

HABITAT USE AND FORAGING BEHAVIOR OF FOUR PARULID WARBLERS IN A SECOND-GROWTH FOREST

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Abstract.—Habitat use and foraging behavior of the Chestnut-sided Warbler (*Dendroica pensylvanica*), Canada Warbler (*Wilsonia canadensis*), Mourning Warbler (*Oporornis philadelphia*) and Nashville Warbler (*Vermivora ruficapilla*) were studied in a second-growth forest in northern Wisconsin (USA) during the breeding season. Our objective was to determine if interspecific and intersexual foraging differences exist among these species. The warblers concentrated foraging activities on a few species of trees and shrubs. Compared to other species, Canada Warblers more frequently used coniferous trees that were scattered through the primarily deciduous habitat. All species most frequently used branches of trees, but male Nashville Warblers also made considerable use of leaves and twigs. Warblers foraged at a variety of heights in the vegetation, with male Nashville Warblers foraging highest in the midstory and canopy of mature trees. Females of all species tended to be active lower in the vegetation than males. Gleaning was the most frequently used foraging method, except for male Canada Warblers, which used foraging methods involving flight in about 70% of prey pursuits. When 30 foraging-related characters were considered simultaneously in a multivariate analysis, it was found that intersexual differences within a species were less pronounced than interspecific differences, except Nashville Warbler males, which were distinct in their foraging. When designing a conservation strategy for these species, biologists must recognize that these birds require heterogeneous second-growth forests.

UTILIZACIÓN DEL HÁBITAT Y CONDUCTA DE FORRAJEО DE CUATRO ESPECIES DE PARÚLIDOS EN UN BOSQUE SECUNDARIO

Síopsis.—Se estudió, en un bosque secundario al norte de Wisconsin, el uso de hábitat y la conducta de forrajeo de *Dendroica pensylvanica*, *Wilsonia canadensis*, *Oporornis philadelphia* y *Vermivora ruficapilla*, durante le época reproductiva de dichas aves. El objetivo fue determinar si había diferencias interespecíficas e intersexuales entre las diferentes especies. Las aves concentraron su actividad de forrajeo en un grupo reducido de especies de árboles y arbustos. En comparación a otros estudios *Wilsonia* utilizó, con mayor frecuencia, coníferos que estaban esparcidos a través de un hábitat de deciduos. Todas las especies utilizaron con mayor frecuencia las ramas de los árboles, aunque los machos de *Vermivora* utilizaron considerablemente a las hojas y a las ramitas. La altura de forrajeo fue variable con *Vermivora* utilizando la parte más alta del docel y el estrato medio de la vegetación madura. A menor altura en la vegetación, las hembras de todas las especies tendieron a estar más activas que los machos. El rebusque resultó ser el método de forrajeo utilizado con mayor frecuencia, a excepción de los machos de *Wilsonia* que utilizaron métodos asociados al vuelo en el 70% de los casos. Cuando se consideraron en una análisis de multivarianza, simultáneamente, 30 caracteres relacionados al forrajeo, se encontró que las diferencias intersexuales dentro de una especie eran menos pronunciadas que las diferencias interespecíficas, excepto para los machos de *Vermivora* que fueron distintos en su forrajeo. Cuando se planifique diseñar una estrategia de conservación para estas especies, los biólogos deben reconocer que estas aves requieren de bosques secundarios heterogéneos.

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This study describes the habitat use and foraging behavior of four wood warblers (Emberizidae, Parulinae), the Chestnut-sided Warbler (*Dendroica pensylvanica*), Canada Warbler (*Wilsonia canadensis*), Mourning Warbler (*Oporornis philadelphia*) and Nashville Warbler (*Vermivora ruficapilla*) on their breeding grounds in the upper Midwest, USA. Relatively little is known about the foraging ecology of these four species. Our objectives were to determine how the four species differ in their use of habitat elements and in their foraging patterns, and to compare behavior between the sexes within species. Numerous previous studies have reported interspecific or intersexual foraging differences among co-occurring wood warblers (e.g., Holmes 1986, MacArthur 1958, Morse 1968). The ultimate causes of these differences, and the role of processes such as competition for food, remain unresolved (Martin and Karr 1990, Morrison 1981, Price 1991).

The species considered here characteristically breed in heterogeneous second-growth forests that are mixtures of deciduous and coniferous tree species. Bird populations using some early successional stages may be more vulnerable to decline than previously realized (Hagan 1993, Martin 1993). Information on the ecological requirements of species using early successional stages is thus needed so that effective management decisions can be made regarding these birds.

METHODS

Data were collected in an area centered at the University of Wisconsin Trout Lake Station and the adjacent Mann Creek Wildlife Area, Vilas County, Wisconsin (46°01'N, 89°40'W) between 6 Jun. and 27 Jul. 1977. The area supported second-growth forest, which had been logged and/or burned repeatedly during the previous 100 yr. Stands were a mixture of aspen, northern hardwoods and conifers, that correspond to Curtis's (1959) "northern dry-mesic forest" (for further description see Paszkowski 1984).

Data were collected from 3–10 individuals of each sex of each species. Sexes of all these species show some plumage differences and can be distinguished in the field. Total observation times (in hours) were as follows: Chestnut-sided Warbler male = 9.5, female = 1.8; Canada Warbler male = 1.3, female = 0.2; Mourning Warbler male = 3.0, female = 0.9; Nashville Warbler male = 0.3, female = 0.2.

Data were collected by locating an individual and composing a timed, continuous record of the bird's movement until it was lost (maximum 10 min). We recorded: (1) plant species or genus (plants which could not be rapidly identified to species, e.g., *Acer*, *Alnus*, *Corylus*, *Populus* and *Prunus*) where a bird searched for and/or captured prey, (2) foraging height (visually estimated), (3) substrate used during locomotion (leaf, twig [wood <1 cm diameter], branch [1.0–2.5 cm diameter], limb [2.6–12 cm diameter], trunk [>12 cm diameter], ground and air), (4) direction moved relative to the trunk or center of a plant (up, down, towards and away), (5) flight distances (to a new substrate or plant; if direction

changed dramatically while a bird was flying, the move was considered a new flight) and (6) foraging method used for prey capture. We recognized the following foraging methods: (1) glean (picked prey from substrate while perched), (2) pounce (flew towards prey located on a substrate, alighted on substrate while capturing prey), (3) hover (picked prey from substrate while in flight without landing) and (4) sally (captured prey in mid-air while in flight). It was not always possible to determine if a foraging maneuver resulted in a prey capture, as many prey were small (e.g., Diptera), thus foraging methods encompass both successful and unsuccessful capture attempts.

From our continuous records we extracted a number of other variables for analysis. We defined a "sequence" as a series of moves that began when a bird moved to a new tree or shrub and ended when it left that plant. We used sequences that were observed completely to calculate movement rate (number of hops and flights/s; cf. Robinson and Holmes 1982). As heights within a movement sequence can be correlated (Sherry 1975), we used only the height of the first move within a sequence when analyzing foraging height. Visual inspection of data revealed that warblers usually did not change their foraging heights appreciably during a foraging sequence.

We used chi-squared tests of independence to compare the distribution of movement sequences among vegetation types, the distribution of moves among substrates, and the frequency of foraging behaviors across warbler species. Data from males and females were handled separately. For these tests, plants were pooled into four categories: "shrubs" (alder, *Alnus crispa* and *rugosa*; hazelnut, *Corylus americana* and *cornuta*), "hardwoods" (black oak, *Quercus borealis*; cherry, *Prunus virginiana*, *serotina* and *pensylvanica*; paper birch, *Betula papyrifera*; and maple, *Acer saccharum* and *rubrum*), "aspens" (*Populus tremuloides* and *grandidentata*), and "conifers" (white pine, *Pinus strobus*; red pine, *P. resinosa*; jack pine, *P. banksiana*; black spruce, *Picea mariana*; and balsam fir, *Abies balsamea*). Substrate categories were also combined (twig with leaves, and limb with trunk). Movement rates and heights, along with flight distances, were compared for males and for females of the four species using one-way analysis of variance (ANOVA) coupled with Tukey's test.

To compare foraging behavior and habitat use between sexes and among species simultaneously, we performed cluster analysis on a data matrix consisting of eight rows (species \times sexes) and 30 characteristics (columns), following Holmes et al. (1979). Analysis used the unweighted pair-group clustering method with arithmetic averages (UPGMA) and Euclidian distance coefficients (NTSYS-pc; Rohlf 1987). Twenty-seven variables were percentages that were log transformed ($\log_{10}[x + 1]$) to reduce skewness. These were: (a) percentage use of four foraging methods, (b) percentage of moves in four directions, (c) percentage of moves on seven substrates and (d) percentage of movement sequences in 12 plant species/genera. Specific categories were the same as described for univariate analyses. The remaining three variables were: mean foraging

height, standard error of foraging heights and sex-specific body masses (obtained from Dunning 1984). All columns were standardized by subtracting the column mean from each value in the column (see Holmes et al. 1979).

Our data are non-independent and may be autocorrelated (Hurlbert 1984). Such data may give inaccurate estimates of variance and should be interpreted with care (Hejl et al. 1990).

RESULTS

Males and females of each warbler species concentrated their activities in relatively few of the available tree and shrub species. The five woody plants most frequently used by all warbler species were: trembling/big-toothed aspen, sugar/red maple, paper birch, hazelnut and white pine. When woody plant species were combined into four categories, interspecific comparisons revealed significant differences in the use of these vegetation types among males ($\chi^2 = 80.4$, $df = 9$, $P < 0.001$) and among females ($\chi^2 = 28.5$, $df = 9$, $P < 0.001$) of the four warbler species (Fig. 1). Male Chestnut-sided and Nashville Warblers foraged more frequently in hardwood trees than the other species, whereas male Canada and Mourning Warblers foraged more frequently in aspens. In addition, male Canada Warblers made greater use of conifers than the other species. Female Canada Warblers also foraged more frequently in conifers than females of the other species (Fig. 1). Female Chestnut-sided, Mourning, Canada and Nashville Warblers foraged frequently in aspen trees, shrubs, aspen trees and hardwood trees, respectively.

All species were active at a wide range of heights in the vegetation (Table 1), but mean foraging heights differed significantly among species for both males and females ($F = 38.9$, $df = 3,521$, $P < 0.001$; $F = 3.60$, $df = 3,187$, $P = 0.015$, respectively). For males, all species differed significantly from each other in foraging heights, with Nashville > Chestnut-sided > Canada > Mourning Warbler (Tukey pair-wise comparisons; $P < 0.05$). For females, Nashville Warblers foraged significantly higher than Chestnut-sided or Mourning Warblers (Tukey pair-wise comparisons; $P < 0.05$).

All warblers travelled most frequently by hopping along branches (Fig. 2). Comparisons across species, however, revealed significant differences in substrate use for males ($\chi^2 = 78.1$, $df = 9$, $P < 0.001$) and females ($\chi^2 = 52.1$, $df = 9$, $P < 0.001$). Nashville Warbler males used twigs and leaves more frequently than any other species. Chestnut-sided Warbler females made minimal use of tree limbs and trunks (Fig. 2).

Flights were relatively rare, accounting for <20% of observed moves for each sex and species (Fig. 2, "air"). They were also short, typically <1 m (Table 1). Flight distance varied significantly among male warblers ($F = 4.34$, $df = 3,685$, $P = 0.005$), but not among females ($F = 0.39$, $df = 3,244$, $P = 0.76$). Male Chestnut-sided Warblers made significantly longer flights than male Mourning Warblers ($P < 0.05$, Tukey test).

Frequency of movement differed significantly among species for both

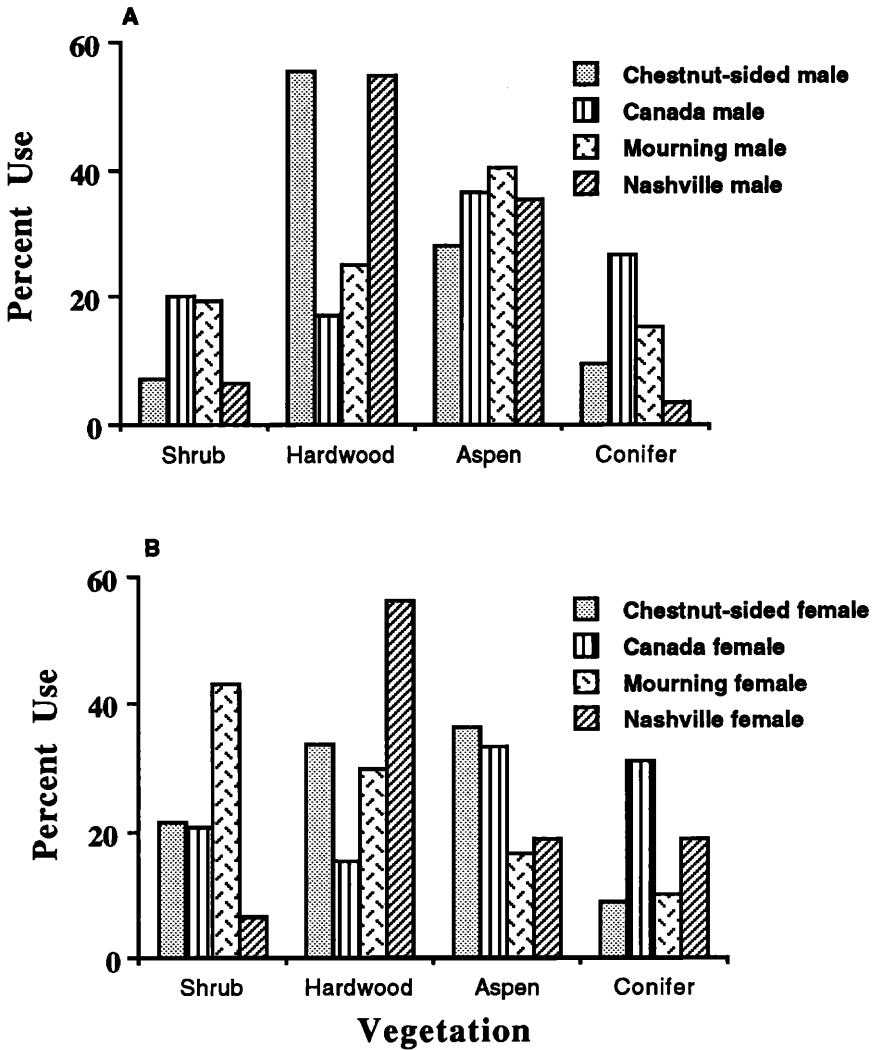


FIGURE 1. Vegetation use by four warbler species in a second-growth forest (% occurrence of movement sequences). Total numbers of sequences used in the analysis were: Chestnut-sided male = 267, female = 107; Canada Warbler male = 129, female = 39; Mourning Warbler male = 92, female = 30; Nashville Warbler male = 31, female = 16.

males and females ($F = 58.3$, $df = 3,648$; $F = 9.03$, $df = 3,223$, respectively, $P < 0.001$; Table 1). Among males, movement rates differed significantly between all pair-wise combinations ($P < 0.05$, Tukey test) except the species with the highest rates, Canada and Nashville Warblers. Similarly, female Canada and Nashville Warblers had high movement

TABLE 1. Activity heights, flight distances and movement rates of male and female warblers recorded during the breeding season in a second-growth forest. Values reported as mean \pm SE. Range and sample sizes in parentheses.

Warbler species	Sex	Movement height (m)	Flight distances (m)	Movement frequency (hops and flights/s)
Chestnut-sided	M	5.47 \pm 0.16 (0.3–11.7; 269)	0.98 \pm 0.05 (0.3–10.0; 334)	0.13 \pm 0.01 (0.0–0.9; 375)
	F	2.59 \pm 0.23 (0.7–12.0; 103)	1.01 \pm 0.06 (0.3–6.7; 172)	0.20 \pm 0.01 (0.0–1.0; 150)
Canada	M	4.06 \pm 0.25 (0.3–23.0; 122)	0.98 \pm 0.04 (0.3–4.0; 210)	0.40 \pm 0.03 (0.0–2.0; 150)
	F	3.18 \pm 0.27 (1.0–8.3; 39)	0.85 \pm 0.10 (0.3–2.7; 33)	0.33 \pm 0.04 (0.0–0.9; 30)
Mourning	M	3.07 \pm 0.26 (0.3–11.0; 105)	0.74 \pm 0.06 (0.3–5.0; 118)	0.23 \pm 0.02 (0.0–1.0; 101)
	F	2.68 \pm 0.46 (0.7–10.0; 32)	0.90 \pm 0.18 (0.3–6.7; 32)	0.20 \pm 0.03 (0.0–6.7; 34)
Nashville	M	8.22 \pm 0.57 (1.3–13.0; 29)	0.57 \pm 0.05 (0.3–1.0; 27)	0.38 \pm 0.06 (0.0–1.2; 26)
	F	4.49 \pm 0.74 (1.7–11.7; 17)	0.91 \pm 0.19 (0.3–2.7; 11)	0.36 \pm 0.07 (0.1–1.0; 13)

rates and differed significantly ($P < 0.05$, Tukey test) from Chestnut-sided and Mourning Warbler females which had low movement rates.

Overall, gleaning was the most commonly observed foraging method except in male Canada Warblers (Fig. 3). Males of the four species differed significantly in their use of gleaning versus non-gleaning behaviors that required flight ($\chi^2 = 37.6$, $df = 9$, $P < 0.001$). Male Nashville Warblers gleaned more frequently and male Canada Warblers less frequently than the other species. Females of three species (Mourning Warbler could not be included because of low sample size) did not differ significantly in use of gleaning versus methods involving flight ($\chi^2 = 5.86$, $df = 6$, $P > 0.10$).

Cluster analysis, which integrated detailed measures of habitat use and foraging patterns, indicated that for Chestnut-sided, Canada and Mourning Warblers, males and females were more similar to each other in their behavior than to either sex of the other species (Fig. 4). Male Nashville Warblers proved to be the most distinct of all sex-species categories, and females of this species were more similar to males and females of the other three species than to conspecific males.

DISCUSSION

The predominance of activity in *Populus* species and understory elements, such as *Corylus*, reflected the fact that warblers in our study were using relatively young, disturbed forests which characteristically have high

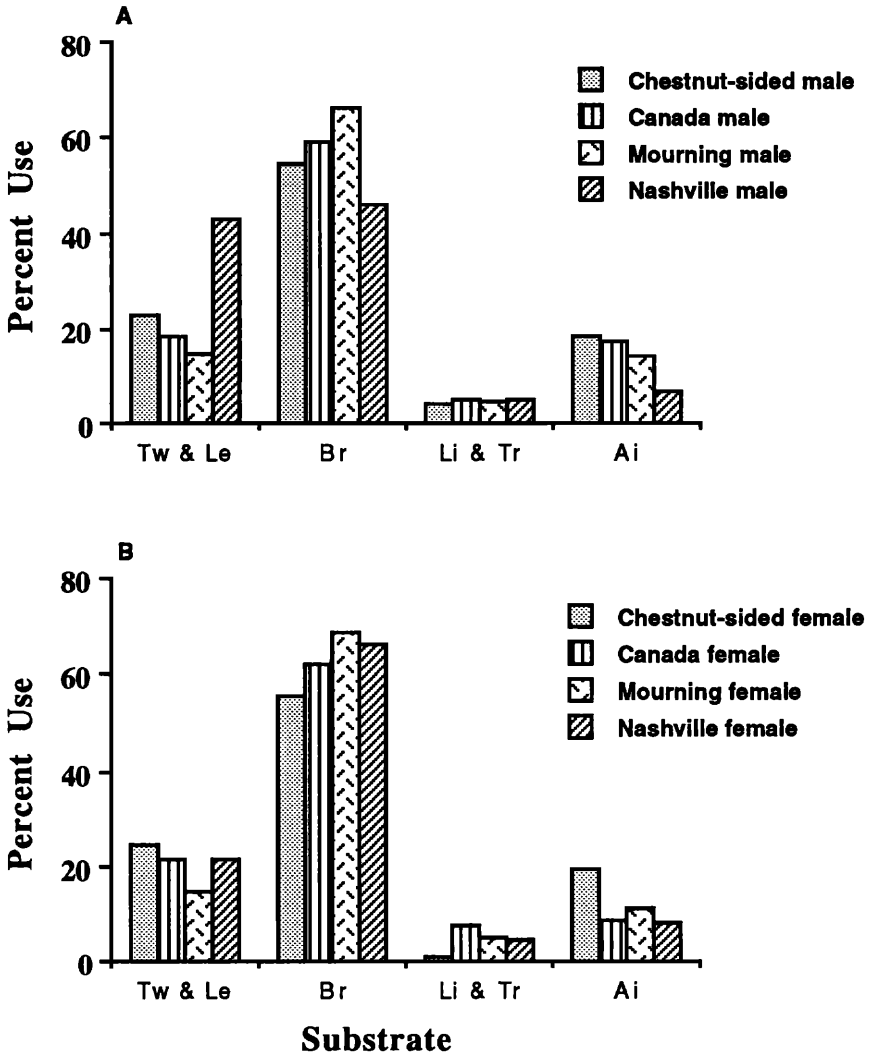


FIGURE 2. Substrates used by four warbler species in a second-growth forest (% of moves observed). Tw & Le = twig and leaves, Br = Branch, Li & Tr = limb and trunk, and Ai = Air. Total numbers of movements used in the analysis were: Chestnut-sided Warbler male = 1189, female = 695; Canada Warbler male = 598, female = 93; Mourning Warbler male = 729, female = 260; Nashville Warbler male = 142, female = 103.

light penetration and a well-developed layer of shrubs and herbs. Although this habitat was quite heterogenous, males and females of the four warbler species did not use a particularly wide variety of the shrub and tree species present. The Canada Warbler was the most distinctive of the

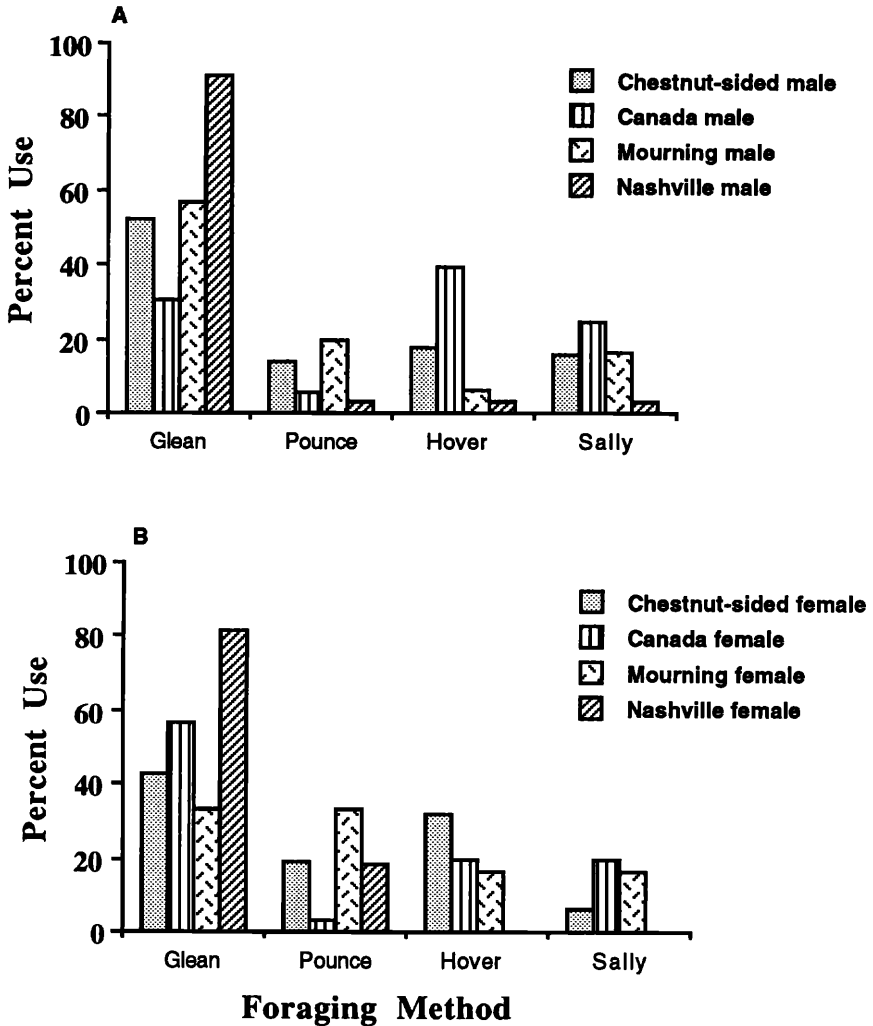


FIGURE 3. Foraging methods used by four warbler species in a second-growth forest. Total numbers of prey capture attempts observed were: Chestnut-sided male = 116, female = 47; Canada Warbler male = 89, female = 30; Mourning Warbler male = 30, female = 6; Nashville Warbler male = 34, female = 11.

four as it foraged in coniferous trees scattered through a forest dominated by deciduous species (Fig. 1).

Mourning Warblers frequently moved along wider branches, limbs and trunks, where they walked (alternating footfalls) rather than hopped (simultaneous footfalls). In contrast, male Nashville Warblers often captured prey while perched on flexible, unstable surfaces such as leaves and twigs

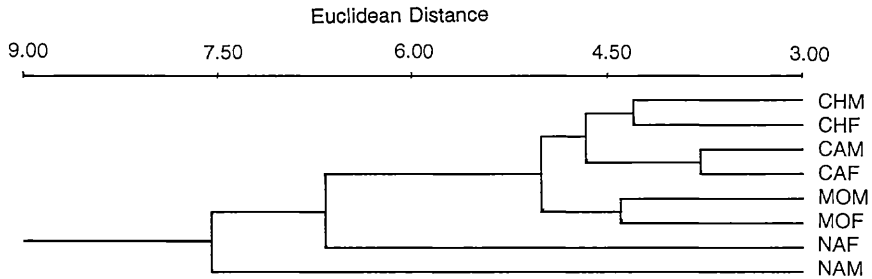


FIGURE 4. Cluster dendrogram showing intersexual and interspecific relationships of four warbler species in a second-growth forest, based on multivariate analyses of habitat use and foraging behavior. CHM = Chestnut-sided Warbler male; CHF = Chestnut-sided Warbler female; CAM = Canada Warbler male; CAF = Canada Warbler female; MOM = Mourning Warbler male; MOF = Mourning Warbler female; NAM = Nashville Warbler male; and NAF = Nashville Warbler Female.

(Fig. 2). The ability to exploit these foraging locations may be an outcome of the small body size of the Nashville Warbler; males on average weigh 8.9 g (vs. 9.8–13.0 g for the other species; Dunning 1984). Airola and Barrett (1985) also found that Nashville Warblers foraged more frequently on foliage than Yellow-rumped Warbler (*D. coronata*) or Hermit Warbler (*D. occidentalis*) and depended almost exclusively on gleaning.

Flight was used moderately by the other species to capture prey. Similar to the results of Martin and Karr (1990), we found Chestnut-sided Warblers used flight in about 50% of prey capture attempts. Tramer and Kemp (1980) reported that Wilson's Warbler (*W. pusilla*), a congener of the Canada Warbler, used flight in about 40% of foraging maneuvers. We observed that male and female Canada Warblers flew in 70% and 43% of their prey capture attempts, respectively.

Movement rates differed among species for both sexes, with Nashville and Canada Warblers displaying higher rates than Chestnut-sided and Mourning Warblers (Table 1). What ultimate or proximate causes were responsible for these differences is difficult to determine. Vegetation structure could be a factor limiting speed, as could morphology (Moermond 1990). Both factors could also contribute to interspecific differences in foraging methods (Robinson and Holmes 1984).

Our cluster analysis indicated that males and females were most similar to each other in their foraging patterns for Chestnut-sided, Canada and Mourning Warblers. Morse (1971) and Holmes (1986) likewise reported that foraging behavior of the parulid warbler species that they studied were most similar between males and females of the same species. Our study indicated that male and female Nashville Warblers were the most divergent from each other and from the other species. We had the least data on the Nashville Warbler, but propose that it was truly distinctive because of its use of the overstory created by mature trees of aspen and birch.

Although males and females of three of the species examined strongly resembled each other in behavior (Chestnut-sided, Canada and Mourning Warblers), the sexes were by no means identical in their foraging. A number of hypotheses have been put forward to explain why such differences occur between the sexes in passerine birds. It has been suggested that differences are related to the center of foraging activity during the breeding season (space-restrained foraging hypothesis; Morse 1968, 1989). Males forage at greater heights where they can alternate foraging with singing to communicate effectively inter- and intrasexually. Females forage in lower strata close to their nests, thereby saving energy while travelling between the nest and foraging locations (Morse 1968, Holmes 1986). Foraging heights in males and females are, therefore, correlated with singing perch heights and nest heights, respectively. As reported for other parulid warblers (Busby and Sealy 1979, Franzreb 1983, Morrison 1982, Morse 1968), males of the four species examined here were active on average 0.4–3.7 m higher than females. Nests of all four species are typically on or near the ground (Ehrlich et al. 1988).

Morse (1968) argued that female warblers forage faster than males because they: (1) need supplemental energy to produce eggs and (2) are time-constrained as they must alternate incubation/brooding with foraging. The patterns of sex-based differences we observed did not support this argument, as only Chestnut-sided Warbler females moved faster than males.

Rand (1952) and Selander (1966) suggested that sexual differences in foraging niche occur in response to intersexual competition. Consistent with this hypothesis, Peters and Grubb (1983) and Desrochers (1989) have shown in wintering Downy Woodpeckers (*Picoides pubescens*) and Black-capped Chickadees (*Parus atricapillus*), respectively, that females avoid microhabitats used by dominant males. Contradicting this hypothesis, Morton et al. (1987) found that habitat use of non-breeding female Hooded Warblers (*W. citrina*) did not change when males were experimentally removed.

Morse (1989) suggested that the degree of sexual difference in foraging niche is related to the intensity of both intra- and interspecific competition. He found that male and female warblers foraged more similarly on islands with low numbers of competitors (both intra- and interspecific) when compared to warblers on the mainland where the number of potential competitors was high (Morse 1971). We did not document diet composition or food abundance, thus the role of resource competition in shaping observed intersexual and interspecific differences in foraging patterns and habitat use cannot be addressed in a meaningful fashion.

In summary, the four species of warblers displayed interspecific and intersexual differences in behavior, yet males and females obviously coexist on the same breeding territory and species coexist in the same habitat. In designing a conservation strategy for this suite of birds, biologists must recognize that co-occurring species require different elements provided by the heterogeneous environment of second-growth forest.

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LITERATURE CITED

- AIROLA, D. A., AND R. H. BARRETT. 1985. Foraging and habitat relationships of insect-gleaning birds in a Sierra Nevada mixed-conifer forest. *Condor* 87:205-216.
- BUSBY, D. G., AND S. G. SEALY. 1979. Feeding ecology of a population of nesting yellow warblers. *Can. J. Zool.* 57:1670-1681.
- CURTIS, J. T. 1959. *Vegetation of Wisconsin*. Univ. of Wisconsin Press, Madison, Wisconsin. 657 pp.
- DESROCHERS, A. 1989. Sex, dominance, and habitat use in wintering black-capped chickadees: a field experiment. *Ecology* 70:636-645.
- DUNNING, J. B., JR. 1984. *Body weights of 686 species of North American birds*. Western Bird Banding Assoc., Monogr. 1, Cave Creek, Arizona.
- EHRlich, P. R., D. S. DOBKIN, AND D. WHEYE. 1988. *The birder's handbook*. Simon and Schuster Inc., New York, New York. 785 pp.
- FRANZREB, K. E. 1983. Intersexual habitat partitioning in Yellow-rumped Warblers during the breeding season. *Wilson Bull.* 95:581-590.
- HAGAN, J. M., III. 1993. Decline of the Rufous-sided Towhee in the eastern United States. *Auk* 110:863-874.
- HEJL, S. J., J. VERNER, AND G. W. BELL. 1990. Sequential versus initial observations in studies of avian foraging. *Stud. Avian Biol.* 13:166-173.
- HOLMES, R. T. 1986. Foraging patterns of forest birds: male-female differences. *Wilson Bull.* 98:196-213.
- , R. E. BONNEY, JR., AND S. W. PACALA. 1979. Guild structure of the Hubbard Brook bird community: a multivariate approach. *Ecology* 60:512-520.
- HURLBERT, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* 54:187-211.
- MACARTHUR, R. H. 1958. Population ecology of some warblers of northeastern conifer forests. *Ecology* 39:599-619.
- MARTIN, T. E. 1993. Nest predation among vegetation layers and habitat types: revising the dogmas. *Am. Nat.* 141:897-913.
- , AND J. R. KARR. 1990. Behavioral plasticity of foraging maneuvers of migratory warblers: multiple selection period for niches. *Stud. Avian Biol.* 13:353-359.
- MOERMOND, T. C. 1990. A functional approach to foraging: morphology, behavior, and the capacity to exploit. *Stud. Avian Biol.* 13:427-430.
- MORRISON, M. L. 1981. The structure of western warbler assemblages: analysis of foraging behavior and habitat selection in Oregon. *Auk* 98:578-588.
- . 1982. The structure of western warbler assemblages: ecomorphological analysis of the Black-throated Gray and Hermit Warblers. *Auk* 99:503-513.
- MORSE, D. H. 1968. A quantitative study of foraging male and female spruce-woods warblers. *Ecology* 49:779-784.
- . 1971. The foraging of warblers isolated on small islands. *Ecology* 52:216-228.
- . 1989. *American warblers*. Harvard Univ. Press, Cambridge, Massachusetts. 406 pp.
- MORTON, E. S., J. F. LYNCH, K. YOUNG, AND P. MEHLHOP. 1987. Do Hooded Warblers exclude females from nonbreeding territories in tropic forest? *Auk* 104:133-135.
- PASZKOWSKI, C. A. 1984. Macrohabitat use, microhabitat use, and foraging behavior of the Hermit Thrush and Veery in a northern Wisconsin forest. *Wilson Bull.* 96:286-292.
- PETERS, W. D., AND T. C. GRUBB, JR. 1983. An experimental analysis of sex-specific foraging in the downy woodpecker, *Picoides pubescens*. *Ecology* 64:1437-1443.
- PRICE, T. 1991. Morphology and ecology of breeding warblers along an altitude gradient in Kashmir, India. *J. Anim. Ecol.* 60:643-664.
- RAND, A. L. 1952. Secondary sexual characters and ecological competition. *Fieldiana Zool.* 34:65-70.

- ROBINSON, S. K., AND R. T. HOLMES. 1982. Foraging behavior of forest birds: the relationships among search tactics, diet, and habitat structure. *Ecology* 63:1918-1931.
- , AND ———. 1984. Effects of plant species and foliage structure on the foraging behavior of forest birds. *Auk* 101:672-684.
- ROHLF, F. L. 1987. Numerical taxonomy and multivariate analysis system. Exeter Publishing, Setauket, New York. 37 pp.
- SELANDER, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. *Condor* 68:113-151.
- SHERRY, T. W. 1975. Foraging behavior and niche relationships of breeding American redstarts (*Setophaga ruticilla*) and least flycatchers (*Empidonax minimus*): the flycatcher guild in a New England hardwoods forest. M.Sc. thesis, Dartmouth College, Hanover, New Hampshire.
- TRAMER, E. J., AND T. R. KEMP. 1980. Foraging ecology of migrant and resident warblers and vireos in the highlands of Costa Rica. Pp. 285-296, in A. Keast and E. S. Morton, eds. *Migrant birds in the neotropics: ecology, behavior, distribution, and conservation*. Smithsonian Institution Press, Washington, D.C.

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