INTERSEXUAL HABITAT PARTITIONING IN YELLOW-RUMPED WARBLERS DURING THE BREEDING SEASON

KATHLEEN E. FRANZREB

Intersexual differences in foraging behavior have been noted for a number of avian species (Selander 1966; Jackson 1970; Kilham 1970; Willson 1970; Kisiel 1972; Grubb 1975; Williams 1975, 1980; Winkler 1979; Jenkins 1979), mainly members of the order Piciformes. Relatively limited research has been conducted on variation in foraging ecology between sexes of passerines (Morse 1967, 1968; Williamson 1971; Holmes et al. 1978).

The objective of this study was to ascertain if there were any significant differences between the foraging behavior of male and female Yellow-rumped Warblers (*Dendroica coronata*) during the breeding season in mixed-coniferous forest. Three possible explanations to account for any such differences are examined including: (1) habitat partitioning in order to facilitate efficient exploitation of resources by reducing intra-pair competition; (2) the influence of reproductive responsibilities (territorial advertisement and defense, location of nests, incubation duties, etc.) and its relationship to optimal foraging behavior; and (3) the hypothesis that foraging strategy merely reflects, and is strongly influenced by, what is available in the portions of the habitat actually used.

STUDY AREA

The Willow Creek watershed is located in the Apache-Sitgreaves National Forest approximately 80 km south of Springerville, Greenlee Co., in the White Mountains of Arizona. The watershed is covered by a mixed-coniferous forest and elevation ranges from 2682–2805 m.

The overall tree density was estimated at 626.2 trees per ha with Douglas-fir (*Pseudotsuga menziesii*) having the highest density followed by ponderosa pine (*Pinus ponderosa*) and southwestern white pine (*Pinus strobiformis*). Douglas-fir also had the highest relative dominance and relative frequency values. For a more thorough description of the vegetation components, please see Franzreb (1978) or Franzreb and Ohmart (1978).

METHODS

Vegetation analysis.—A 15.5-ha study plot was established using a system of nine parallel, flagged transect lines 390 m in length and 50 m apart. The plotless point-quarter method was used to sample the vegetation. Tree heights of 400 mature trees were estimated using a clinometer and subsequently classified into 3-m intervals. Additional details of the vegetation analysis are available in Franzreb (1978) and Franzreb and Ohmart (1978).

Foraging behavior.—Foraging data on male and female Yellow-rumped Warblers were obtained from mid-May through August in 1973 and 1974 as I systematically traversed the transect lines. Observations were taken under skies that were generally clear to less than

TABLE 1

FORAGING METHOD USED BY MALE AND FEMALE YELLOW-RUMPED WARBLERS

| Method[a] | No. of observations and percent | | | |
	Male		Female	
Glean	427	87.0%	199	87.7%
Hover	50	10.2%	18	7.9%
Hawk	14	2.8%	10	4.4%
Total	491	100.0%	227	100.0%
Niche overlap	0.98			

[a] No significant difference (G = 2.0, df = 2, $P > 0.25$).

30% overcast and wind conditions varied from no wind to light wind (Beaufort scale 0–2). Although data were collected throughout the day, the majority of observations were taken during morning hours (06:00–10:00).

Data were obtained by recording observations on an individual for as long as it was visible (frequently several minutes). For statistical purposes it is desirable to use just the first observation to reduce sampling bias. However, males are more conspicuous than females, especially during the nesting season when singing is prevalent; thus, if just the first observation is used during the analysis, the results may be biased to foraging locations near song posts. To test the effect of enhanced male detectability, I segregated the data into "first observations" and "all observations combined" and compared them using the G-test (Sokal and Rohlf 1969). There were no significant differences ($P \leq 0.05$) in any of the seven foraging variables tested, hence, data reported here represent first observations.

Data were collected on seven variables related to the foraging niche of the species: method of prey procurement, perch type, perch diameter, distance from the branch tip to the perch site, tree species preferences, tree height, and bird location in the tree relative to the ground. Nine types of trees (eight species and dead trees) were identified as foraging substrates. With each observation the height of the tree in which the bird foraged was recorded using a clinometer. Also, the distance of the bird relative to the ground was estimated and denoted as "height from ground."

The G-statistic was used to determine if statistically significant ($P \leq 0.05$) differences in foraging behavior between male and female Yellow-rumped Warblers existed for the seven foraging variables. Mean tree height selection and foraging height for males and females were compared using a t-test.

Niche overlap between males and females was determined from $O_{xy} = 1 - \frac{1}{2} \Sigma \mid P_{xi} - P_{yi} \mid$ (Schoener 1968) where P_{xi} is the proportion of observations of use of resource state i by males (x) and P_{yi} the use of resource state i by females (y). O_{xy} represents the extent of niche overlap between males (x) and females (y) with total overlap along a dimension yielding a value of 1. An indication of niche breadth was estimated by calculating the proportional similarity index (Feinsinger 1981) whereby $PSI = 1 - \frac{1}{2} \Sigma \mid p_i - q_i \mid$. Here p_i is the proportion of resource items in state i used by male (or female) warblers and q_i is the proportion of items in state i available to the birds. The PSI was calculated separately for each sex and was only determined for those variables for which it was possible to quantify resource availability (distance from tip, tree species, tree height, foraging height).

TABLE 2
PERCH TYPE SELECTED BY MALE AND FEMALE YELLOW-RUMPED WARBLERS WHILE FORAGING

Perch type[a]	No. of observations and percent			
	Male		Female	
Trunk	2	0.5%	0	0.0%
Branch/twig	381	85.4%	189	85.9%
Leaf	63	14.1%	31	14.1%
Total	446	100.0%	220	100.0%
Niche overlap	0.99			

[a] No significant difference (G = 1.8, df = 3, P > 0.50).

RESULTS

Foraging behavior.—There were no significant differences between the sexes in method of prey procurement (Table 1), perch type (Table 2), diameter of the perch (Table 3), or distance from the branch tip to the foraging site (Table 4). Niche overlap for these foraging variables ranged from 0.91 to 0.99 (Tables 1–4). Niche breadth was high for distance from the tip because each sex was quite generalized in the portion of the branch selected.

Tree species selection was significantly different (G = 65.2, df = 8, P < 0.001) in that females relied heavily on Douglas-fir (34.1%) which was used by males only 18.2% of the time (Table 5). In contrast, males selected Engelmann spruce (*Picea engelmanni*) considerably more frequently than females (28.7% vs 19.2%). Tree species use showed the lowest degree of niche overlap (0.71) of any foraging variable (Table 5). Females were more generalized than males in this regard as demonstrated by the proportional similarity indices (0.76 female, 0.65 male) (Table 5).

The sexes differed significantly (G = 20.2, df = 3, P < 0.001) in terms of the heights of the trees used for foraging purposes (Table 6). In addition, the mean tree height used by males was significantly higher (t = 2.37, df = 647, P < 0.02) than the mean tree height for females (male $\bar{x}$ = 26.9 ± 10.1 m; female $\bar{x}$ = 24.1 ± 10.4 m), although there was considerable overlap (niche overlap = 0.85) (Table 6). Males were also decidedly more specialized than females in tree height selection (PSI = 0.37 male, 0.52 female); in fact, both sexes were more specialized in this variable than in any other foraging characteristic.

Males and females foraged at significantly different heights (G = 33.2, df = 3, P < 0.001) above the ground (Table 7). Also, female mean foraging

TABLE 3

DIAMETER OF PERCHES SELECTED BY FORAGING MALE AND FEMALE YELLOW-RUMPED
WARBLERS

Perch diameter[a]	No. of observations and percent			
	Male		Female	
>5.10 cm	32	7.0%	12	6.3%
>2.54 ≤ 5.10 cm	47	10.2%	8	4.2%
>1.27 ≤ 2.54 cm	55	12.0%	23	12.2%
≤1.27 cm	325	70.8%	146	77.3%
Total	459	100.0%	189	100.0%
Niche overlap 0.91				

[a] No significant difference (G = 7.4, df = 3, P > 0.05).

height was significantly lower than that of males ($t = 2.45$, df $= 649$, $P <$ 0.05) (female $\bar{x} = 14.7 \pm 7.1$ m; male $\bar{x} = 17.7 \pm 7.0$ m); over 80% of female foraging observations occurred up to 18 m from the ground, whereas approximately 60% of the male foraging observations occurred within that height interval. There was substantial niche overlap (0.78) in foraging height; and females were slightly less specialized (PSI = 0.56 male, 0.61 female) (Table 7).

DISCUSSION

There are at least three possible explanations for the differences in foraging behavior displayed by male and female Yellow-rumped Warblers.

TABLE 4

MALE AND FEMALE YELLOW-RUMPED WARBLER FORAGING SITES WITH RESPECT TO
DISTANCE FROM THE BRANCH TIPS

Distance from branch tip[a]	No. of observations and percent			
	Male		Female	
0–33% from tip	215	48.5%	93	39.1%
>33–66% from tip	138	31.2%	87	36.5%
>66% from tip	90	20.3%	58	24.4%
Total	443	100.0%	238	100.0%
Niche overlap 0.91				
Proportional similarity index		0.85		0.91

[a] No significant difference (G = 5.6, df = 2, P > 0.10).

TABLE 5

TREE SPECIES SELECTED BY FORAGING MALE AND FEMALE YELLOW-RUMPED WARBLERS

Tree species[a]	No. of observations and percent			
	Male		Female	
Ponderosa pine	128	28.7%	21	10.1%
Southwestern white pine	52	11.7%	24	11.6%
Douglas-fir	81	18.2%	71	34.1%
Alpine fir	5	1.1%	10	4.8%
White fir (*Abies concolor*)	21	4.7%	22	10.6%
Blue spruce (*Picea pungens*)	4	0.9%	4	1.9%
Engelmann spruce	128	28.7%	40	19.2%
Quaking aspen (*Populus tremuloides*)	23	5.1%	16	7.7%
Snag (dead tree)	4	0.9%	0	0.0%
Total	446	100.0%	208	100.0%
Niche overlap 0.71				
Proportional similarity index[b]		0.65		0.76

[a] Significant difference (G = 65.2, df = 8, P < 0.001).
[b] Based on relative density data.

These are: (1) that the differences promote habitat partitioning and thus a reduction in intraspecific competition between the pair resulting in more thorough and efficient use of available resources (alternative 1); (2) that males forage closer to song posts and females forage nearer to nest-sites, thereby reducing energy expenditures and maximizing fitness (alternative

TABLE 6

COMPARISON OF TREE HEIGHT SELECTION BY FORAGING MALE AND FEMALE YELLOW-RUMPED WARBLERS

Tree height[a] (m)	No. of observations and percent			
	Male		Female	
≤9 m	36	8.1%	21	10.2%
>9 m ≤ 18 m	50	11.3%	50	24.3%
>18 m ≤ 27 m	144	32.5%	60	29.1%
>27 m	213	48.1%	75	36.4%
Total	443	100.0%	206	100.0%
Niche overlap 0.85				
Proportional similarity index		0.37		0.52

[a] Significant difference (G = 20.2, df = 3, P < 0.001).

TABLE 7

VARIATION IN FORAGING SITE WITH RESPECT TO DISTANCE FROM THE GROUND FOR MALE
AND FEMALE YELLOW-RUMPED WARBLERS

| Height from ground[a] (m) | No. of observations and percent | | | |
	Male		Female	
≤9 m	78	17.4%	45	22.3%
>9 m ≤ 18 m	193	43.0%	121	59.9%
>18 m ≤ 27 m	162	36.1%	31	15.3%
>27 m	16	3.5%	5	2.5%
Total	449	100.0%	202	100.0%
Niche overlap 0.78				
Proportional similarity index[b]		0.56		0.61

[a] Significant difference ($G = 33.2$, df = 3, $P < 0.001$).
[b] Based on tree height frequency data (Franzreb, unpubl.).

2); and (3) that because the sexes forage in different parts of the habitat which are probably different with respect to the abundance and distribution of prey, dissimilar foraging patterns emerge to allow the birds to forage most efficiently (alternative 3). All three alternative explanations can be tied in varying degrees to optimal foraging theory. Models dealing with this theory assume that the fitness of a foraging animal is dependent on its foraging efficiency which is usually measured in terms of net energy, and that it is selectively advantageous to forage so as to maximize fitness (Pyke et al. 1977).

In examining the merits of alternative 1, it may be argued that a reduction in intraspecific competition is largely dependent on morphological divergence. Although morphological variation is often reflected in differential foraging behavior, it is not a requisite for such differences (Ligon 1968, Jackson 1970, Kisiel 1972). Results from extensive research on woodpeckers (Picidae), including cases where sexes are morphologically similar, indicate intersexual differences in diameter of foraging perch, tree species preferences, foraging heights from the ground, and method of foraging.

In this study food may not have been limiting; hence, the high niche overlap values observed for several foraging variables should not be construed as indicative of substantial competition because there may have been no severe competition in regard to those particular variables. Schoener (1974) noted that high overlap along certain dimensions may not be relevant in appraising competition if the dimensions are not those important in partitioning the resources. Overlap indices may fail as measures

of competition if the resource examined is not in short supply; in such cases even complete overlap will not result in competition (Colwell and Futuyma 1971, Hurlbert 1978). These same limitations apply to proportional similarity indices.

The first alternative indicates that warblers segregate the habitat via differences in foraging behavior to promote a reduction in competition. If this is the main reason for the variation in foraging behavior between the sexes, one might expect to see similar partitioning during the winter, assuming that food is not more abundant then than in the summer (a reasonable assumption given the primarily insectivorous diet of this species). Yellow-rumped Warblers frequently forage in intraspecific or mixed-species flocks during the winter (Wilz and Giampa 1978). The cohesive intraspecific flocks frequently formed by Yellow-rumped Warblers suggest that males and females are foraging in the same locations (similar tree heights, tree species, foraging heights, etc.) (K. J. Wilz, pers. comm.). These foraging variables are the primary distinguishing factors in habitat partitioning during the breeding season. If intersexual differences in foraging behavior were necessary to efficiently partition resources to obtain sufficient food and diminish competition, one would assume such partitioning would be evident in the winter as well as in the summer. Limited information suggests this is not the case. Hence, although the evidence is circumstantial, it would seem that intraspecific competitive influences are not the sole or primary motivating forces behind the differences observed during the breeding season in warbler foraging behavior. Alternative 1, therefore, appears to be unlikely.

Alternative 2 implies that the sexes segregate the habitat to increase foraging efficiency and maximize fitness. Net dietary food gain for energy purposes depends upon such factors as searching time, handling time, and food values (Pyke et al. 1977). In addition, other activities aside from foraging (such as time devoted to territorial advertisement and defense, escape from predators, and nesting duties), must also be considered in a bird's overall energy budget. Studying the foraging behavior of male and female spruce-woods warblers in coastal Maine, Morse (1968) noted that male Magnolia Warblers (*D. magnolia*), Myrtle (=Yellow-rumped) Warblers, Black-throated Green Warblers (*D. virens*), and Blackburnian Warblers (*D. fusca*) foraged nearer to the heights of their singing perches than to the heights of their nests. In contrast, the females foraged closer to their nests than to the males' singing perches. He suggested that the basic differences arose because males must be conspicuous in maintaining their territories; since a considerable amount of time is spent in that pursuit, it behooves males to forage close to the singing posts which are generally at or near the tops of the trees. On the other hand, females generally nest

considerably lower than singing perch heights. Nests of Yellow-rumped Warblers are usually constructed 1–15 m from the ground, near the ends of branches generally in conifers (Reilly 1968). Thus, it should be more energy efficient for females to forage lower in the vegetation, all other factors being equal. Less energy would then be expended in movement and hunting for prey, therefore the total caloric intake necessary for body maintenance should be at least slightly reduced, and depending on conditions, may even be substantially less.

Regarding tree height use, the preference of male warblers to select tall trees may also reflect foraging near the most conspicuous locations which are well-suited as song posts. Indeed, males not only foraged higher in the trees than females, but also selected substantially taller trees.

Tree species selection may be influenced by differences in food availability, abundance, and distribution among various locations within the vegetation profile. Males were more selective of tree species, possibly the result of their greater propensity for selecting taller trees and/or foraging higher above the ground. This may result because certain tree species generally are taller than others. The majority of male observations occurred in the three tree species which tended to be the tallest trees on the watershed (ponderosa pine, Douglas-fir, and Engelmann spruce). Tree height use and tree species selection also lend support to alternative 2 in that both appear related to reproductive duties and concomitant differences in foraging to maximize both energy intake and success in care of young. This appears to be the most pursuasive alternative.

Alternative 3 implies that because sexes forage in different parts of the habitat, they, not unsurprisingly, forage differently because abundances and distributions of food items would undoubtedly be dissimilar. The basic question that then can be asked is why the birds seek food in different portions of the habitat. This alternative does little in terms of explaining the reasons for the observed differences. To answer this, one is left to ponder the other two alternatives.

SUMMARY

Variation in foraging behavior between male and female Yellow-rumped Warblers (*Dendroica coronata*) was examined during the breeding season in a mixed-coniferous forest, White Mountains, Arizona. Of seven foraging variables analyzed, the male and female Yellow-rumped Warblers displayed no significant differences (G-statistic, $P > 0.05$) in method, perch type, perch diameter, or in distance from the branch tip. However, pronounced significant differences ($P \leq 0.05$) in foraging behavior were noted for tree species selection, and for the correlated variables tree height preference and foraging location with respect to distance from the ground. Males tended to forage in taller trees and at a greater distance from the ground. Females spent considerably more time in Douglas-fir than did males. Most

of the variation in foraging behavior may be attributable to males foraging in the vicinity of song posts, whereas females spent a greater proportion of time nearer the nest-sites.

Of the three possible alternatives examined to account for these differences, it appears that the alternative reflecting related energy savings gained by each member of the pair concentrating its foraging activities near the location of its most important reproductive duties, is the most persuasive. This alternative is also the one most closely aligned with optimal foraging theory.

ACKNOWLEDGMENTS

LITERATURE CITED

COLWELL, R. K. AND D. J. FUTUYMA. 1971. On the measurement of niche breadth and overlap. Ecology 52:567–576.

FEINSINGER, P., E. SPEARS, AND R. POOLE. 1981. A simple measure of niche breadth. Ecology 62:27–32.

FRANZREB, K. E. 1978. Tree species used by birds in logged and unlogged mixed-coniferous forest. Wilson Bull. 90:221–238.

——— AND R. D. OHMART. 1978. The effects of timber harvesting on breeding birds in a mixed-coniferous forest. Condor 80:431–441.

GRUBB, T. C. 1975. Weather-dependent foraging behavior of some birds wintering in a deciduous woodland. Condor 77:175–182.

HOLMES, R. T., T. W. SHERRY, AND S. E. BENNETT. 1978. Diurnal and individual variability in the foraging behavior of American Redstarts (*Setophaga ruticilla*). Oecologia 36:141–149.

HURLBERT, S. H. 1978. The measurement of niche overlap and some relatives. Ecology 59:67–77.

JACKSON, J. A. 1970. A quantitative study of the foraging ecology of Downy Woodpeckers. Ecology 51:318–323.

JENKINS, J. M. 1979. Foraging behavior of male and female Nuttall Woodpeckers. Auk 96:418–420.

KILHAM, L. K. 1970. Feeding behavior in Downy Woodpeckers. I. Preference for paper birches and sexual differences. Auk 87:544–556.

KISIEL, D. 1972. Foraging behavior of *Dendrocopos villosus* and *D. pubescens* in eastern New York state. Condor 74:393–398.

LIGON, D. 1968. Sexual differences in foraging behavior in two species of *Dendrocopos* woodpeckers. Auk 85:203–215.

MORSE, D. H. 1967. Competitive relationships between Parula Warblers and other species during the breeding season. Auk 84:490–502.

———. 1968. A quantitative study of foraging of male and female spruce-woods warblers. Ecology 49:779–784.

PYKE, G. H., H. R. PULLIAM, AND E. L. CHARNOV. 1977. Optimal foraging: a selective review of theory and tests. Qtr. Rev. Biol. 52:137–154.

REILLY, E. M., JR. 1968. The Audubon illustrated handbook of American birds. McGraw-Hill Co., New York, New York.

SCHOENER, T. W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. Ecology 49:704–726.

———. 1974. Some methods for calculating competition coefficients from resource-utilization spectra. Am. Nat. 108:332–340.

SELANDER, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. Condor 68:113–151.

SOKAL, R. R. AND F. J. ROHLF. 1969. Biometry. W. H. Freeman and Co., San Francisco, California.

WILLIAMS, J. B. 1975. Habitat utilization by four species of woodpeckers in a central Illinois woodland. Am. Midl. Nat. 93:354–367.

———. 1980. Intersexual niche partitioning in Downy Woodpeckers. Wilson Bull. 92:439–451.

WILLIAMSON, P. 1971. Feeding ecology of the Red-eyed Vireo (*Vireo olivaceous*) and associated foliage-gleaning birds. Ecol. Monogr. 41:129–152.

WILLSON, M. F. 1970. Foraging behavior of some winter birds of deciduous woods. Condor 72:169–174.

WILZ, K. J. AND V. GIAMPA. 1978. Habitat use by Yellow-rumped Warblers at the northern extremities of their winter range. Wilson Bull. 90:566–574.

WINKLER, H. 1979. Foraging ecology of Strickland's Woodpecker in Arizona. Wilson Bull. 91:244–254.

ENDANGERED SPECIES OFFICE, U.S. FISH AND WILDLIFE SERVICE, 2800 COTTAGE WAY, SACRAMENTO, CALIFORNIA 95825. ACCEPTED 1 NOV. 1982.