

THE STRUCTURE OF WESTERN WARBLER ASSEMBLAGES: ECOMORPHOLOGICAL ANALYSIS OF THE BLACK-THROATED GRAY AND HERMIT WARBLERS

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ABSTRACT.—This study analyzes ecological and morphological relations of the Black-throated Gray (*Dendroica nigrescens*; BTG) and Hermit (*D. occidentalis*; HW) warblers in western Oregon. Wing and tail lengths differed between the male and female of each species. Wing shapes, however, were similar between sexes within each species. Playback experiments showed strong responses to homospecific songs by the HW and BTG in areas of allopatry and sympatry. Response to heterospecific song was evident only in areas of allopatry for the two species. Habitats used by the HW were characterized by relatively heavy total conifer cover. The BTG used habitats with relatively heavy deciduous tree cover. Territories of the two species overlapped in an ecotone between stands dominated by conifer and those dominated by oak. The habitat utilization functions of the species did not overlap. The type and proportion of foraging maneuvers used were also similar for both species and sexes. Use of trees usually occurred at different heights for sexes of HW. Comparison of male BTG with both male and female HW showed a slight possibility of encounter while foraging. Indices of foraging height diversity (J') were similar between species and sexes, except for the female HW, which had a higher J' . Overlap while foraging was minimized because of the lack of substantial overlap in habitat use for the two species. The division of foraging zones is discussed in relation to morphology and habitat use. Received 11 November 1981, accepted 5 February 1982.

THE study of groups of closely related organisms living together in the same area has long intrigued biologists (see Hutchinson 1975, Morse 1980a: 253, for reviews). Of particular interest here is the work initiated by MacArthur (1958) and later refined and expanded by Morse (1968, 1971, 1980a) and others. The major conclusion of these authors—that competition for certain resources was primarily responsible for structuring warbler species assemblages in the eastern United States—has become an axiom of current avian ecological theory. Variations of this theory have also been invoked to explain intersexual differences in foraging behavior and habitat use in other species (Rand 1952, Selander 1966, Williams 1980).

The present study seeks to broaden my previous work on warbler assemblages in the western United States (Morrison 1981) by examining the ecological and morphological relations of two species of western *Dendroica*. My specific objectives were to (1) analyze the foraging behavior, habitat use, interspecific song recognition, and morphological relationships

of the Black-throated Gray (*D. nigrescens*; BTG) and Hermit (*D. occidentalis*; HW) warblers in western Oregon, and (2) compare aspects of foraging behavior between males and females of both species.

The BTG and HW are common breeding species throughout much of western North America. The BTG frequents both deciduous and coniferous forests, constructing nests at low to moderate heights in both types of substrates (Barlow 1899a, Bowles 1902, Bent 1953, Griscom and Sprunt 1979). The HW concentrates foraging and nesting activities in coniferous trees, apparently preferring stands of moderately dense Douglas-fir (*Pseudotsuga menziesii*) and true fir (*Abies*) (Barlow 1899b, 1900; Bowles 1906; Bent 1953; Griscom and Sprunt 1979). Both species are primarily summer residents in western Oregon, the BTG arriving during mid-April and the HW during early May.

STUDY AREAS

The primary study area was located near the west entrance of the William L. Finley National Wildlife

Refuge (FINLEY), Benton County, Oregon. The study area, encompassing about 30 ha, was characterized by a mixture of mature Oregon white oak (*Quercus garryana*) and Douglas-fir; bigleaf maple (*Acer macrophyllum*) were scattered throughout the stand. Douglas-fir was dominant on a broad, low ridge running through the center of the study area, and oak dominated throughout the remainder of the site. The understory was a mixture of Douglas-fir and oak saplings, with occasional individuals of hazelnut (*Corylus cornuta*), cherry (*Prunus* sp.), red alder (*Alnus rubra*), and madrone (*Arbutus menziesii*). The low shrub-herb layer was dominated by a nearly continuous cover of Pacific poison oak (*Rhus diversiloba*) and scattered clumps of sword-fern (*Polystichum munitum*) and snowberry (*Symphoricarpos albus*). This plant association is described by Franklin and Dyrness (1973: 110). The extreme west edge of the study area had been silviculturally thinned, leaving a nearly pure stand of widely spaced (2–6 m) mature Douglas-fir. Both species of warblers were common breeding birds at FINLEY.

Two additional areas were chosen for study. (1) SOUTH was located near the southwest edge of the Finley refuge, Benton County, Oregon. Vegetation on this area ranged from the same oak-Douglas-fir mixture as at FINLEY to a nearly pure oak stand. The BTG, but not the HW, was observed on this area. (2) MARY'S was located on the middle to upper slopes of Mary's Peak, Benton County, Oregon at an elevation of 410–1,000 m in the western hemlock (*Tsuga heterophylla*)-Douglas-fir zone of western Oregon (Franklin and Dyrness 1973), which is the dominant vegetation zone of the Oregon Coast Range. The HW, but not the BTG, was observed on this area.

METHODS

Morphological measurements.—Museum specimens (adult males and females) of BTG and HW were measured with vernier calipers for the following external characters: length of the outermost seven primaries (P9 to P3; chord of the arc made by the folded wing); tail length; length (anterior edge of nostril to tip), width (at anterior edge of nostril), and depth (at anterior edge of nostril) of bill; length of hallux minus claw; claw length; and tarsus length (diagonal distance between the tibiotarsal-tarsometatarsal joint and the last undivided scute). Date and location were transcribed for all specimens. To reduce error caused by possible geographic variation in characters, I analyzed only nonmigratory (breeding) birds collected in western Oregon, southwestern Washington, and northwestern California.

Playback experiments.—Songs of BTG and HW were recorded at each study area using a Nagra III recorder and a Gibson parabolic microphone. Tapes used for playback experiments were made by trans-

ferring the original recordings to cassette tapes. For most of the experiments, a Realistic CTR-41 cassette recorder connected by 7 m of cord to a speaker (without amplification) was used. Experiments were also conducted using the Nagra and the original tapes for playback.

Experiments were conducted by placing the speaker within 30 m of a singing, and thus probably territorial, male warbler. In the areas of allopatry (SOUTH and MARY'S), the song of the heterospecific species was presented first; in the area of sympatry (FINLEY), the sequence was randomized (Milligan 1966, Ficken and Ficken 1969, Gill and Murray 1972, Emlen et al. 1975). If the first playback produced no response, the second song was played after a delay of 60 s. If the male showed a positive reaction (approach) to the first playback, the second playback was delayed for at least 15 min.

Each experiment consisted of a preliminary 3-min control (silent) period, followed immediately by a 3-min playback, followed by another 3 min of silence. Another song was played following the last silent period, depending on the response of the bird to the first playback. During each 3-min period, the rate of singing, song type, and activity and location of the bird (e.g. distance from speaker) were recorded. An "attack" was considered any flight directly over and within 2 m of the speaker.

Songs of the Townsend's (*D. townsendi*; TW) and Yellow-rumped (*D. coronata auduboni*; YRW) warblers were also played to BTG and HW at all study areas; the sequence of playback (homo- and heterospecific) was randomized. Songs of the TW and YRW, recorded in western habitats outside of our study areas, were obtained from the Library of Natural Sounds, Laboratory of Ornithology, Cornell University. TW and YRW are spring and fall migrants in the study areas but are not known to breed there. The use of TW and YRW songs was designed to increase the choices presented to each breeding species and to avoid some of the problems associated with playback experiments (see Fitzpatrick 1980).

Foraging behavior.—Foraging activities of BTG and HW were recorded during the breeding season (May and June). Data recorded for each individual included: species, sex, foraging location (e.g. foliage, limb), foraging height, species and height of foraging substrate, limb length and distance of bird out on limb from tree bole, and mode of attack (i.e. gleaning, hover-gleaning, or flycatching). These data were recorded once per min when a bird was actively foraging, to a maximum of 10 min observation time for a single individual. Mean observation time for all individuals was 4 min (SD = 3.5).

The percentage of foraging observations at five height intervals (0.0–4.0, 4.1–10.0, 10.1–20.0, 20.1–30.0, >30.0 m) was used to calculate a measure of vertical foraging diversity using the equation $H' = -\sum p_i \log p_i$, where p_i is the proportion of observa-

TABLE 1. Morphological measurements of male and female Black-throated Gray and Hermit warblers (units = mm). Data are the length of the variable unless noted otherwise.

	Black-throated Gray Warbler			Hermit Warbler			P ^a
	\bar{x}	SD	Range	\bar{x}	SD	Range	
MALES (n = 25) ^d							
P8 ^{b,c}	61.9	1.56	59.0-64.6	67.0	0.88	65.0-68.4	*
Tail	49.8	1.74	46.7-52.7	51.8	1.23	49.0-53.4	*
Tarsus	16.8	0.43	16.2-17.7	17.5	0.49	16.6-18.6	*
Bill length	6.9	0.28	6.5-7.7	6.8	0.19	6.5-7.2	ns
Bill width	3.0	0.16	2.7-3.2	2.7	0.14	2.5-3.1	*
Bill depth	3.2	0.14	3.0-3.5	3.0	0.12	2.8-3.3	*
Hallux	4.7	0.28	4.3-5.3	4.9	0.24	4.4-5.3	ns
Claw	4.5	0.20	4.1-4.8	4.8	0.17	4.5-5.1	*
FEMALES (n = 11) ^d							
P8 ^{b,c}	59.3	1.23	58.0-62.4	63.0	0.85	62.1-64.7	*
Tail	47.9	1.50	46.1-51.3	49.7	1.46	47.5-52.5	*
Tarsus	16.7	0.35	16.2-17.4	16.8	0.43	16.1-17.5	ns
Bill length	6.8	0.23	6.4-7.2	6.8	0.18	6.6-7.1	ns
Bill width	2.9	0.15	2.7-3.2	2.6	0.14	2.4-2.8	*
Bill depth	3.2	0.19	2.9-3.6	2.9	0.13	2.8-3.2	*
Hallux	4.7	0.21	4.3-5.1	4.9	0.20	4.6-5.3	ns
Claw	4.4	0.16	4.1-4.7	4.7	0.09	4.7-4.9	*

^a * = P < 0.01, ns = nonsignificant; t-test.
^b P = primary number.
^c P9 to P3 plotted in Fig. 1.
^d n = number of specimens per species.

tions in the *i*th category. All values appear as the ratio $J' = H'/H'_{max}$, where H'_{max} is the maximum possible diversity (Pielou 1966). J' corrects for the effect of different numbers of categories.

To help evaluate the extent of overlap in foraging zones between species at FINLEY, I calculated a measure of niche overlap based on the use of vertical vegetative strata in relation to availability of such strata. I used the index, *L*, developed by Hurlbert (1978), which considers both resource availability and use of such resources by the species. *L* assumes a value of zero when no resource state is shared by two species, a value of 1 when both species use each resource state in proportion to its abundance, and a value over 1 when both species use certain resources more intensively than others and their use of such resource states tends to coincide.

Habitat use and availability.—Habitats used during the breeding season by the two species at FINLEY were quantified as follows: a randomly placed point was situated in the territory of an individual. Territories were roughly outlined by following the movements of individual birds and watching for intraspecific encounters (especially during playback experiments). Actual territory size was not determined. Centered on each point, three 15-m lines were paced off, each line at 120°-intervals (the direction of the initial line was randomized). An 8-m-radius plot was then placed at the end of each of the three lines (totalling three 8-m-radius plots in each territory). A visual estimate of the variables listed in

Appendix 1 was made for each plot; a dbh tape was used to measure tree diameter. Five BTG and three HW territories were measured.

Vertical vegetation complexity was determined by taking a vertical reading at 3-m intervals along each of the three 15-m lines at each point in a territory. The presence or absence of live vegetation in each of the five previously defined height intervals was measured by sighting through a 2-cm diameter tube held perpendicular to the ground at each 3-m interval. A measure of foliage height diversity (J') was calculated.

Vegetation available to the birds (site vegetation) was determined by placing seven points (21 8-m-radius plots) on FINLEY following a random sampling scheme. Measurements were recorded at each point as described for habitat-use (territorial) parameters.

To help determine whether or not the warblers were using a specific set of habitat variables (from Appendix 1), I applied an index developed by Jacobs (1974), which identified the use of a variable in proportion to its availability:

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

where D_{hb} is the index of habitat use, r is the proportional use of a given variable, and p is the proportional availability of that variable. D_{hb} ranges from -1 to 0 for negative use, and from 0 to 1 for positive use. To ease interpretation, D_{hb} values were categorized as follows: D_{hb} of 0 to $\pm 0.15 = 0$ (no

TABLE 2. Ratios for wing measurements for male and female Black-throated Gray and Hermit warblers.

	Black-throated Gray		Hermit	
	Male	Female	Male	Female
Wing ratios ^a				
P6/P9	1.01	1.01	0.99	0.99
P4/P9	0.88	0.89	0.85	0.86
P4/P8	0.87	0.88	0.84	0.85

^a P = primary number.

preference); $\pm 0.16-0.40 = +$ or $-$ (slight preference or avoidance); $\pm 0.41-0.80 = ++$ or $--$ (moderate preference or avoidance); and $\pm 0.81-1.0 = +++$ or $---$ (strong preference or avoidance). The overlap index (*L*) of Hurlbert (1978) was used to assess the extent of overlap in habitat use by the species.

RESULTS

Morphological variation.—Male and female Black-throated Gray Warblers differed only in wing and tail lengths (Table 1). The shape of the wings (based on primary length), however, did not vary between sexes (Table 2, Fig. 1). Wing and tail measurements differed between male and female Hermit Warblers (Table 1). As with BTG, wing shape was nearly identical between sexes of HW (Table 2, Fig. 1). Male HW, however, had a slightly longer tarsal measurement than females.

There were marked differences in wing length between BTG and HW of the same sex (intrasexual) (Table 1, Fig. 1). A difference in wing shape was also noted but was confined to differences between P9 and P6 (Table 2). P9 was shorter in BTG, and longer in HW, compared to P6. Wing length of female HW was similar to that of male BTG. Thus, HW had longer, more pointed wings relative to BTG.

Playback experiments.—Results of playback experiments showed a strong response to homospecific songs by HW and BTG in areas of allopatry and sympatry (Table 3). Responses to heterospecific songs, however, were only evident in areas of allopatry for the two species. Both species showed a weak response ("mild interest") to playback of allopatric Townsend's and Yellow-rumped warblers on all study areas.

On at least three occasions at FINLEY, the playback of the BTG was initiated directly below a foraging male HW. While the HW

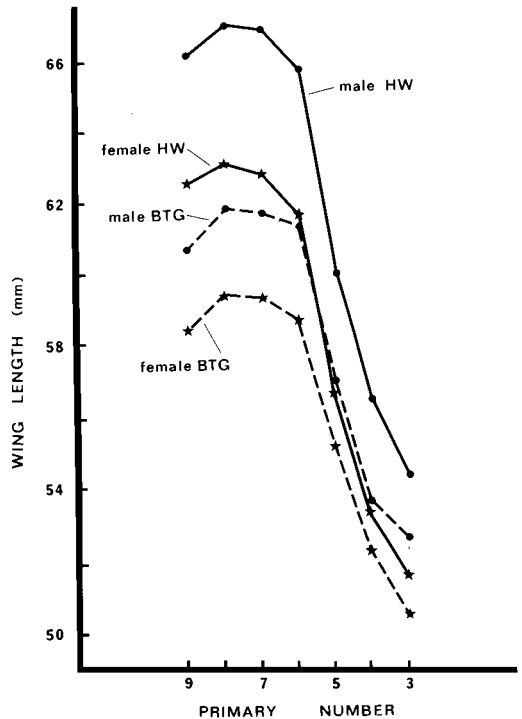


Fig. 1. Length and shape of the wings of male (dots) and female (stars) Black-throated Gray (dashed lines) and Hermit (solid lines) warblers. Sample sizes given in Table 1.

showed no apparent response to playback, two male BTG flew into the area and began chasing one another through the conifers, often approaching to within 2 m of the HW. The HW again showed no antagonism toward either BTG.

Stein (1962) concluded that it is not possible to distinguish the BTG from the HW or TW by voice in every instance. Thus, it is possible that the response by allopatric BTG and HW to each other's songs was a case of "mistaken identity." One would then expect a similar response to playback of TW, however, rather than the relatively weak response noted. By an error in planning, songs of both the TW and YRW were not presented to the HW and BTG until well after territorial establishment. Response by territorial males usually decreases markedly after territorial establishment (Morse 1976a). Thus, even the relatively weak response may be significant, given the complete lack of response by HW and BTG to each other's songs in areas of sympatry (FINLEY).

TABLE 3. Response of male Black-throated Gray and Hermit warblers to playback of homo- and heterospecific songs in areas of sympatry (FINLEY) and allopatry (SOUTH and MARY'S) for the two species.

Location Species tested	Response to playback of ^{a,b}			
	Black-throated Gray	Hermit	Townsend's	Yellow-rumped
FINLEY				
Black-throated Gray Warbler	S 6 (13)	W-N 7 (16)	W-N 3 (4)	W-N 2 (2)
Hermit Warbler	N 5 (15)	S 5 (14)	W-N 3 (3)	W-N 2 (2)
SOUTH				
Black-throated Gray Warbler	S 4 (10)	s 4 (10)	W-N 2 (3)	W-N 1 (2)
MARY'S				
Hermit Warbler	S 7 (15)	S 5 (11)	W-N 4 (6)	W 2 (2)

^a S = strong response including frequent "attacks"; s = moderate response including frequent approaches to within 9 m of speaker; W = weak response seldom including more than change in orientation or perch; N = no obvious response. Two letters listed together (e.g. W-N) indicate even response between the two scores.

^b Sample sizes = number of different birds tested (number of tests).

Habitat use.—Data for vegetation analysis of HW, BTG, and the overall study site are given in Appendix 1. For ease of interpretation, D_{hb} values in Table 4 should be consulted. The D_{hb} values generally follow the significance identified by ANOVA (i.e. a variable with a + or – was also usually significant at $P < 0.05$).

The habitat used by HW at FINLEY was characterized by relatively heavy total conifer cover. This cover was the result of a large number of Douglas-fir with greater than 31 cm dbh. Although large (>30 cm dbh) oaks were scattered throughout their territories, total deciduous tree cover was relatively low. There was relatively little vegetation cover for the first (0.0–4.0 m) and second (4.1–10.0 m) vertical layers but relatively greater cover in the fourth (20.1–30.0 m) and fifth (>30.0 m) layers in HW territories. At least two territories of both the HW and BTG overlapped in the ecotone between stands dominated by oak and those dominated by Douglas-fir, a situation that existed along the slightly elevated ridge bisecting the study area and where an oak stand abutted the thinned stand.

The BTG used habitats with relatively heavy deciduous tree cover. This cover was supplied primarily by a high density of small oaks (<30 cm dbh). Although the number of conifers in BTG territories did not differ significantly from that available, D_{hb} values revealed a tendency for avoidance of conifer cover. BTG included

a relatively heavy cover of vegetation in the lower two vertical layers in their territories, although this again was nonsignificant. Although the height of the deciduous trees used by both species did not differ significantly from the height of trees generally available in the habitat, trees used by the HW were significantly shorter than those used by BTG.

Indices of overlap in habitat use (L) for the HW and BTG, calculated for use of conifer and deciduous tree cover, was 0.83. A slightly higher L of 0.93 was obtained when use of cover by height intervals was used to calculate overlap. The utilization functions of these species did not overlap. That is, values of less than 1.0 indicate that the species are distributed randomly with respect to one another (Hurlbert 1978).

Foraging behavior.—The types and proportions of foraging maneuvers used were similar for both species and sexes (Table 5). Gleaning was employed during more than 80% of the foraging time. Use of foraging substrate was virtually identical for male and female HW, with both sexes using Douglas-fir more than 90% of the time. Both male and female BTG used a greater proportion of oak (and thus less Douglas-fir) for foraging than did HW. Male BTG, however, spent a greater proportion of time in Douglas-fir, and thus less in oak, than did females of the species.

Indices of foraging overlap (L) reflected the

TABLE 4. Indices of habitat use (D_{hb}) for Black-throated Gray and Hermit warblers at FINLEY.

Variable	Index of habitat use ^a	
	Black-throated Gray	Hermit
Conifer		
Percentage cover (total)	-	++
<30 cm dbh	0	0
31-90 cm dbh	-	+
>90 cm dbh	0	+
Total number	0	0
\bar{x} height (m)	0	0
Deciduous trees		
Percentage cover (total)	+	--
<30 cm dbh	+	--
>30 cm dbh	0	0
Total number	+	--
\bar{x} height (m)	0	-
Shrub cover (%)	0	0
Layer cover (%)		
0.0-4.0 m	+	--
4.1-10.0	+	--
10.1-20.0	0	0
20.1-30.0	-	+
>30.0 m	0	+
Total cover	0	0

^a List of D_{hb} values given in text; in general, + = preference, - = avoidance.

results of the percentage use of tree species for foraging (Table 6). Male and female HW tended to coincide in use of trees—an L of 1.59 indicated that there existed a 59% greater chance of encounter than would be expected if the sexes were distributed randomly with respect to trees selected. The overlap for male and female HW dropped to nearly 1.0, however, when use of vegetative layers was considered, indicating that use of Douglas-fir by the sexes occurred at different heights. Comparison of male BTG with both male and female HW also revealed a slight (23% and 26%, respectively) possibility of encounter. Males of both species also tended to overlap slightly in use of vegetation by height layers. Female BTG showed no intra- or interspecific overlap in tree species use. Overlap values greater than 1.0 in use of vegetative layers for female BTG are biologically insignificant, given that foraging by these

TABLE 5. Type of maneuver and species of tree used during foraging by Black-throated Gray and Hermit warblers at FINLEY (sample sizes given in Table 7).

Variable	Black-throated Gray		Hermit	
	Male	Female	Male	Female
Foraging type (%)				
Gleaning	82.4	88.2	85.5	82.9
Hover-gleaning	14.2	7.8	12.4	14.6
Flycatching	3.4	3.9	2.1	2.4
Tree species (%)				
Douglas-fir	71.3	34.3	91.4	95.0
Oak	28.7	65.8	8.6	5.0

individuals takes place in different species of trees compared to male BTG and both male and female HW.

The slight overlap in foraging between male BTG and both sexes of HW was also misleading. BTG spent the majority of foraging time in relatively tall Douglas-fir that were scattered throughout their otherwise oak-dominated territories. Male BTG concentrated activities in Douglas-fir in apparent response to the need to use relatively tall structures as song posts. BTG and HW did not overlap in habitat use ($L < 1.0$). Therefore, even the small chance of encounter (26%) noted should be considered extreme.

Male BTG foraged higher in Douglas-fir and oak than did female BTG; the maximum foraging height of males exceeded that of females (Table 7). The absolute height of Douglas-fir, but not oak, used for foraging by male BTG was also greater than that used by females. These results are reflected in the slightly higher

TABLE 6. Indices of foraging overlap (L) for male and female Black-throated Gray (BTG) and Hermit (HW) warblers at FINLEY.

	Male HW	Female HW	Male BTG
Height layers			
Female HW	1.09		
Male BTG	1.56	1.17	
Female BTG	1.25	1.23	1.33
Tree species			
Female HW	1.59		
Male BTG	1.23	1.26	
Female BTG	0.69	0.66	0.86

TABLE 7. Foraging behavior of male and female Black-throated Gray and Hermit warblers at FINLEY; values = \bar{x} (SD) and range; n = number of observations.

Variable	Black-throated Gray Warbler		Hermit Warbler	
	Male ($n = 397$)	Female ($n = 157$)	Male ($n = 400$)	Female ($n = 61$)
Bird height (m)				
Douglas-fir	12.7 (4.75) 0.9-28.0	8.6 (3.71) 2.5-15.0	15.1 (4.81) 0.9-31.0	9.7 (3.61) 2.0-16.0
Oak	11.3 (2.34) 3.0-17.0	9.9 (2.41) 5.5-14.5	12.1 (3.50) 4.0-16.5	— ^a
Total	12.3 (4.27) 0.9-28.0	9.3 (3.11) 2.5-15.0	14.9 (4.78) 0.9-31.0	9.7 (3.61) 2.0-16.0
Tree height (m)				
Douglas-fir	18.9 (5.08) 5.0-30.0	15.4 (4.82) 6.0-25.0	22.9 (6.86) 7.0-35.0	20.1 (7.57) 14.0-40.0
Oak	13.6 (2.36) 9.0-17.0	13.3 (2.66) 7.0-16.0	14.2 (3.40) 6.5-17.0	— ^a
Total	17.4 (5.09) 5.0-30.0	13.8 (4.01) 6.0-25.0	22.3 (7.10) 6.5-35.0	20.1 (7.57) 14.0-40.0
Limb length (m)	2.7 (1.10) 0.5-6.0	3.5 (2.35) 0.5-6.5	2.6 (1.00) 1.1-5.0	2.1 (0.52) 1.5-3.0
Bird on limb (m) ^b	2.2 (1.18) 0.5-5.5	2.6 (2.46) 0.7-6.0	1.5 (0.60) 0.4-3.0	1.2 (0.28) 0.4-2.5

^a Could not be calculated; see text.

^b Distance of bird (on limb) from tree bole.

proportional use of foraging substrates (Table 8).

Although male and female HW used Douglas-fir of similar heights, males foraged considerably higher in conifers than did females (Tables 7 and 8). As female HW were seldom observed in oak, sufficient data could not be obtained for a comparison of male and female positions in this substrate.

Female BTG foraged on longer limbs than

male BTG (Table 7). The relative positions of the sexes were similar, however, with both male and female foraging towards the tips of branches (Table 8). Male HW used slightly longer limbs than did females (Table 7). Both sexes, however, concentrated foraging activities near the center of limbs (Table 8).

The length of limbs used did not differ be-

TABLE 8. Proportional positions of Black-throated Gray and Hermit warblers during foraging at FINLEY; original data given in Table 7.

Variable	Black-throated Gray		Hermit	
	Male	Female	Male	Female
Bird height/substrate height (%)				
Douglas-fir	67.2	55.8	65.9	48.3
Oak	83.1	74.4	85.2	— ^a
Total	70.7	67.4	66.8	48.3
Bird distance/limb length (%) ^b	81.5	74.3	57.7	57.1

^a Could not be calculated; see text.

^b Distance of bird (on limb) from tree bole/length of limb.

TABLE 9. Percentage of foraging observations by height intervals, and a measure of vertical foraging diversity (J'), for male and female Black-throated Gray and Hermit warblers at FINLEY; sample sizes given in Table 7.

Variable	Black-throated Gray		Hermit	
	Male	Female	Male	Female
Height interval (m) ^a				
0.0-4.0	3.0	8.8	1.1	8.9
4.1-10.0	27.5	44.1	16.7	44.4
10.1-20.0	66.4	47.1	73.6	37.8
20.1-30.0	3.0	0.0	7.6	8.9
>30.0	0.0	0.0	1.1	0.0
Foraging height diversity (J')	0.520	0.578	0.510	0.720

^a Values = percentage occurrence.

tween male BTG and male HW. Female BTG, however, used longer branches than did female HW. The difference in limb lengths for females is likely related to the different species of trees used for foraging.

Male BTG and male HW concentrated foraging activities in the third (10.1–20.0 m) height interval (Table 9). Females of both species foraged primarily in the second and third height intervals. Indices of foraging height diversity (J') were similar between species and sexes, except for female HW, which had a higher J' (Table 9). The higher J' for female HW resulted from a more even apportionment of foraging time between the first and fourth, and second and third, height intervals relative to the BTG and male HW.

DISCUSSION

Resource partitioning.—As reviewed by Bloom (1981), interspecific competition is the most often cited explanation for resource partitioning. The absence of observable competition is often taken to mean that competition was so effective in the past (as during community formation) that it is no longer expressed in visible encounters (see Rosenzweig 1981). Under such reasoning, the competition hypothesis becomes nonfalsifiable (Bloom 1981). The critical question thus becomes whether resource partitioning leads to specialization or specialization leads to resource partitioning (Bloom 1981).

Certain *Dendroica* in the eastern United States are known to respond aggressively to one another in areas of territorial overlap; such interactions may be indicative of competition between the species for resources (Morse 1967, 1976b; Ficken et al. 1968). The species in this study, however, displayed no interspecific antagonism in an area of territory overlap. Although the species foraged in the same manner and often in the same types of substrates, overlap was minimal as a result of the use of different habitats. The Black-throated Gray and Hermit warblers apparently evolved from a common ancestor but did so in areas dominated by differing flora (Mengel 1964, Hubbard 1969). The relatively broad differences in habitat use that developed in allopatry are thus probably responsible for the patterns of resource use evident in this study—competition

in the current area of sympatry need not be invoked to explain these utilization patterns.

Development of intersexual foraging differences.—Males of both species spent the majority of time during the reproductive period singing from the upper portion of Douglas-fir trees. Females foraged at lower mean heights than males, concentrating feeding activities near the nest. Similar intersexual differences in foraging zones were found for four species of *Dendroica* in Maine spruce forests (Morse 1968).

Reduction of intersexual competition for food has been given as a reason for sexual foraging differences (Rand 1952, Selander 1966, Williams 1980). Morse (1980a, b) hypothesized that apparent sexual partitioning of foraging zones left an “undiluted” food supply around the nest for the female to utilize (see also Robins 1971). Considerable overlap in foraging heights was noted in this study, however, and by Morse (1968). It seems more parsimonious to assume that intersexual partitioning of foraging zones results from the need for males to use conspicuous perches for territorial establishment and defense and for females to remain near the nest site (see also Morse 1968, Robins 1971, Williamson 1971, Smith 1978). Partitioning of foraging zones may ultimately be the result of sexual selection, which has preadapted the sexes for different types of prey exploitation (Power 1980). Other forms of selection (e.g. avoidance of competition for resources) could exaggerate pre-existing sexual differences (see Power 1980).

Development of interspecific wing morphology.—It has been hypothesized that a relatively short, blunt wing enhances foraging in lower, denser foliage, while longer, pointed wings improve movement in more open sites and taller vegetation (Poole 1938, Hamilton 1961). This could be the ultimate reason for the smaller and differently shaped wings of Black-throated Gray Warblers compared to Hermit Warblers. Shorter wings may enhance foraging in the oak woodlands that Black-throated Gray Warblers occupy over much of their range and apparently preferred in this study. The greater vertical development of conifer forests used by Hermit Warblers may require relatively longer wings for efficient movement within and between trees. The physical requirements of migration, as expressed in wing morphology,

may also influence the length of the primaries. That is, wing length may be related to migratory distance (Hamilton 1961, but see Keast 1980). Thus, differences in habitat and/or migratory patterns may account for interspecific differences in wing length and shape.

ACKNOWLEDGMENTS

I am grateful to R. Greenberg, J. P. Hubbard, H. M. Power, J. D. Rising, E. C. Meslow, and an anonymous referee for critically reviewing drafts of this paper. P. Sekora and D. Boone facilitated use of the Finley National Wildlife Refuge. J. W. Hardy, Florida State Museum, supplied the Nagra recorder and several playback tapes; his help is deeply appreciated. The curators and staff of the following museums are acknowledged for providing me with study skins: Western Foundation Vert. Zool.; Mus. Comp. Zool.; Mus. Nat. Hist., Univ. Puget Sound; U.S. Natl. Mus. Nat. Hist.; Mus. Vert. Zool.; Thomas Burke Memorial Washington State Mus., Univ. Washington; California Acad. Sci.; Denver Mus. Nat. Hist.; Delaware Mus. Nat. Hist.; San Diego Nat. Hist. Mus.; Zool. Mus., Univ. Montana; Univ. Alaska Mus.; Charles R. Conner Mus., Washington State Univ.; Los Angeles County Nat. Hist. Mus.; Univ. Wyoming; Univ. Colorado Mus.; Oregon State Univ. Fish. and Wildl. Mus.; British Columbia Provincial Mus.; Royal Ontario Mus.; and Dept. Zool., Univ. British Columbia. Special thanks are due R. A. Paynter, N. K. Johnson, A. M. Rea, and D. M. Niles for supplying me with data on numerous occasions; their patience is appreciated. B. J. Verts provided work space at Oregon State. L. Mauer is thanked for preparation of the manuscripts. Funds for this study were provided by the Frank M. Chapman Memorial Fund of the American Museum of Natural History, and the U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Cooperative Agreement 14-16-0009-78-977. This study was conducted under the auspices of the Oregon Cooperative Wildlife Research Unit: Oregon State University, Oregon Department of Fisheries and Wildlife, U.S. Fish and Wildlife Service, and the Wildlife Management Institute, cooperating. This is Oregon State University Agricultural Experiment Station Technical Paper 6228.

LITERATURE CITED

- BARLOW, C. 1899a. The nesting haunts of the Black-throated Gray Warbler. *Condor* 1: 96.
 ———. 1899b. Nesting of the Hermit Warbler in the Sierra Nevada Mountains, California. *Auk* 16: 156-161.
 ———. 1900. Nest and eggs of the Hermit Warbler. *Condor* 2: 45.
- BENT, A. C. 1953. Life histories of North American wood warblers. Part 1. U.S. Natl. Mus. Bull. 203.
 BLOOM, S. A. 1981. Specialization and noncompetitive resource partitioning among sponge-eating dorid nudibranchs. *Oecologia* 49: 305-315.
 BOWLES, C. W. 1902. Notes on the Black-throated Gray Warbler. *Condor* 4: 82-85.
 BOWLES, J. H. 1906. The Hermit Warbler in Washington. *Condor* 8: 40-42.
 EMLEN, S. T., J. D. RISING, & W. L. THOMPSON. 1975. A behavioral and morphological study of sympatry in the Indigo and Lazuli buntings of the Great Plains. *Wilson Bull.* 87: 145-179.
 FICKEN, M. S., & R. W. FICKEN. 1969. Responses of Blue-winged Warblers and Golden-winged Warblers to their own and the other species' song. *Wilson Bull.* 81: 69-74.
 FICKEN, R. W., M. S. FICKEN, & D. H. MORSE. 1968. Competition and character displacement in two sympatric pine-dwelling warblers (*Dendroica*, Parulidae). *Evolution* 22: 307-317.
 FITZPATRICK, J. W. 1980. Review of "Revision of the *Myiarchus* flycatchers of South America." *Auk* 97: 906-908.
 FRANKLIN, J. F., & C. T. DYRNESS. 1973. Natural vegetation of Oregon and Washington. USDA Forest Serv. Gen. Tech. Rept. PNW-8.
 GILL, F. B., & B. G. MURRAY, JR. 1972. Discrimination behavior and hybridization of the Blue-winged and Golden-winged warblers. *Evolution* 26: 282-293.
 GRISCOM, L., & A. SPRUNT, JR. 1979. The warblers of America, revised ed. Garden City, New York, Doubleday and Co.
 HAMILTON, T. H. 1961. The adaptive significance of intraspecific trends of variation in wing length and body size among bird species. *Evolution* 15: 180-195.
 HUBBARD, J. P. 1969. The relationships and evolution of the *Dendroica coronata* complex. *Auk* 86: 393-432.
 HURLBERT, S. H. 1978. The measurement of niche overlap and some relatives. *Ecology* 59: 67-77.
 HUTCHINSON, G. E. 1975. Variations on a theme by Robert MacArthur. Pp. 492-521 in *Ecology and evolution of communities* (M. L. Cody and J. M. Diamond, Eds.). Cambridge, Massachusetts, Harvard Univ. Press.
 JACOBS, J. 1974. Quantitative measurement of food selection. *Oecologia* 14: 413-417.
 KEAST, A. 1980. Spatial relationships between migratory parulid warblers and their ecological counterparts in the neotropics. Pp. 109-130 in *Migrant birds in the neotropics: ecology, behavior, distribution, and conservation* (A. Keast and E. S. Morton, Eds.). Washington, D.C., Smithsonian Inst. Press.
 MACARTHUR, R. H. 1958. Population ecology of

- some warblers of northeastern coniferous forests. *Ecology* 39: 599-619.
- MENGEL, R. M. 1964. The probable history of species formation in some northern wood warblers (Parulidae). *Living Bird* 3: 9-43.
- MILLIGAN, M. 1966. Vocal responses of White-crowned Sparrows to recorded songs of their own and another species. *Anim. Behav.* 14: 356-361.
- MORRISON, M. L. 1981. The structure of western warbler assemblages: analysis of foraging behavior and habitat selection in Oregon. *Auk* 98: 578-588.
- MORSE, D. H. 1967. The contexts of songs in Black-throated Green and Blackburnian warblers. *Wilson Bull.* 79: 64-74.
- . 1968. A quantitative study of foraging of male and female spruce-woods warblers. *Ecology* 49: 779-784.
- . 1971. The foraging of warblers isolated on small islands. *Ecology* 52: 216-228.
- . 1976a. Variables affecting the density and territory size of breeding spruce-wood warblers. *Ecology* 57: 290-301.
- . 1976b. Hostile encounters among spruce-woods warblers (Dendroica: Parulidae). *Anim. Behav.* 24: 764-771.
- . 1980a. Behavioral mechanisms in ecology. Cambridge, Massachusetts, Harvard Univ. Press.
- . 1980b. Foraging and coexistence of spruce-woods warblers. *Living Bird* 18: 7-25.
- PIELOU, E. C. 1966. Species-diversity and pattern-diversity in the study of ecological succession. *J. Theoret. Biol.* 10: 370-383.
- POOLE, E. L. 1938. Weights and wing areas in North American birds. *Auk* 55: 511-517.
- POWER, H. W. 1980. The foraging behavior of Mountain Bluebirds. *Ornithol. Monogr.* No. 28.
- RAND, A. L. 1952. Secondary sexual characters and ecological competition. *Fieldiana-Zool.* 34: 65-70.
- ROBINS, J. D. 1971. Differential niche utilization in a grassland sparrow. *Ecology* 52: 1065-1070.
- ROSENZWEIG, M. L. 1981. A theory of habitat selection. *Ecology* 63: 327-335.
- SELANDER, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. *Condor* 68: 113-151.
- SMITH, J. N. M. 1978. Flycatching by male Song Sparrow, *Melospiza melodia*. *Can. Field-Natur.* 92: 195-196.
- STEIN, R. C. 1962. A comparative study of songs recorded from five closely related warblers. *Living Bird* 1: 61-71.
- WILLIAMS, J. B. 1980. Intersexual niche partitioning in Downy Woodpeckers. *Wilson Bull.* 92: 439-451.
- WILLIAMSON, P. 1971. Feeding ecology of the Red-eyed Vireo (*Vireo olivaceus*) and associated foliage-gleaning birds. *Ecol. Monogr.* 41: 129-152.

APPENDIX I. Use and availability of habitat variables for Black-throated Gray and Hermit warblers at FINLEY.

Variables	Black-throated Gray (15) ^a				Hermit (9)				Study area (21)				AN-OVA ^b
	\bar{x}	SD	Range		\bar{x}	SD	Range		\bar{x}	SD	Range		
Conifer													
Percentage cover	36.8	19.94	12.3-81.7		68.1	11.40	53.3-90.0		46.0	22.55	12.0-90.0		B
Number <30 cm dbh	7.2	2.69	4.3-12.7		6.0	1.31	4.0-8.0		6.8	2.42	4.0-13.0		D
Number 31-90 cm dbh	2.2	1.52	0.3-6.3		5.2	2.15	2.3-8.3		3.2	2.27	0.3-8.5		B
Number >90 cm dbh	0.1	0.15	0.0-0.3		0.2	0.34	0.0-1.0		0.1	0.23	0.0-1.0		D
Total number	9.5	2.82	5.6-15.4		11.3	1.61	9.0-14.6		10.1	2.70	5.0-16.0		D
Mean height (m)	17.7	4.99	4.0-35.0		22.0	7.10	4.0-40.0		19.9	6.05	3.0-40.0		D
Deciduous trees													
Percentage cover	50.5	18.20	15.0-86.7		11.3	11.81	0.0-31.7		37.5	25.63	0.0-90.0		B
Number <30 cm dbh	19.8	10.97	5.0-39.7		3.1	3.12	0.0-7.7		14.4	12.38	0.0-40.0		B
Number >30 cm dbh	0.9	1.10	0.0-4.0		0.6	0.76	0.0-2.3		0.8	1.02	0.0-4.0		D
Total number	20.7	10.78	5.7-41.0		3.7	3.68	0.0-9.0		15.2	12.42	0.0-45.0		B
Mean height (m)	13.4	1.66	9.7-16.2		8.3	6.73	0.0-15.0		11.3	4.97	0.0-17.0		B, C
Shrubs													
Percentage cover	58.9	13.55	35.0-78.3		47.8	20.04	20.0-76.7		54.8	16.24	20.0-80.0		D
Mean height (m)	0.3	0.20	0.1-0.9		0.4	0.37	0.1-1.2		0.3	0.28	0.1-1.2		D
Height intervals (percentage cover)													
1.5-4.0 m	43.3	17.04	20.0-86.7		14.8	12.82	0.0-33.3		33.6	21.61	0.0-90.0		B
4.1-10.0	80.0	12.88	53.3-93.3		41.5	24.44	0.0-73.3		66.1	26.73	0.0-95.0		B
10.1-20.0	76.2	14.39	46.7-100.0		84.4	15.27	66.7-100.0		80.0	15.66	45.0-100.0		D
20.1-30.0	33.8	17.62	6.7-73.3		60.0	16.99	40.0-86.7		41.7	21.29	6.5-87.0		B
>30.0 m	5.0	7.10	0.0-20.0		9.6	10.60	0.0-26.7		6.4	8.41	0.0-30.0		D
Total cover (%)	238.3	25.58	193.4-300.0		210.4	44.60	133.4-280.0		227.8	36.39	130.0-300.0		D
Diversity (FHD, H')	1.40	—	—		1.37	—	—		1.42	—	—		—

^a Sample size in parenthesis; n = number of circular plots, which correspond to five BTG and three HW territories.

^b Analysis of variance: Black-throated Gray (BTG) = Hermit (HW) (A); BTG = Study area (B); HW = Study area (C); BTG = HW = Study area (D).