 km of the Wyoming Willow site) during May 1975 and August 1975, respectively.

　　Upon encountering a foraging bird, I collected data pertaining to six variables that are generally thought to be important in distinguishing insectivorous birds ecologically (MacArthur 1958, Root 1967, Williamson 1971, Lack 1971, Cody 1974, Landres and MacMahon 1980): absolute foraging height—whether the bird was seen from 0–0.6 m, 0.6–1.2 m, 1.2–2.4 m, 2.4–4.9 m, 4.9–9.8 m, 9.8–19.5 m, or greater than 19.5 m, as estimated by eye; relative foraging height—the lower, second, third, or top quartile of the vegetation within which the bird was seen foraging; vegetation density—the estimated percentage area (0–15, 15–50, 50–85, 85–100%) covered by vegetation within an imaginary 1 m^2 surrounding the foraging bird; horizontal foraging position—the inner, middle, or outer third of the lateral distance from the center of the vegetation within which the bird was seen foraging; feeding method—the method of obtaining food (glean, to pick food from a surface while stationary; sally, to fly out after airborne prey; hover, to pick food from a surface while in stationary flight; or jump, to jump upwards and pick food from the underside of a surface; and foraging substrate—the surface from which food was seen to be taken (water, ground, bark, foliage, or air).

　　The sex of a foraging individual was not recorded. This could produce biased estimates of the species' foraging behavior if males and females differ in their behavior and if different proportions of each sex were recorded among the four species. Sexual differences in foraging height that have been documented for some wood warblers (Morse 1968, Holmes et al. 1978), however, apparently result from the fact that foraging activities are constrained by sexually related breeding activities (singing for males, nest attendance for females); consistent sexual differences in wood warbler foraging behavior outside the breeding season are therefore unlikely and have yet to be documented. In addition, because my breeding-season observations originated from a willow habitat that is only one-fourth as tall as the vegetation where such sexual differences have been documented, the magnitude of intersexual differences is unlikely to be greater than that of interspecific differences in foraging height.

　　I used the *G*-statistic to test the significance of differences in the use of each of the variables among the four species and to test the significance of association between pairwise combinations of the six variables (Sokal and Rholf 1969). Uncertainty coefficients (Nie et al. 1975) were also calculated for all pairwise tests of association among the six variables to assess the strength of the associations. The

uncertainty coefficient varies from 0.0, when knowledge of the category of one variable does not reduce the uncertainty of predicting the category of another, to 1.0, when uncertainty is completely eliminated and each category of one variable is associated with only one category of the other variable.

The similarity in foraging behavior of a single species from one site to another or from one time to another within the same site was determined by use of Schoener's (1970) formula:

$$S_{ih} = 1 - \frac{1}{2}\Sigma(P_{ij} - P_{hj}),$$

where P_{ij} is the proportion of observations of behavior j in site i and P_{hj} is the proportion of observations of behavior j in site h. The resultant value (S_{ih}) takes its minimum (0) when no behaviors are shared by the two sites and its maximum (1) when the proportional distributions of the behaviors between sites are identical. The same method was used to determine the overlap in use of a single variable by two species.

I censused the warbler species within a given site by walking strip transects that were normally 1 km long and 40 m wide. Each bird seen or heard was recorded as a single detection, and species densities were estimated from the number of detections per unit area censused.

Foliage-height profiles of the principal study areas were established from counts of the number of times foliage hit a 5 m extendable pole, which was raised through the vegetation at 75 points (one every 25 steps) 5 m to either side of the census route. An imaginary extension for taller vegetation was provided by a camera and telephoto lens.

RESULTS

Summer.—Common Yellowthroats and Yellow, MacGillivray's and Wilson's warblers are broadly sympatric throughout much of western North America during the breeding season (Robbins et al. 1966, for example). Briefly, the habitat preferences of these four species run along a vegetation-height and moisture gradient, with the Common Yellowthroat relatively abundant in cattails and tules, MacGillivray's preferring wet thickets, Wilson's predominating in willow habitats, and Yellow most common in the taller alder, aspen, or cottonwood situations (Grinnell and Miller 1944; pers. obs.). All four species can be found nesting syntopically in the intermediately tall willow habitats of Wyoming, and the microhabitats utilized by each reflect the rather more broad habitat preferences just outlined. For example, the foraging-height preferences of the four species observed breeding in the Wyoming willows (Fig. 2) correspond with the relative position of each along the gradient of breeding-habitat types. This finding is essentially the same as that reported by Cody (1974) for the same habitat, except that he found MacGillivray's Warbler to forage much higher in the vegetation. His observations of this species were rare, however, and he illustrated its height preference only tentatively.

The use of each of the six variables (Appendix) was significantly heterogeneous among the four species (G-tests, $P < 0.05$), indicating that the variables are at least potentially important in distinguishing the species ecologically. Each of the six variables I chose to measure is significantly interrelated with every other variable (G-tests, $P < 0.05$), as determined from the breeding-season (late May–June) data. The significance, however, is largely due to strong couplings between single categories from each of two variables. For example, feeding method is associated with foraging substrate primarily because of the necessary dependence between "sally" and "air." Similarly, height and relative height are interrelated, principally because records in the highest absolute height category had to be recorded in the highest relative height category. It is important to note that a tremendous amount of independence among the variables does exist despite the statistically significant associations. The scatter around the intercorrelations can be demonstrated by examining uncertainty coefficients, or some other statistic that reflects the strength of the association. The average of the 15 uncertainty coefficients was 0.10 (SD = 0.13, range = 0.02–0.49), which
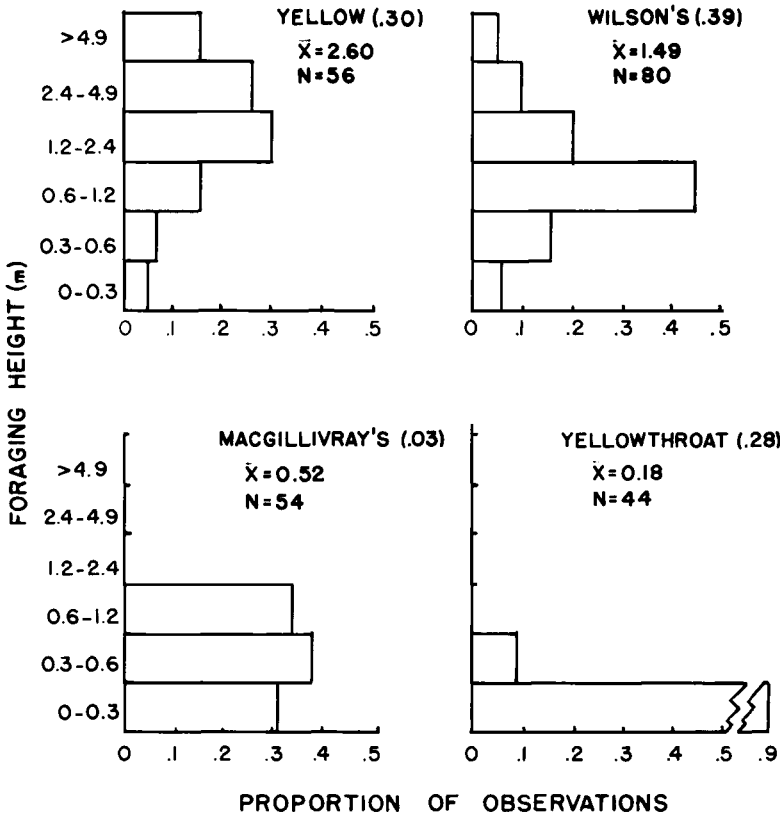
Fig. 2.   Frequency histograms of the foraging heights of four warbler species during the nesting period in the willow habitat of Wyoming. Parenthetical numbers indicate relative abundances of the four species, $\bar{x}$ = mean foraging height, and n = number of observations.

can be interpreted to mean that, on average, only 10% of the complete uncertainty of predicting the category of one variable is removed, given the category of another variable. Thus, there still exists a good deal of meaningful independence among the variables. Consider, for example, Common Yellowthroats and MacGillivray's Warblers: they have statistically indistinguishable feeding methods (both glean nearly exclusively) and would be expected to use indistinguishable substrates as well, as those two variables are significantly interrelated. Common Yellowthroats take food from the ground, bark, and foliage with nearly equal frequency (Appendix), however, while MacGillivray's Warbler differs significantly from the Common Yellowthroat in substrate use (Table 1) by gleaning from bark surfaces relatively more frequently. This difference in substrate use presumably contributes to their ecological isolation.

For each of the variables, I also tested the six possible species pairs for heterogeneity. During late May and June, each species pair differed significantly with respect to absolute foraging height, and all possible pairs except Yellow-Wilson's differed significantly with respect to relative foraging height, foraging position and foraging substrate (Table 1). Feeding methods were more similar among the 4

TABLE 1. Variables for which behaviors differ significantly (*G*-tests, asterisk indicates *P* < 0.05) between given species pairs in summer (left of slash) and winter (right of slash).

Species pair	Absolute foraging height	Relative foraging height	Vegetation density	Foraging position	Foraging substrate	Feeding method
Yellow-Yellowthroat	*/*	*/*	*/*	*/NS	*/*	*/*
Yellow-MacGillivray's	*/*	*/*	*/*	*/*	*/*	*/*
Yellow-Wilson's	*/*	NS/*	NS/*	NS/NS	NS/NS	NS/NS
Yellowthroat-MacGillivray's	*/*	*/NS	NS/*	*/*	*/*	NS/NS
Yellowthroat-Wilson's	*/*	*/*	*/NS	*/NS	*/*	*/*
MacGillivray's-Wilson's	*/*	*/*	*/*	*/*	*/*	*/*

species, but the 2 high-foraging species differed significantly from the 2 low-foraging species in this respect because they sallied more often for aerial insects.

To rank the six variables in terms of their ability to separate or distinguish the warbler species, I calculated the overlap between each of the six possible species pairs and averaged these to obtain a mean overlap value (Table 2). On average, the four species are least similar in the absolute heights at which they forage and most similar in their feeding methods. Whether these rankings reflect the relative ecological importance of these variables is uncertain (see discussion), but they do permit an objective seasonal comparison.

Winter.—Common Yellowthroats and Yellow, MacGillivray's and Wilson's warblers are commonly found syntopically in several distinctive low-elevation habitats that occur throughout coastal western México. These habitats include mangroves, second-growth areas, plantations, and tropical evergreen forests. Each of the four species is restricted in its habitat use at higher elevations, and it is more difficult to find all four species syntopically, because each tends to occur only where the habitat is most appropriate, e.g. marshes for Common Yellowthroat, tall riparian for Yellow, and forest undergrowth for MacGillivray's and Wilson's. Even though the four species show rather broad habitat tolerances at lower elevations, they are not equally abundant in all these lowland habitat types or all parts of a given habitat (Hutto 1980). Near San Blas the densest aggregation of the four species occurred along the edges of tropical evergreen forests, where they were about three times as dense as in any of the other local habitat types (Table 3).

In January 1976, 11 individuals, including 1 Nashville Warbler (*Vermivora ruficapilla*), 2 Yellow, 2 MacGillivray's, 2 Common Yellowthroats, 3 Wilson's, and 1 American Redstart (*Setophaga ruticilla*), were color banded on the second-growth plot. Banded individuals of all these species were found in the same locations within the plot for the remainder of the winter (through March). This site tenacity, coupled

TABLE 2. Average overlaps (±SD) from the six possible pairwise combinations of Common Yellowthroat and Yellow, MacGillivray's and Wilson's warblers for the six variables.

Behavioral variable	Summer	Winter
Absolute foraging height	0.40 ± 0.24	0.30 ± 0.25
Relative foraging height	0.44 ± 0.34	0.42 ± 0.29
Vegetation density	0.55 ± 0.26	0.65 ± 0.18
Horizontal foraging position	0.60 ± 0.20	0.73 ± 0.17
Feeding method	0.73 ± 0.18	0.73 ± 0.16
Foraging substrate	0.63 ± 0.12	0.61 ± 0.20

TABLE 3. Densities (number/10 ha) of the four warbler species in five habitat types around San Blas, Nayarit, México.

	Habitat type				
Species	Mangroves	Plantation	Second growth	Evergreen forest edge	Thornscrub
Yellow Warbler	27.3	8.5	17.0	31.2	0.0
MacGillivray's Warbler	10.0	50.7	27.8	84.9	56.0
Common Yellowthroat	38.8	0.0	12.4	20.0	0.0
Wilson's Warbler	5.0	20.0	38.1	176.0	14.1
Totals	81.1	79.2	95.3	312.1	70.1

with occasional observations of intra- and interspecific aggression, lead me to believe that most of the migrants maintained individual territories.

As in summer, the use of each of the six variables was significantly heterogenous among the four species (G-tests, $P < 0.05$). The variable that provided the greatest separation of (lowest overlap among) the four species in winter was absolute foraging height (Table 2). The greatest overlap among species was in their feeding method and horizontal foraging position. Each species differed significantly (G-tests, $P < 0.05$) from all others in absolute foraging height and 5 of the 6 species pairs differed significantly in relative foraging height, vegetation density, and foraging substrate (Table 1).

Between-season patterns.— I calculated the similarity in each species' use of a given behavioral variable between the summer and winter study sites. The degree of between-season behavioral similarity for each of the four species (Table 4) indicates that, in all cases, feeding method was the least changed behavior from summer to winter and that absolute foraging height and substrate use involved greater behavioral flexibility. Over a year, a species can be most safely characterized by how it feeds and least safely by the substrate from which or height (relative or absolute) at which it feeds.

DISCUSSION

The variables that best distinguish the four warbler species in summer are the same ones that best distinguish them in winter. The four species are best separated by their absolute and relative foraging heights and least well separated by their feeding methods. Whether foraging height is the most important niche dimension in terms of ecological separation is uncertain (Abrams 1980), but behaviors that are

TABLE 4. Values representing the similarity in use of a given variable between the summer and winter study sites for each of the four warbler species. Asterisks indicate the behaviors that are significantly different between seasons (G-tests, $P < 0.05$).

Behavioral variable	Yellow	MacGil-livray's	Yellow-throat	Wilson's	Mean similarity
Absolute foraging height	0.34*	0.95	0.88	0.63*	0.70 ± 0.28
Relative foraging height	0.74	0.60*	0.85	0.86	0.76 ± 0.12
Vegetation density	0.86	0.80	0.61*	0.71*	0.75 ± 0.11
Horizontal foraging position	0.60*	0.86	0.86	0.84	0.79 ± 0.13
Feeding method	0.95	0.97	1.00	0.84	0.94 ± 0.07
Foraging substrate	0.68*	0.58*	0.87	0.58*	0.68 ± 0.14

FORAGING HEIGHT (M)

16

8

4

2

1

0.5

(31) YR
(27) — (16)
(8) N
(77) YR

YELLOW
(46)
(20)
(104) YR
(63) N
(108) OC
(36)

(78)
(12)
(44) YR
(10) YR
(84) — (22)
(53)
(14)
(105) — (99)
(12)
(14)
(25)
(57)
(53)

(56)

(80)
(21)
(45)
WILSON'S

(6)
(126)
(63) N
(28) OC
(12) YR

(54)
(20) YR MACGILLIVRAY'S
(30)
(15)
(77) OC

YR(47)
(54)
CY(14)
(33) — (14) — (55) — (53) — (34)
(12) — (20)
(21)
(8) CY

(44)
COMMON YELLOWTHROAT

GEOGRAPHIC LOCATION

CHRISTIAN BRIDGE WYOMING / LODGEPOLE PINE WYOMING / WILLOW WYOMING-JUNE / WILLOW FLATS WYOMING-AUGUST / ALAMO CANYON ARIZONA / MANGROVES NAYARIT / WET FOREST NAYARIT / FOREST EDGE NAYARIT / SECOND GROWTH NAYARIT / COCONUT PLANTATION NAYARIT / RIO CUCHUJAQUI SONORA / WOLVERTON CALIFORNIA
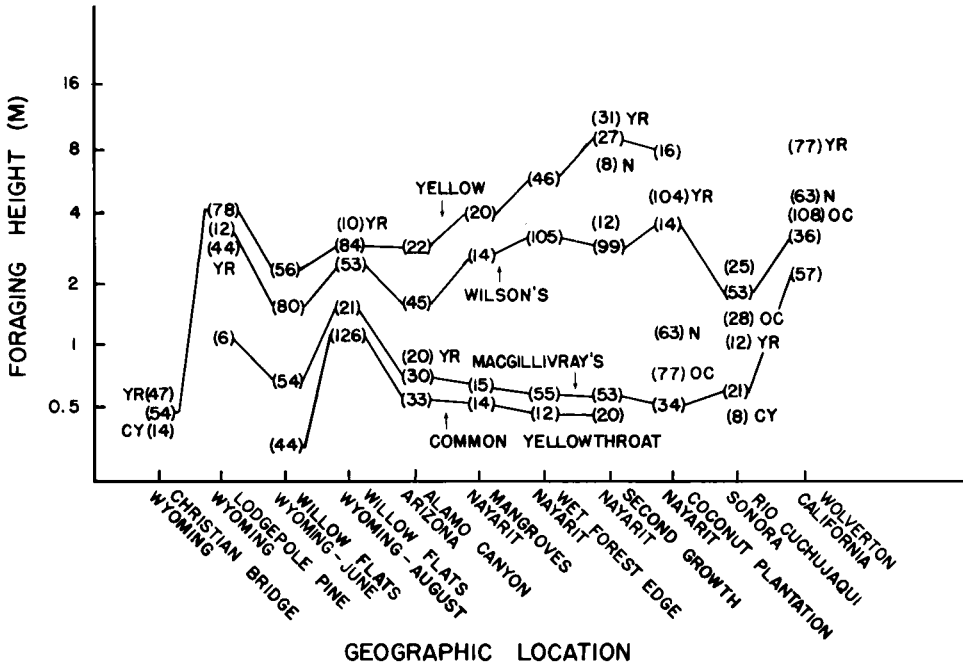
Fig. 3. The mean foraging heights of the four warbler species from various localities and seasons. The foraging height for a given observation was defined as the midpoint of that height category within which the bird was recorded. Numbers indicate sample sizes and are connected merely to emphasize the consistency in relative positions of the four species. CY = Common Yellowthroat, YR = Yellow-rumped Warbler, OC = Orange-crowned Warbler, N = Nashville Warbler.

indeed important in reducing competition among species must at least be statistically distinguishable (Gatz 1979); foraging locations rather than feeding methods may therefore be relatively important in promoting ecological isolation among the warbler species. The seasonally similar rankings of the six variables with respect to their ability to distinguish the species is a result of the general seasonal similarity in each species' foraging behavior. Such similarity in the foraging behavior of migrants between seasons has been expressed by others as well (Eaton 1953, MacArthur 1958, Schwartz 1964, Moreau 1972, Lack 1976—but see Rabenold 1980, Chipley 1980).

The seasonal variability in foraging behavior that does exist is of considerable interest. The average seasonal similarity in use of each variable by the four species (Table 4) reveals that the behaviors associated with foraging locations are more flexible than those associated with feeding methods. This result could reflect the differences in the number of categories that I created for each of the variables; the number of categories, however, should not necessarily be the same for all variables. The most critical problem is creating enough categories for a given variable so that real behavioral differences that exist can be detected. I chose qualitatively distinct categories that corresponded either with categorical feeding behaviors or with categorical distinctness in vegetation structure and was able to detect significant differences among species in their use of each of the six variables. The creation of additional categories beyond the number necessary to detect behavioral differences is not a problem, because the similarity index I used is insensitive to the number of

categories (Abrams 1980). Numerous categories will merely facilitate the detection of more subtle behavioral differences. The fact that the different variables reflect different behavioral operations, and that it might be "easier" for a bird to shift its foraging height than its feeding method, is also not a problem—it is precisely the point.

How can differences in the magnitudes of seasonal similarity in foraging behavior be explained? It has been argued from a theoretical standpoint (MacArthur and Pianka 1966, MacArthur and Wilson 1967, Hespenheide 1975) that space is more easily subdivided than food and that, for a species exposed to a changing competitive milieu, we should expect shifts in those behaviors associated with foraging locations as opposed to feeding methods. In addition, at least in the case of migratory birds, some behaviors must be more flexible than others as a result of the predictability of that aspect of the environment upon which a given variable is based. For example, behavioral flexibility in foraging height is demanded of canopy birds by the environment because the ranges of vegetation heights vary from habitat to habitat. Similarly, foraging substrates may differ from place to place or season to season and flexibility in substrate use is also necessary (there is very little foliage in the thorn forests that are traversed by many migrants in spring, and there were no leaves on the willows of Wyoming in May). Feeding method, on the other hand, is relatively similar in a seasonal sense because of the way food presents itself: there are most always insects for which to glean, sally, hover, and jump.

Those niche components (e.g. foraging height) that are most variable for these ultimate reasons may then be least constrained in a proximate sense by bird morphology and therefore the most likely to reveal niche shifts in the presence of additional competitors. It is not surprising that those behavioral parameters that have been shown to be relatively closely related to morphology—feeding method (Engels 1940, Root 1967, Ficken et al. 1968, Karr and James 1975, Norberg 1979), horizontal foraging position (Richardson 1942, Osterhaus 1962, Norberg 1979), and density of vegetation used (Hamilton 1961, Pearson 1977)—are just those that are the least flexible among the six variables that I measured. Diamond (1970a, b; 1975) and Diamond and Marshall (1977) also conclude from studies of niche shifts in New Guinean and New Hebridean birds that spatial rather than feeding-technique shifts are the rule and that feeding changes are most always accompanied by subspecific morphological change.

The fact that foraging heights are so variable seasonally does not detract from the possibility that foraging-height differences may promote ecological isolation among the four warbler species. Even though foraging heights varied markedly, the height at which a species foraged relative to the other three species remained constant (Fig. 3). Of 12 sites where at least two of the four species were present, each site revealed the same relative ordering of species along the height dimension. This could be a result of the fact that (a) each species is adapted to forage most effectively in a particular microenvironment (as determined by, say, light intensity or branch configuration), which occurs at a different height in each study site; (b) species forage at different heights from site to site in response to changes in the availability of food, independent of microenvironmental conditions or the presence of other species, or (c) changes in the foraging height of a species represent a response to interference or exploitative competition from other species.

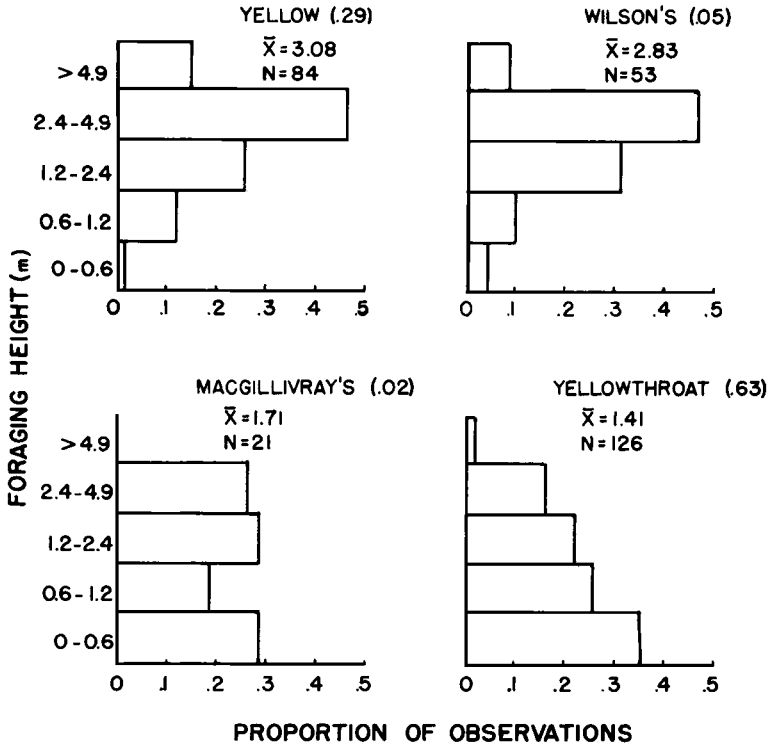It is unlikely that the microenvironments are the same over the range of heights

Fig. 4. Frequency histograms of the foraging heights of four warbler species during late summer 1975 in the willow habitat of Wyoming. Parenthetical numbers indicate relative abundances of the four species, $\bar{x}$ = mean foraging height, and n = number of observations.

occupied by some species (Fig. 3), although I have no data to refute this hypothesis. It is impossible to distinguish between (b) and (c) above without controlled field experiments, but it is tempting to speculate that the heights at which the birds forage are determined at least in part by each other's presence. An uncontrolled experiment presented itself in late summer in Wyoming when most of the Yellow, Wilson's, and MacGillivray's warblers had departed before the Common Yellowthroats. The decrease in abundance of the three species was accompained by dramatic shifts in the foraging heights of the Common Yellowthroat (Fig. 4). Although all species observed in August foraged a bit higher on average than in June, the shift in average foraging height for Common Yellowthroats was four times that of any other species. While Common Yellowthroats spend 90% of their time less than 0.3 m off the ground in June, their mean foraging height was 7.8 times greater in late August, and it was striking to find them foraging at 5 m on occasion.

Observations of interspecific aggression among the four species are scattered throughout my summer field notes, and it is likely that interference competition helps maintain the foraging height differences among these species. Edington and Edington (1972) also concluded that maintenance of vertical and horizontal separation among several insectivorous bird species that they studied depends on interaction and not exclusively on noninteractive habitat selection. Furthermore, Morse (1971) reported changes in the foraging locations of two warbler species in the ab-

sence of the socially dominant *Dendroica virens* on small islands, and Primack and Howe (1975) produced an excellent example of interference competition maintaining vertical separation between butterflies and hummingbirds. It therefore appears as if those aspects of foraging behavior that need be flexible for reasons associated with the unpredictability of the physical environment, or with the economics of foraging, are the same behaviors that are least constrained by morphology and most responsive to changes in the numbers of competitors. This is an important conclusion in light of recent attempts (e.g. Karr and James 1975, Ricklefs and Cox 1977, Ricklefs and Travis 1980) to make inferences about community structure by using morphological data in the absence of behavioral information. Because those behaviors that are most responsive (in a short-term sense) to the presence or absence of competitors are seemingly the least well related to morphology, ecological relationships among species may never be fully derivable from morphological information alone (see also Hespenheide 1973, 1975).

The observation that birds occupy the same relative heights at all study sites could mean that morphology is a poor predictor of foraging heights but an accurate predictor of the species' positions along some physical gradient that varies consistently with height and that is actually the parameter being divided. I believe, however, that morphological information can predict (in other than very general terms) neither the absolute niche position of a single species nor the relative positions of potential competitor species for the reasons that follow. As mentioned previously, microenvironmental conditions are probably not the same at heights as different as, say, the Yellow Warbler occupied in the various localities depicted in Fig. 3, and its absolute niche position at any one site could, therefore, not have been predicted from morphological data alone. Second, although the foraging positions of the four warbler species remained consistent relative to one another, the foraging locations of the four species relative to Yellow-rumped (*Dendroica coronata*), Nashville, and Orange-crowned (*Vermivora celata*) warblers did not remain so orderly (Fig. 3). These additional species did not appear to hold small, individual territories but foraged over larger areas in either intraspecific (Yellow-rumped Warbler) or interspecific (Orange-crowned and Nashville warblers) flocks (Hutto 1980, pers. obs.). This difference in social behavior apparently precluded the possibility of maintaining an orderly segregation with the four nonflocking species. It is interesting to note that the two species that foraged together in interspecific flocks also maintained consistent foraging-height positions relative to one another. Some species do, therefore, change relative positions along the gradient of vegetation height, and their relative niche positions along this gradient would not be possible to predict from morphological traits alone.

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APPENDIX. The numbers of observations of each of four warbler species in various categories of six behavioral variables in summer (May–June 1975; data to left of slash) and winter (January–February 1975, 1976; data to right of slash).

1. *Absolute foraging height*

	0–0.6 m	0.6–1.2 m	1.2–2.4 m	2.4–4.9 m	4.9–9.8 m	>9.8 m	Total
Yellow	6/0	9/0	17/6	15/4	9/14	0/30	56/54
Yellowthroat	44/49	0/3	0/1	0/3	0/0	0/0	44/56
MacGillivray's	36/38	18/16	0/3	0/0	0/0	0/0	54/57
Wilson's	17/14	35/12	16/25	8/26	4/12	0/3	80/92

2. *Relative foraging height*

	Lower quartile	Second quartile	Third quartile	Top quartile	Total
Yellow	5/0	10/4	19/15	22/35	56/54
Yellowthroat	36/40	6/13	0/3	2/0	44/56
MacGillivray's	54/34	0/19	0/4	0/0	54/57
Wilson's	15/9	15/21	27/41	23/21	80/92

3. *Vegetation density*

	0–15%	15–50%	50–85%	85–100%	Total
Yellow	21/25	26/28	6/1	3/0	56/54
Yellowthroat	0/7	10/28	22/21	12/0	44/56
MacGillivray's	0/6	8/14	24/20	22/17	54/57
Wilson's	22/14	39/29	14/40	5/9	80/92

4. *Foraging position*

	Inner	Middle	Outer	Total
Yellow	9/29	7/8	40/17	56/54
Yellowthroat	22/28	12/7	10/21	44/56
MacGillivray's	40/50	14/7	0/0	54/57
Wilson's	19/34	19/25	42/33	80/92

5. *Feeding method*

	Glean	Sally	Hover	Total
Yellow	127/42	48/12	11/4	186/58
Yellowthroat	48/46	0/0	0/0	48/46
MacGillivray's	60/67	0/0	0/2	60/69
Wilson's	124/93	82/42	13/37	219/172

6. *Foraging substrate*

	Ground	Bark	Foliage	Air	Total
Yellow	4/1	56/2	78/43	48/12	186/58
Yellowthroat	18/21	19/12	11/13	0/0	48/46
MacGillivray's	6/6	42/20	12/43	0/0	60/69
Wilson's	4/15	77/11	56/104	82/42	219/172