FORAGING ECOLOGY OF THE RED-FACED WARBLER DURING THE BREEDING SEASON

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The Red-faced Warbler (*Cardellina rubrifrons*) is primarily a Mexican species which breeds from central Arizona and southwestern New Mexico south through the mountains of northwestern Mexico. During the breeding season it inhabits montane forests; nests are constructed on the ground and are well concealed by vegetation. Although not shy, this species is relatively quiet and inconspicuous in spite of its striking coloration, and little is known about its ecology.

In 1973 and 1974 we studied the Red-faced Warbler to analyze quantitatively its foraging behavior during the nesting season. Such information should add to our understanding of the ecology of this little-studied species.

STUDY AREA AND METHODS

The Willow Creek watershed is located approximately 80 km south of Springerville in the Apache-Sitgreaves National Forest, Greenlee County, White Mountains, Arizona. Elevation ranges from 2682-2805 m. The watershed is covered by a mixed-coniferous forest composed predominantly of Douglas-fir, Ponderosa Pine and Southwestern White Pine. We established a 15.5 ha study plot using a system of 9 parallel, flagged transect lines 390 m in length and 50 m apart.

Vegetation Analysis

We sampled the vegetation using the plotless point-quarter method (Cottam and Curtis 1956); 400 mature trees (diameter at breast height greater than or equal to 7.6 cm) were measured. Dominance values were based on basal area estimations. We estimated the height of each tree using a clinometer. Results were segregated into 3 m height intervals and provided frequency data for each height class. Additional details of the methods used in the vegetation analysis are available in Franzreb (1978).

Foraging Behavior

We obtained foraging data on Red-faced Warblers from mid-May through August in 1973 and 1974 by systematically traversing transect lines. Observations were taken under skies that were generally clear to less than 30% over-

cast; wind conditions varied from no wind to light wind (Beaufort scale 0 to 2). Although we collected data throughout the day, the majority of observations were made during morning hours (0600-1000).

We collected foraging data for eight niche dimensions: method of prey procurement, stance, 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. One observation per bird per sighting was taken to reduce sampling bias.

Method of foraging referred to the manner in which food was collected. Categories included glean, hover, hawk (sallying from a branch to catch flying insects), and peck-probe. Stance employed while foraging was either standing upright, hanging upside down, or clinging in a sideways position. Birds observed on the trunk were recorded as being in the sideways position.

We denoted the kind of material on which the bird perched as perch type. We further categorized each observation in the branch and twig perch class on the basis of perch diameter. The bird's position relative to the branch tip was categorized by subdividing the branch into thirds. The height and species of tree and the bird's distance from the ground were recorded for each observation.

Table 1. Vegetation analysis of mixed-coniferous forest, White Mountains, Arizona.

Species	Density[1] #/ha	Relative density	Relative dominance	Relative frequency
Ponderosa Pine (*Pinus ponderosa*)	112.7	18.0	30.5	19.3
Southwestern White Pine (*Pinus strobiformis*)	109.6	17.5	10.6	18.6
Douglas-fir (*Pseudotsuga menziesii*)	194.1	31.0	35.2	26.1
Alpine Fir (*Abies lasiocarpa*)	3.1	0.5	0.3	0.7
White Fir (*Abies concolor*)	51.7	8.3	7.6	8.6
Blue Spruce (*Picea pungens*)	12.5	2.0	0.7	2.5
Engelmann Spruce (*Picea engelmanni*)	31.3	5.0	2.7	5.4
Quaking Aspen (*Populus tremuloides*)	50.1	8.0	4.1	8.2
Snag (dead tree)	61.1	9.8	8.3	10.7
Total	626.2	100.0%	100.0%	100.0%

[1]Total density of all species = unit area/(mean plant-to-point distance)^2.

Foraging behavior diversity was calculated using Shannon's (1948) formula. Evenness (Pielou 1975) values were then calculated ($J' = H'/H'_{max}$) and indicated the degree of foraging specialization for each dimension. Evenness values range from 0 to 1, with values approaching 1 indicating more even utilization of available resource categories, hence, a species that is more of a generalist with regard to that particular foraging trait.

RESULTS

Vegetation

Douglas-fir was the dominant tree comprising the highest density (194.4 trees/ha) and being the most common (Table 1). In this mixed-coniferous forest Ponderosa Pine and Southwestern White Pine were also substantial components of the vegetative community. Total tree density was estimated at 626.2 tree/ha.

Trees 9 m or less in height constituted 46.2% of the total tree composition (Table 6). The tallest trees on the watershed (e.g., greater than 27 m) occurred with only a 6.3% frequency. Additional details of the vegetation analysis may be found in Franzreb (1978) and Franzreb and Ohmart (1978).

Foraging Behavior

Gleaning was the predominant foraging method (89.4%) (Table 2). Virtually all foraging (130 observations) occurred on branches/twigs (99.2%) rather than on trunks (0.8%), leaves (0%), or cones (0%). Over 75% of the branches selected were 1.3 cm or less in diameter (Table 3). Warblers tended to use the third of the branch closest to the tip more often than either the middle portion or that closest to the trunk (Table 4).

Red-faced Warblers foraged most frequently in Douglas-fir (40.8% of observations) and Southwestern White Pine (26.1%) (Table 5). Considering the number and size of Ponderosa Pines, they were little used (8.4%).

Table 2. Method of foraging of Red-faced Warblers during the breeding season.

Method	Number and Percent of Observations	
Glean	126	89.4%
Hover	12	8.5%
Hawk	3	2.1%
Total	141	100.0%

Table 3. Diameter of perch utilized by foraging Red-faced Warblers.

Perch Diameter	Number and Percent of Observations	
> 5.1 cm	5	4.7%
> 2.5 ≤ 5.1 cm	6	5.6%
> 1.3 ≤ 2.5 cm	13	12.1%
≤ 1.3 cm	83	77.6%
Total	107	100.0%

Table 4. The portion of the branch used by Red-faced Warblers while foraging.

Distance From Branch Tip	Number and Percent of Observations	
0 - 33%	51	39.2%
> 33 - 66%	43	33.1%
> 66%	36	27.7%
Total	130	100.0%

Table 5. Tree species selected by foraging Red-faced Warblers.

Species	Number and Percent of Observations	
Ponderosa Pine	12	8.4%
Southwestern White Pine	37	26.1%
Douglas-fir	58	40.8%
Alpine Fir	2	1.4%
White Fir	4	2.8%
Blue Spruce	5	3.5%
Englemann Spruce	13	9.2%
Quaking Aspen	9	6.4%
Snag	2	1.4%
Total	142	100.0%

Table 7. Distance from ground of Red-faced Warbler foraging sites.

Height from Ground	Number and Percent of Observations	
⩽ 9 m	74	55.6%
> 9 ⩽ 18 m	55	41.4%
> 18 ⩽ 27 m	4	3.0%
> 27 ⩽ 36 m	0	0
> 36 m	0	0
Total	133	100.0%

Table 8. Diversity (H') and evenness (J') values for foraging characteristics of Red-faced Warblers.

Foraging Category	Diversity	Evenness
Method	0.39	0.36
Stance	0	0
Perch type	0.05	0.07
Perch diameter	0.76	0.55
Distance from tip	1.09	0.99
Tree species	1.66	0.76
Tree height	1.45	0.90
Distance from ground	0.80	0.50
Mean evenness		0.52

Table 6. Tree height selection by foraging Red-faced Warblers and tree height frequency.

Tree Height	Number and Percent of Observations		Tree Height Frequency[1]
⩽ 9 m	22	15.6%	46.2%
> 9 ⩽ 18 m	50	35.4%	29.8%
> 18 ⩽ 27 m	42	29.8%	17.7%
> 27 ⩽ 36 m	19	13.5%	5.0%
> 36 m	8	5.7%	1.3%
Total	141	100.0%	100.0%

[1]Based on measurements obtained during vegetation analysis.

Most foraging occurred in the medium to tall trees—those greater than 9 m but less than or equal to 27 m (Table 6). The shortest trees (9 m or less) were used considerably less frequently than the proportion they comprised of the vegetation profile.

The Red-faced Warbler frequently foraged relatively close to the ground (Table 7). In fact over 55% of the observations occurred within 9 m of the forest floor. An estimated 97% of foraging activities were conducted in trees within 18 m from the ground, even though substantial foliage volume was available higher in the trees.

Distance from the tip was the most generalized foraging characteristic as indicated by the evenness value (0.99) (Table 8). Tree height selection was also relatively generalized. In contrast, stance was a highly specialized foraging category showing no diversity. Perch type was also highly stereotyped.

DISCUSSION

Warbler foraging ecology has been the subject of a number of studies (MacArthur 1958; Morse 1967a,b, 1968, 1971, 1976; Wilz and Giampa 1978; Szaro and Balda 1980; Hutto 1981). However, none of these studies examined foraging ecology of the Red-faced Warbler, a primarily Mexican species whose breeding range northernmost extension is central Arizona and southwestern New Mexico.

Red-faced Warblers preferred to forage in Douglas-fir, the dominant tree species. Disproportionately more observations occurred in this tree species even considering its dominance and relatively high foliage volume (17.6% of all foliage) (Franzreb 1978) in the habitat. Szaro and Balda (1980) noted that Red-faced Warblers were not present below a certain foliage volume. In this study they tended to utilize the tree species with the densest foliage. Thus, they were less frequent in Ponderosa Pine than expected on the basis of plant density and relative frequency data. Their increased use of Southwestern White Pine may perhaps be attributed to the fact that this tree's foliage density is generally higher than that of Ponderosa Pine. Foliage density may be important because of its influence on food availability, quantity and distribution. The degree to which a particular tree species is capable of providing suitable cover (necessary for protection against predators and inclement weather) is partly dependent on the density of foliage.

Red-faced Warblers selected moderate (>9 m), moderately tall ($\leq$ 27 m), and tall (> 27 m) trees for foraging considerably more often than anticipated based on the proportion of trees of these heights in the habitat. However, their use of these trees was not as pronounced as that of other species on the study plot such as Mountain Chickadee (*Parus gambeli*) and Ruby-crowned Kinglet (*Regulus calendula*).

Red-faced Warblers showed a decided preference to forage relatively close to the ground (i.e., within 9 m). Again, this is quite different from the behavior

of the most common species on the study area: Mountain Chickadee, Ruby-crowned Kinglet and Yellow-rumped Warbler (*Dendroica coronata*).

Studies examining niche overlap between subordinate and dominant species have usually found a decrease in niche breadth in the subordinate species when in the presence of a dominant (Colwell and Futuyma 1971, Morse 1974). However, other workers have noted an increase in niche breadth along certain niche dimensions when dominants were present (Willis 1966, Morse 1970, Yeaton 1974). In this study, it may well be that interspecific competition resulted in the restriction of the Red-faced Warbler to the lowest areas of the vegetation profile.

The Red-faced Warbler was present in relatively low density when compared to other species such as the Yellow-rumped Warbler, possibly its closest potential competitor because of morphological similarities. Red-faced Warbler densities were 10.6 birds/40 ha in 1973 and 25.6/40 ha in 1974 compared to 131.6/40 ha and 89.8/40 ha for the Yellow-rumped Warbler (Franzreb and Ohmart 1978). Mountain Chickadees and Ruby-crowned Kinglets were also considerably more numerous than Red-faced Warblers (Franzreb and Ohmart 1978). In a Maine spruce fir forest, Morse (1967a) found that kinglets and other warblers were an important factor limiting the distribution of the Northern Parula (*Parula americana*). A similar situation may be occurring in this study area.

It also was noted, in an investigation of four species of *Dendroica* warblers, that males tended to forage closer to their song posts than to their nests, whereas females tended to forage closer to the nests than to the male song perches (Morse 1968). This behavior presumably results in partitioning the habitat to provide for the most efficient resource exploitation. Because the Red-faced Warbler is a ground nester, it would be reasonable to predict that it would forage closer to the ground than tree-nesting species, especially once eggs hatch and the substantial food requirements of nestlings place an additional burden on the adults.

The most specialized foraging categories (method, stance and perch type) as indicated by diversity and evenness values were the most constrained by morphological considerations. The other characteristics were less stereotyped and behaviorally more plastic.

SUMMARY

We examined the foraging ecology of the Red-faced Warbler in a mixed-coniferous forest, White Mountains, Arizona, during the breeding season in 1973 and 1974. Foraging characteristics addressed included method, stance, type of perch, diameter of perch, position on the branch, tree species selection, tree height preferences, and height from the ground. Diversity (H′) and evenness (J′) values indicated that this warbler was most diverse in distance from the branch tip and in tree height selection. Red-faced Warblers over-

whelmingly preferred to glean on branches/twigs and usually selected the smallest ($\leq$ 1.3 cm) branches with a slight preference for the third of the branch closest to the tip. Over 66% of the observations occurred within Douglas-fir and Southwestern White Pine. Although trees of all heights were utilized, warblers preferred to forage relatively close to the ground. This preference may have resulted from interspecific competitive pressures, or possibly, because this species is a ground nester, foraging closer to the ground may be energetically more efficient.

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LITERATURE CITED

Colwell, R.K & D.J. Futuyma. 1971. On the measurement of niche breadth and overlap. Ecology 52:567-576.

Cottam, G. & J. Curtis. 1956. The use of distance measures in phytosociological sampling. Ecology 37:451-460.

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

Franzreb, K.E. & R.D. Ohmart. 1978. The effects of timber harvesting on breeding birds in a mixed-coniferous forest. Condor 80:431-441.

Hutto, R.L. 1981. Seasonal variation in the foraging behavior of some migratory western wood warblers. Auk 98:765-777.

MacArthur, R.H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39:599-619.

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

Morse, D.H. 1967b. Foraging relationships of Brown-headed Nuthatches and Pine Warblers. Ecology 48:94-103.

Morse, D.H. 1968. A quantitative study of foraging of male and female spruce-woods warblers. Ecology 49:779-784.

Morse, D.H. 1970. Ecological aspects of some mixed species foraging flocks of birds. Ecol. Monogr. 40:119-168.

Morse, D.H. 1971. The insectivorous bird as an adaptive strategy. Ann. Rev. Ecol. Syst. 2:177-200.

Morse, D.H. 1974. Niche breadth as a function of social dominance. Amer. Nat. 108: 818-830.

Morse, D.H. 1976. Variables affecting the density and territorial size of breeding spruce-woods warblers. Ecology 57:290-301.

Pielou, E.C. 1975. Ecological diversity. John Wiley & Sons, New York.

Shannon, C.E. 1948. The mathematical theory of communication. Bell Syst. Tech. J. 27:379-423; 623-656.

Szaro, R.C. & R.P. Balda. 1980. Bird community dynamics in a Ponderosa Pine forest. Studies in Avian Biol. No. 3.

Willis, E.O. 1966. Interspecific competition and the foraging behavior of Plain-brown Woodcreepers. Ecology 47:667-672.

Wilz, K.J. & V. Giampa. 1978. Habitat use by Yellow-rumped Warblers at the northern extremities of their winter range. Wilson Bull. 90:566-574.

Yeaton, R.I. 1974. An ecological analysis of chaparral and pine forest bird communities on Santa Cruz Island and mainland California. Ecology 55:959-973.

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Sketch by Narca Moore