

# THE STRUCTURE OF WESTERN WARBLER ASSEMBLAGES: ANALYSIS OF FORAGING BEHAVIOR AND HABITAT SELECTION IN OREGON

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**ABSTRACT.**—This study examines the foraging behavior and habitat selection of a MacGillivray's (*Oporornis tolmiei*)—Orange-crowned (*Vermivora celata*)—Wilson's (*Wilsonia pusilla*) warbler assemblage that occurred on early-growth clearcuts in western Oregon during breeding. Sites were divided into two groups based on the presence or absence of deciduous trees. Density estimates for each species were nearly identical between site classes except for Wilson's, whose density declined on nondeciduous tree sites. Analysis of vegetation parameters within the territories of the species identified deciduous tree cover as the variable of primary importance in the separation of warblers on each site, so that the assemblage could be arranged on a continuum of increasing deciduous tree cover. MacGillivray's and Wilson's extensively used shrub cover and deciduous tree cover, respectively; Orange-crowns were associated with both vegetation types. When the deciduous tree cover was reduced, Orange-crowns concentrated foraging activities in shrub cover and maintained nondisturbance densities. Indices of foraging-height diversity showed a marked decrease after the removal of deciduous trees. All species except MacGillivray's foraged lower in the vegetative substrate on the nondeciduous tree sites; MacGillivray's concentrated foraging activities in the low shrub cover on both sites. Indices of foraging overlap revealed a general pattern of decreased segregation by habitat after removal of deciduous trees.

I suggest that the basic patterns of foraging behavior and habitat selection evidenced today in western North America were initially developed by ancestral warblers before their invasion of the west. Species successfully colonizing western habitats were probably preadapted to the conditions they encountered, with new habitats occupied without obvious evolutionary modifications. *Received 18 August 1980, accepted 20 February 1981.*

STUDIES of similar coexisting species usually enumerate ecological differences that presumably reduce the demand upon common resources and allow coexistence (Williams and Batzli 1979). MacArthur's (1958) classic study of niche segregation by sympatric *Dendroica*, followed by a series of similar studies by Morse (1967, 1968, 1971, 1973, 1976) and Ficken et al. (1968), which dealt with several genera, led to the conclusion that competition for limited resources played the primary role in structuring warbler species assemblages in the eastern United States. The identification of ecological differences alone, however, does not demonstrate the role of competition in structuring avian communities (Schoener 1974). Experimental manipulations are useful means of examining the role of foraging plasticity in species coexistence (Williams and Batzli 1979, Landres and MacMahon 1980).

This study was designed to (1) document the foraging behavior, habitat selection, and population densities of a MacGillivray's (*Oporornis tolmiei*)—Orange-crowned (*Vermivora celata*)—Wilson's (*Wilsonia pusilla*) warbler assemblage that occurred on clearcuts in the Oregon Coast Range, and (2) assess the response of this assemblage to removal of the deciduous tree component on the clearcuts. Results are related to an hypothesis about the formation and structure of western warbler assemblages.

The species observed in this study breed commonly in many communities in western North America. In addition, races of the Wilson's Warbler range eastward

TABLE 1. Description of study sites.

Site name	USFS number	Site size (ha)	Elevation (m)	Aspect	Years post-planting <sup>a</sup>	Location
Deciduous tree (DT) group						
Benner <sup>b,c</sup>	3403-51	21	300-450	NE	5	Lincoln County, Oregon (T14S, R9W; sec. 14, 23)
Dill Pickle <sup>b</sup>	3502-16	31	110-280	NE	7	Lane County, Oregon (T15S, R9W; sec. 17)
Non-deciduous tree (ND) group						
Green Divide <sup>b,c</sup>	3503-38	36	150-400	N	5	Lane County, Oregon (T15S, R9W; sec. 31)
Bear Creek <sup>b</sup>	3404-51	24	150-370	NE/SE	5	Lincoln County, Oregon (T15S, R10W; sec. 4, 5)

<sup>a</sup> Age of conifer at beginning of study.

<sup>b</sup> Studied in 1979.

<sup>c</sup> Studied in 1980.

across Canada and the northern United States to Newfoundland, Ontario, Vermont, and Maine (A.O.U. 1957). These warblers are usually described as common inhabitants of brushlands and second-growth forests, although the Wilson's and, to a lesser extent, the Orange-crown, are often associated with riparian vegetation (Gabrielson and Jewett 1940, Bent 1953). In western Oregon, the species are primarily summer residents, arriving in early May and departing in August or September for southern wintering grounds (Gabrielson and Jewett 1940, A.O.U. 1957).

#### STUDY AREAS AND METHODS

##### STUDY AREAS

From May to August during 1979 and 1980, I obtained data from four clearcuts in the Oregon Coast Range, Siuslaw National Forest; all sites were as similar in size and topography as possible (Table 1). These sites had been clearcut logged (all standing wood cut, including noncommercial species) and the logging slash burned. About 1 yr after burning, and 5-7 yr before this study, each site was hand planted with Douglas fir (*Pseudotsuga menziesii*) seedlings at 3 × 3-m spacings. The vegetation in this early (5-7 yr) stage of succession is heterogeneous and characterized by a dominance of shrubs. Red alder (*Alnus rubra*), ranging to 7 m in height, was the major deciduous overstory during this period. The shrub-dominated, seral stage persists until the understory is overtopped by conifer saplings, usually 15-20 yr after planting. Plants typical of this shrub layer included salmonberry (*Rubus spectabilis*), thimbleberry (*R. parviflorus*), vine maple (*Acer circinatum*), and salal (*Gaultheria shallon*). Dominants in the low shrub-herb layer included sword fern (*Polystichum munitum*), tansy ragwort (*Senecio vulgaris*), foxglove (*Digitalis purpurea*), pearly everlasting (*Anaphalis margaritacea*), Oregon oxalis (*Oxalis oregana*), and various grasses.

Study sites were placed into two groups based on whether or not their deciduous tree component had been removed; these groups will be referred to as deciduous tree (DT) and nondeciduous tree (ND) sites, respectively. The deciduous trees (primarily red alder) on ND had been removed by aerial herbicide application. Because of the similarity in the vegetative and avian community parameters on the sites within each group, data for sites were combined by group and reported as DT and ND only.

##### AVIAN PARAMETERS

*Foraging behavior.*—Foraging behavior of each species was determined by recording movements of individual birds. Data recorded included: species, sex, foraging location (e.g. foliage, limb), foraging height, foraging-substrate height, and weather conditions. These data were recorded once per minute for each individual depending upon the visibility of the bird. The mean observation time for all individuals

TABLE 2. Vegetation variables used in analyses of warbler habitat selection and assemblage structure, and general vegetative structure of study sites.

Variable	Mnemonic
Percentage shrub cover	SHBCV
Height of shrubs (m)	SHBHT
Percentage conifer cover	CONCV
Height of conifers (m)	CONHT
Number of conifers	CONNO
Percentage deciduous tree cover	DECCV
Height of deciduous trees (m)	DECHT
Number of deciduous trees	DECNO
Number of snags	SNAG
Number of stumps	STMP
Total percentage ground cover	TOTCV
Total number of trees	TOTNO

was  $11.5 \pm 5.03$  min. As females are rather secretive during breeding, only data for males are analyzed herein. Data are likely biased towards singing males, which, through their conspicuousness, would be expected to be disproportionately represented in the samples relative to nonsinging males.

A primary measure of foraging behavior concerns the spatial distribution of foraging zones. The percentage of observations of foraging at different height intervals (0.0–1.0, 1.1–3.0, and >3.0 m) was used to calculate vertical foraging diversity using the equation  $H' = -\sum p_i \log p_i$ , where  $p_i$  is the proportion of the  $i^{\text{th}}$  category. All values appear as the ratio  $J' = H'/H'_{max}$  (Pielou 1966), where  $H'_{max}$  is the maximum possible diversity.  $J'$  corrects for the effects of different numbers of categories. As tree height seldom exceeded 5 m, finer division of the vertical strata was not warranted.

To assess the extent of overlap in foraging between species on DT and ND, I calculated niche overlap based on the use of vertical vegetative strata in relation to the availability of such strata on the study areas. I used an index,  $L$ , developed by Hurlbert (1978; equations 9, 10, and 11), which takes into account the resources available to the species (see also Petraitis 1979). For a given resource state (using  $L$ ), the number of interspecific encounters will be proportional to the densities of two species and the abundance of the resource state.  $L$  assumes a value of zero when no resource state is shared by two species, a value of 1.0 when both species use each resource state in proportion to its abundance, and a value over 1.0 when both species use certain resource states more intensively than others and the utilization functions (or preferences) of two species tend to coincide (Hurlbert 1978). Following Hurlbert (1978), niche overlap is defined as "the degree to which frequency of interspecific encounters is higher or lower than it would be if each species utilized each resource state in proportion to its abundance."

*Avian census technique.*—The census technique used was the variable-circular plot method. Reynolds et al. (1980) gave a thorough description of this census technique. In this study, 10 census stations were systematically established on each study area. No station was closer than 100 m to the clearcut edge nor closer than 100 m to the nearest station. Birds were censused using both visual and auditory signals for 8 min at each station on a study area beginning at sunrise. Censusing the 10 stations on an area required about 2 h; only one area was censused per day. All study areas were censused once per week for a total of five censuses per year during the breeding season (mid-May–July). Densities reported represent the number of males observed.

*Habitat use.*—Analysis of vegetation within breeding territories has been used to describe the habitat requirements of birds (James 1971; Anderson and Shugart 1974; Whitmore 1975, 1977; Noon and Able 1978). To document the habitat selected by the warblers, I sampled vegetation in 5-m-radius plots within the territories of birds on each site; singing males served as the center of each plot (James 1971). A visual estimate of the vegetation variables given in Table 2 was made for each plot.

These data were analyzed by Discriminant Function Analysis (DFA) with stepwise inclusion of variables using the Statistical Package for the Social Sciences (Klecka 1975). DFA identifies the variables of primary importance in separating the habitats used by each species. The procedure began with a test of the null hypothesis of homogeneity of within-species variance-covariance matrices (Cooley and Lohnes 1971: 224). These data did not meet the assumption of equality of variance-covariance matrices, indicating that the multivariate representation of the groups differed in dispersion. Thus, the test of the null hypothesis of equality of group centroids in measurement space was not strictly valid. The test of equality of group centroids is fairly robust, however, under departures from equality of group dispersions (Cooley and Lohnes 1971: 228).

The discriminant program also evaluated the original set of cases to determine how many were correctly classified by the variable(s) selected by the stepwise procedure. The number of groups to which a species is misclassified and the extent of misclassification were used as an index of habitat niche breadth for each species (Noon and Able 1978). The program also computed *F*-statistics between all pairs of species (referred to as the *F*-matrix) based on the variables entered in the stepwise procedure. The *F*-matrix was used to give a general index of similarity in habitat use.

To help determine whether species were utilizing a specific set of habitat variables, an index developed by Jacobs (1974), which identified the use of a variable in proportion to its availability, was applied:

$$D_{hb} = \frac{r - p}{r + p - 2rp}$$

where  $D_{hb}$  is the index of habitat utilization,  $r$  is the proportional use of a given variable, and  $p$  is the proportional availability of that variable.  $D_{hb}$  varies from  $-1$  to  $0$  for negative use, and from  $0$  to  $1$  for positive use. I based  $D_{hb}$  on a comparison of general vegetation structure of the study areas (availability) with vegetation structure used by a bird (use). To aid comparison of habitat utilization between species and sites, the  $D_{hb}$  values were categorized as follows:  $D_{hb}$  of  $0$  to  $\pm 0.15 = 0$  (no preference);  $\pm 0.16$  to  $0.40 = +$  or  $-$  (slight preference or avoidance);  $0.41$  to  $0.80 = ++$  or  $--$  (moderate preference or avoidance); and  $\pm 0.81$  to  $1.0 = +++$  or  $---$  (strong preference or avoidance).

#### VEGETATION SAMPLING

*Vegetation structure.*—Structural characteristics of vegetation on each area were analyzed by placing 50 5-m-radius plots on an area following a stratified random sampling scheme. A visual estimate of variables listed in Table 2 was made for each plot. Data were analyzed by DFA as described for the analysis of avian habitat parameters.

*Vertical complexity.*—At each avian census station, two sampling points were placed about 20 m from the station in two random directions. A 30-m line transect intersecting each of these two points in random directions was used to measure vegetative diversity and cover by height classes. Vertical readings were taken at 2-m intervals along the transect to record presence or absence of vegetation for each of three height classes (0.0–1.0, 1.1–3.0, and >3.0 m). A measure of foliage height diversity ( $J'$ ) was then calculated. Percentage vegetation cover was the sum of percentage covers in each layer over all layers; maximum cover was 300% for all three layers.

*Habitat heterogeneity.*—Foliage height diversity and percentage cover measure complexity in the vertical plane only. The horizontal component, or patchiness, of habitat diversity, however, can also be an important predictor of the avian community (MacArthur 1964, Wiens 1974, Roth 1976).

I calculated an index of habitat heterogeneity in a manner similar to the "closest individual" method of Greig-Smith (1957). Distance in two random directions from each of the points (used for measuring vertical complexity) to the nearest deciduous tree and/or shrub over 2.0 m tall was measured; 40 distances were recorded for each site. Shrubs were defined functionally; that is, a contiguous clump of individuals was considered one "clump." Distances were measured to the center of each clump. Because the distances involved give information about dispersion and diversity, they should measure heterogeneity (Roth 1976). The index of heterogeneity ( $IH$ ) was calculated using the equation for the coefficient of variation,  $IH = 100 \text{ SD}/\bar{x}$ , where  $\text{SD}$  is the standard deviation and  $\bar{x}$  the mean of point-to-plant distances (Roth 1976).

## RESULTS

*Vegetation analysis.*—Nearly all measured variables differed between DT and ND sites (Table 3). The magnitude of difference for variables between sites was relatively minor, however, except for deciduous tree cover (DECCV). On both DT and ND, DECCV was concentrated as scattered pockets of red alder. These trees, averaging about 2.4 m (compared with 1.4 m for conifer and 1.0 m for shrubs), provided the tallest cover on the areas. Of course, deciduous tree cover on DT was substantially greater than on ND. The higher habitat heterogeneity ( $IH$ ) and foliage height diversity ( $J'$ ) indices on DT relative to ND was evidence of the more patchy and thus structurally diverse nature of DT.

TABLE 3. Summary of selected measures of the vegetative characteristics of the deciduous tree (DT) and nondeciduous tree (ND) study sites.

Variable <sup>a</sup>	DT <sup>b</sup>		ND <sup>b</sup>		Difference <sup>c</sup>
	$\bar{x}$	SD	$\bar{x}$	SD	
SHBCV	42.5	26.30	62.4	26.39	***
SHBHT	0.9	0.38	1.0	0.32	**
CONCV	7.0	6.16	3.7	7.38	**
CONHT	1.7	0.75	1.4	0.43	**
DECCV	26.6	27.74	8.0	11.15	***
DECHT	2.8	1.65	2.0	1.59	***
TOTCV	76.1	34.43	79.5	31.48	ns
Layer (%)					
L1 (0–1 m)	88.0		90.2		
L2 (1.1–3 m)	35.8		16.6		
L3 (>3 m)	10.0		1.3		
Evenness ( $J'$ )	0.660		0.492		
IH (%)	65.9		45.9		

<sup>a</sup> For variable codes, see Table 2.

<sup>b</sup> Sample sizes = 50 5-m-radius plots per site.

<sup>c</sup> \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ , ns = nonsignificant;  $t$ -test.

Discriminant analysis identified DECCV as the only variable with the power to separate the site classes based on overall vegetative structure; the stepwise procedure terminated after entering this variable. The function was strong, with 70% of each site class correctly classified.

*Avian density estimates.*—Density estimates for the MacGillivray's and Orange-crowned were nearly identical between site classes, while density for Wilson's was about twice as high on DT relative to ND (Table 4). Although no species was a clear dominant (as measured by population density) on DT, the Orange-crowned composed about 50% of the warbler assemblage on ND.

*Discriminant analysis of warbler assemblages.*—The stepwise procedure identified DECCV as the only variable important in the separation of warblers on DT and ND. The assemblage was thus arranged on a continuum of increasing deciduous tree cover. Ordering of species on the ordinate related MacGillivray's to shrub cover and Wilson's to deciduous trees, with Orange-crowns placed in an intermediate position (Fig. 1).

There was significant separation between species on DT, with each warbler occupying an identifiable pattern of vegetation. No separation existed, however, between MacGillivray's and Orange-crowns on ND; that is, they showed extensive similarity in use of habitat structure ( $F$ -matrix, see Fig. 1).

TABLE 4. Density estimates (males/40.5 ha) for warblers on deciduous tree (DT) and nondeciduous tree (ND) study sites.<sup>a</sup>

Species	DT		ND	
	Density	%	Density	%
Orange-crowned Warbler	41.6 ± 11.1	38.3	47.6 ± 9.3	52.7
MacGillivray's Warbler	29.6 ± 8.4	27.6	25.7 ± 7.1	28.4
Wilson's Warbler	36.0 ± 6.8	33.6	17.1 ± 6.4	18.9
Total	107.2		90.4	

<sup>a</sup> Values =  $\bar{x} \pm 95\%$  C.I.

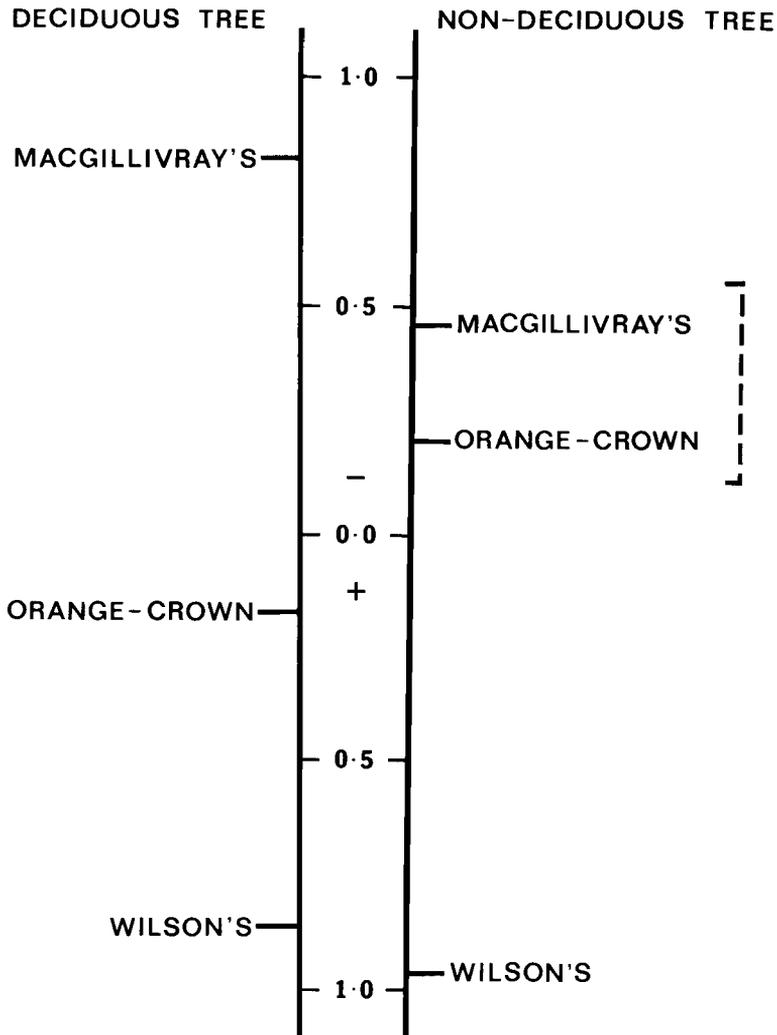


Fig. 1. Ordinations of singing male warblers on deciduous tree and nondeciduous tree study sites based on Discriminant Function Analysis of habitat variables used by the species during breeding. Dashed vertical line denotes nonsignificant separation of species based on the *F*-matrix. Increasing (+) values correspond to increasing deciduous tree cover.

The classification procedure (Table 5) confirmed the generalized nature of habitat utilization for Orange-crowns, with only about 15% correctly classified on each site class; the remaining cases for this species were divided (i.e. misclassified) between MacGillivray's and Wilson's. Between 75% and 88% of the cases were correctly classified as MacGillivray's. The preponderance of shrub cover on all sites made such classification obvious given the frequent use of shrubs by this species on all study areas. Wilson's were rather specific in their use of vegetation (about 60% correctly classified); the majority of the remaining cases for this species were actually classified as Orange-crowned habitat. Here again, the relatively high use of deciduous trees by Wilson's was shown.

TABLE 5. Classification matrix derived from discriminant function program showing actual and predicted species (group) membership for singing male warblers based on habitat use on the deciduous tree and nondeciduous tree sites.

Actual group	Predicted group membership <sup>a</sup>		
	Orange-crowned	MacGillivray's	Wilson's
	<i>Deciduous tree sites</i>		
Orange-crowned Warbler	<u>13.0</u>	47.8	39.1
MacGillivray's Warbler	9.1	<u>87.9</u>	3.0
Wilson's Warbler	25.9	14.8	<u>59.3</u>
	<i>Nondeciduous tree sites</i>		
Orange-crowned Warbler	<u>16.1</u>	58.1	25.8
MacGillivray's Warbler	16.1	<u>74.2</u>	9.7
Wilson's Warbler	26.1	13.0	<u>60.9</u>

<sup>a</sup> Underlined numbers denote percentage correctly classified.

*Habitat use.*—Examination of habitat variables used by singing male warblers showed an increased proportion of shrub cover (SHBCV) by all species and a decreased proportion of DECCV for each species except MacGillivray's on ND compared to DT (Table 6). More important was a species' use of a variable in relation to its availability. Indices of habitat utilization ( $D_{hb}$ ) showed a strong propensity for DECCV and total cover (TOTCV) by Wilson's on both DT and ND; Wilson's showed an increased use of SHBCV on ND (Table 7). MacGillivray's was associated with low DECCV on both site classes and exhibited a positive relationship with SHBCV; Orange-crowns showed a weak relationship with DECCV where this vegetation was available (DT), but otherwise showed no definite pattern of habitat use.

*Foraging behavior.*—Indices of foraging height diversity showed a marked decrease on ND compared to DT (Table 8). The relatively specialized nature of MacGillivray's and Wilson's compared to the generalized foraging habits of Orange-crowns was evident—Orange-crowns showed the widest niche breadth as measured by foraging-site selection. Examination of actual heights and layers of vegetation used for foraging revealed the reason for these lower diversity values on ND—all

TABLE 6. Summary of selected habitat variables for singing male warblers on deciduous tree (DT) and nondeciduous tree (ND) study sites.<sup>a</sup>

Variable <sup>c</sup>	Orange-crowned <sup>b</sup>		MacGillivray's <sup>b</sup>		Wilson's <sup>b</sup>	
	DT	ND	DT	ND	DT	ND
SHBCV	45.7 (26.94)	54.7 (26.89)	44.8 (24.45)	63.9* (26.35)	36.9 (27.98)	71.0* (23.72)
CONCV	8.4 (8.24)	4.8 (11.50)	7.7 (5.19)	3.7* (3.28)	5.1 (4.76)	2.1* (2.94)
DECCV	30.3 (28.54)	10.2* (12.97)	7.6 (10.05)	6.7 (10.92)	46.7 (26.89)	26.9* (18.28)
TOTCV	84.4 (34.72)	69.7 (28.64)	60.2 (27.18)	74.2 (28.60)	88.7 (35.52)	100.0 (30.56)
Sample size <sup>d</sup>	33	41	43	41	37	33

<sup>a</sup> Values =  $\bar{x}$  (SD).

<sup>b</sup> \* $P < 0.05$ ,  $t$ -test.

<sup>c</sup> For variable codes, see Table 2.

<sup>d</sup> Sample size = number of 5-m-radius plots.

TABLE 7. Indices of habitat utilization ( $D_{hb}$ ) based on selected measures of vegetation structure for singing male warblers on the deciduous tree (DT) and nondeciduous tree (ND) sites.

Species	SHBCV <sup>a</sup>		CONCV		DECCV	
	DT	ND	DT	ND	DT	ND
Orange-crowned Warbler	0 <sup>b</sup>	0	0	0	+	0
MacGillivray's Warbler	0	+	0	0	--	-
Wilson's Warbler	0	+	-	-	++	++

<sup>a</sup> For variable codes, see Table 2.

<sup>b</sup> For definition of values, see text; in general, - = avoidance, + = preference, 0 = no preference or avoidance.

species except MacGillivray's foraged lower in the vegetative substrate on ND relative to DT (Table 9).

Indices of foraging overlap revealed a general pattern of decreased segregation by habitat (vertical stratification) on ND relative to DT (Table 10). On the structurally more diverse DT sites, the species concentrated foraging activities in somewhat distinct types of vegetation. Thus, MacGillivray's and Wilson's did not share foraging resources to a significant degree (the former in shrubs, the latter in deciduous trees), Orange-crowns and Wilson's occasionally co-occurred when the former used deciduous trees, and Orange-crowns and MacGillivray's concentrated their activities in shrub cover in rough proportion to its availability. These results parallel the placement of species on the shrub to deciduous tree continuum identified by Discriminant Function Analysis.

On ND, however, all pairwise comparisons were near a value of 1.0, indicating that each resource substrate was used in proportion to its abundance. These results were a function of heavy shrub cover and lack of significant vertical structure on ND. That is, the shrub layer provided ample cover so no two species were forced to co-occupy a relatively scarce habitat patch.

#### DISCUSSION

The species were shown to segregate in habitat preference along an abstract gradient of increasing deciduous tree cover—MacGillivray's and Wilson's warblers utilized shrub cover and deciduous trees, respectively, while Orange-crowned Warblers occupied both of these vegetation types. When the deciduous tree cover was severely reduced, the Orange-crowns concentrated their foraging in the shrub layer and, as a result, maintained nondisturbance densities. The Wilson's Warbler showed limited compensation for habitat alterations, however, and was present in lower density on ND.

Results following habitat manipulation thus confirmed that the density of a species

TABLE 8. Indices of foraging height diversity for singing male warblers on the deciduous tree (DT) and nondeciduous tree (ND) study sites.<sup>a</sup>

Species	Foraging height ( $J'$ )	
	DT	ND
Orange-crowned Warbler	0.824	0.633
MacGillivray's Warbler	0.776	0.484
Wilson's Warbler	0.647	0.523

<sup>a</sup> For sample sizes, see Table 9.

TABLE 9. Summary of selected foraging parameters for singing male warblers on the deciduous tree (DT) and nondeciduous tree (ND) study sites.

Species	Sample size		Foraging height (m) <sup>a</sup>		Percentage use (0–1 m)		Percentage use (1.1–3 m)		Percentage use (>3 m)	
	DT	ND	DT	ND	DT	ND	DT	ND	DT	ND
Orange-crowned Warbler	252	289	1.7 (0.23)	0.8* (0.48)	43.8	86.0	37.8	14.0	18.5	0.0
MacGillivray's Warbler	226	245	0.8 (0.25)	0.6 (0.40)	84.1	91.3	14.1	8.7	1.8	0.0
Wilson's Warbler	158	213	2.4 (0.19)	0.8* (0.59)	17.7	68.5	56.3	28.4	25.9	3.2

<sup>a</sup> Values =  $\bar{x}$  (SD); \* $P < 0.05$ ;  $t$ -test.

was related to the extent of available habitat and its ability to compensate for loss of this habitat. Patterns of habitat use, however, do not address the underlying evolutionary and biogeographic factors that were initially responsible for such utilization patterns. I will now briefly develop an hypothesis concerning the structure of warbler assemblages in the western United States in relation to the results reported herein.

Warblers currently occupying the western United States are apparently descendants of eastern North American species that invaded the west during the Pleistocene (Mengel 1964, 1970). Species successfully invading the west were probably preadapted to the conditions they encountered. Allee et al. (1949: 643) felt that such preadaptation was shown in the fitness of organisms adjusted to new habitats that have many factors in common with the habitats they originally occupied in ancestral forms; new habitats are often invaded without obvious evolutionary modifications. Those species surviving the successive glacial periods during the Pleistocene would thus be in a favorable position to expand into newly developing habitat as the glaciers receded—subsequent invasion by similar species would thus be difficult. Indeed, relatively little invasion has occurred following the most recent glacial period (Mengel 1964).

Species in this study all exhibit patterns of habitat use and foraging behavior similar to those of their hypothesized ancestors, or in the case of the Wilson's Warbler, eastern races of the species (Griscom and Sprunt 1957: 41, Mengel 1964). Therefore, possible competitive forces in western habitats have not greatly altered habitat selection and foraging behavior of these species; that is, competitive exclusion in the west was not necessarily responsible for the species assemblages and behavior seen in this study. Slight modifications in morphological and behavioral attributes

TABLE 10. Indices of foraging overlap ( $L$ ) for singing male warblers on the deciduous tree (DT) and nondeciduous tree (ND) sites.<sup>a</sup>

	Foraging overlap ( $L$ )	
	DT	ND
Orange-crown vs. MacGillivray's	0.80	1.10
Orange-crown vs. Wilson's	1.55	0.96
MacGillivray's vs. Wilson's	0.60	0.91

<sup>a</sup> For sample sizes, see Table 9.

in western warblers as compared to their eastern ancestors or present eastern counterparts may be due to competitive release and differing environments. The distinction between eastern and western assemblages thus lies with the timing given the processes that initially created the structure of the assemblages. It has been theorized that the structure of warbler assemblages in the eastern United States was developed through competitive interactions for essential resources (MacArthur 1958; Ficken et al. 1968; Morse 1968, 1971). The close correspondence between most eastern and western species (east-west phylogenetic species-pairs, Mengel 1970) indicates that these competitive processes had their greatest impact on western warblers before the invasion of western habitats. Differences in habitat selection and foraging behavior should not *a priori* be considered solely a result of competitive forces operating in areas currently occupied by the species.

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## LITERATURE CITED

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