ANNUAL VARIATION IN FORAGING ECOLOGY OF PROTHONOTARY WARBLERS DURING THE BREEDING SEASON

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ABSTRACT.—We studied foraging ecology of Prothonotary Warblers (*Protonotaria citrea*) along the Tennessee River in west-central Tennessee during the breeding seasons of 1984–1987. We analyzed seven foraging variables to determine if this population exhibited annual variation in foraging behavior. Based on nearly 3,000 foraging maneuvers, most variables showed significant interyear variation during the four prenestling and three nestling periods we studied. This interyear variation probably was due to proximate, environmental cues—such as distribution and abundance of arthropods—which, in turn, were influenced by local weather conditions. Researchers should consider the consequences of combining foraging behavior data collected in different years, because resolution of ecological trends may be sacrificed by considering only general patterns of foraging ecology and not the dynamics of those activities. In addition, because of annual variability, foraging data collected in only one year, regardless of the number of observations gathered, may not provide an accurate concept of the foraging ecology in insectivorous birds. *Received 29 September 1988, accepted 16 August 1989.*

DURING the past 20 years, quantitative study of foraging behavior has emerged as one of the major focuses of avian ecologists. This activity has led to the development and testing of theories of optimal foraging, niche partitioning, and community ecology. Typically, foraging data are collected on a study area for several years. These data then are combined across years to produce an overall pattern of species' foraging ecology (e.g. Morse 1968, Holmes et al. 1979, Sabo 1980). Annual variation in foraging behavior, however, generally has been ignored. Recently, there has been concern that, by searching for ecological generalities based upon species' averages across multiple years and areas, information relating environmental factors to behavior is lost (e.g. Wiens 1983, Martin 1987, Wiens et al. 1987). We analyzed the variability in a local population's behavior when exposed to different environmental conditions across consecutive breeding seasons. To date, few in-depth analyses (e.g. Landres 1980, Wagner 1981) of annual variation in species' foraging ecology have been reported, and no analyses of this type have been made on data gathered over >2 yr. Substantial populational (Morse 1971, D. R. Petit et al. 1990), interseasonal (Parnell 1969, Conner 1981), intraseasonal (Williamson 1971, Sherry 1979, L. Petit et al. 1990), and diurnal (Holmes et al. 1978) variability exists in foraging ecology for a number of terrestrial land birds. Consequently it is important to assess the extent of annual behavioral plasticity within a local population. Documentation of the sources of variation in a species' behavior can provide insight into the proximate factors that control those activities.

STUDY AREA AND METHODS

Our study area along the Tennessee River in Benton and Humphreys counties of west-central Tennessee has been described in detail elsewhere (Petit et al. 1987, Petit 1989). Details of the area, its vegetation, our methods, and the analytical techniques that we used are given in the preceding paper (1990, Auk 107: 133–145).

Interyear variation in foraging behavior could have occurred because different environmental conditions existed each year and the warblers simply responded to those changes. This idea was tested indirectly by calculating the magnitude and direction of the deviation of each year from the overall (3 or 4 year) average for all foraging variables. All observations were used to construct these deviations. Because the categories for a given variable are not independent,

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The Auk 107: 146–152. January 1990

we chose for analysis only one category per variable (except substrate), that one in highest overall frequency. For the variable substrate, we chose the 4 most commonly used substrates (fallen branch, willow, maple, and buttonbush) which totaled ca. 50% of all substrates used in each period. Male and female deviations for each period were calculated separately. Thus, for each sex and for each of the 4 substrate types, there were 4 deviations (=4 yr) for the prenestling period (n = 16 total pairs of deviations) and 3 deviations (=3 yr) for the nestling period (n = 12 pairs). For the other 6 variables, there were 24 pairs of deviations (6 variables, 4 yr) for the prenestling period and 18 pairs of deviations (3 yr) for the nestling period. If proximate environmental cues were important, both sexes should alter their foraging behavior in a similar fashion. In that case, a strong positive correlation (Pearson's r) between male and female yearly deviations would be expected.

Results

We recorded 2,978 foraging observations on male (n = 2,023) and female (n = 955) Prothonotary Warblers (*Protonotaria citrea*). Most records were collected during the prenestling (n = 1,972) rather than the nestling (n = 1,006) period because of difficulty in following the nesting birds. In addition, the majority of data was collected during 1984 (51.7%), with the remainder divided more equally among 1985 (22.7%), 1986 (8.0%), and 1987 (17.8%). Samples used in statistical analyses were taken from 373 individuals over 4 yr and totaled 563. For any given year/period combination, sample sizes for females averaged 30.0 ± 14.4 (SD; range = 13–52) and those for males 50.4 ± 26.9 (range = 28–106).

General foraging behavior.—We summarized foraging behavior of male and female Prothonotary Warblers during prenestling (Appendix 1) and nestling (Appendix 2) periods. Prothonotary Warblers foraged primarily by gleaning, but they hovered in up to 31% of observations. Hawking was observed in <5% of observations. Warblers perched most commonly on twigs and branches ≤2.5 cm in diameter. Prothonotary Warblers generally foraged in the subcanopy, usually below 7 m (≥75% of observations), and took prey mostly from leaves and branches in the middle and outer portions of trees and shrubs of all sizes. The most commonly used plant species were willow, maple, sweetgum, and buttonbush, but birds also foraged frequently on dead fallen branches.

Annual variation.—Of the 14 comparisons, 11 (79%) during the prenestling period showed significant annual variation (Table 1, Appendix 1). Males demonstrated statistically significant annual variation for all 7 variables, whereas females showed significant variation across years for foraging method, foraging height, substrate, and prey location. Similarly, marked annual variation in foraging behavior also existed during the nestling period. Of the 14 comparisons, 9 (64%) exhibited significant heterogeneity among the 3 yr (Table 1, Appendix 2). Perch diameter and foraging method varied little by sex during this period, and females showed no significant annual variation in their use of prey location.

Yearly climatological variation.—Mean weekly precipitation and mean daily maximum temperatures varied substantially among years (Table 2). The most striking variation occurred in the amount of rainfall during the prenestling period. Both 1984 and 1985 had relatively high amounts of rainfall, whereas 1986 and 1987 were drier. During May 1984, the Tennessee River rose to >3 m above flood stage and no foraging observations were taken. Mean maximum temperatures were lower in the prenestling periods of 1984 and 1986 than in the other two years. There was less variation in precipitation among years during the nestling period. Mean maximum temperatures were highest in 1984 and lowest in 1985 (Table 2). In summary, the most anomalous period was the prenestling stage of 1984, which was relatively cool and wet compared with other years. Our subjective impression was that this resulted in a reduced number of insects. Other years had local weather conditions closer to normal.

Response to proximate environmental variation.—During both the prenestling (r = 0.75, n = 40) and nestling (r = 0.69, n = 30) periods there was high congruence between sexes in their foraging behavior. This would be predicted if the warblers responded to proximate cues in the environment that varied among years.

Discussion

Prothonotary Warblers undergo marked changes in foraging behavior as the breeding season progresses (L. Petit et al. 1990). This work demonstrates that this behavioral plasticity has an annual component as well.

Only Landres (1980) and Wagner (1981) have investigated annual variability in avian forag-

TABLE 1. Annual variation in foraging ecology of Prothonotary Warblers along the Tennessee River during the prenestling and nestling periods, 1984–1987. *G* represents *G*-statistics based on contingency tables.[a]

	Prenestling period				Nestling period			
	Males		Females		Males		Females	
Foraging variable	*G*	*P*	*G*	*P*	*G*	*P*	*G*	*P*
Foraging method	15.5	**	13.4	*	2.0	NS	4.1	NS
Foraging height	92.1	**	36.2	**	28.6	**	19.8	**
Perch diameter	12.3	*	3.4	NS	5.9	NS	3.9	NS
Substrate	54.3	**	23.6	NS	32.6	**	23.6	**
Substrate height	42.4	**	13.5	*	13.7	**	36.1	**
Location from trunk	20.4	**	0.92	NS	23.8	**	11.1	*
Prey location	36.4	**	12.5	*	14.8	**	7.6	NS

[a] * = $P < 0.05$, ** = $P < 0.01$, NS = not significant.

ing behavior in detail. These studies dealt with data collected for only 2 years. Landres (1980) found significant annual variation for several members of two breeding bird communities in California and Mexico. Likewise, Wagner (1981) documented annual changes in foraging behavior of 3 of 8 species studied during the breeding season, and hypothesized that annual variation in avian foraging behavior may be greater than the well-documented seasonal variation.

The strong correlation between male and female foraging behavior each year suggests that this population of Prothonotary Warblers responded to environmental stimuli. Wiens et al. (1987) were of the opinion that time budgets of and substrate use by two shrubsteppe bird species were not tightly coupled to the environment, although they measured only densities of conspecifics and heterospecifics as environmental variables. We found that local weather conditions varied among years and could have affected warbler foraging. We do not, however, have data on arthropod abundances in all years, and because we do not know how the prey base varied, we can only correlate the variation in weather conditions to observed variation in foraging behavior. Nevertheless, the relative severity of conditions during the prenestling period in 1984 apparently elicited a functional response by the warblers. Specifically, prenestling warblers gleaned more and hovered less than in other years. They foraged mostly below 3 m and increased use of buttonbushes and fallen branches. Larger perches were used also as the birds increased their use of trunks and branches, and foraged less frequently on leaves. We did not take foraging observations during windy or inclement weather, so the data do not reflect a direct response to actual weather conditions. The wet, cool spring of 1984 delayed leafing of trees and shrubs and appeared to suppress abundances of flying and foliage-clinging insects. The foraging data reflect those conditions. We believe that the rainy, cool weather adversely affected arthropod availability (particularly those associated with foliage), and altered the foraging behavior of the warblers. These results also provide indirect evidence that yearly variation in foraging ecology of Prothonotary Warblers is due, in part, to variation in abundance and distribution of prey. This population of Prothonotary Warblers underwent a temporal shift in foraging ecology within the breeding season which correlated well with changes in the availability of arthropod prey (L. Petit et al. 1990). Yearly fluctuations occurred in the arthropod prey base on our study area (L. Petit unpubl.) and on other study areas (e.g. Holmes and Schultz 1988), and forest foliage-using birds responded to changes in prey availability (Holmes and Schultz 1988). Consequently we suggest that the relative abundance of prey items was the most likely proximate cause of the annual variation we observed in foraging ecology. Foliage structure may directly affect foraging ecology of forest birds (e.g. Robinson and Holmes 1984). But foliage structure appeared to remain similar across years for both the prenestling and nestling periods in our study, and change in foliage structure is probably inadequate to explain our results. Simultaneous quantification of at least food resources and local weather conditions in relation to foraging behavior over several years is necessary to fully assess the factors that influence annual variation in avian foraging ecology.

TABLE 2. Local weather conditions ($\bar{x} \pm$ SD) from a NOAA weather station in Waverly, Tennessee, for prenestling and nestling periods (1984–1987).

Weather	1984	1985	1986	1987
Prenestling period				
Weekly precipitation (cm)	13.6 ± 9.1	3.3 ± 3.9	1.4 ± 1.7	1.3 ± 2.5
Daily maximum temperature (°C)	24 ± 5.1	27 ± 3.1	24 ± 5.6	27 ± 3.6
Nestling period				
Weekly precipitation (cm)	1.7 ± 1.9	1.7 ± 1.5	—	2.2 ± 1.9
Mean daily maximum temperature (°C)	32 ± 2.1	29 ± 3.2	—	31 ± 1.7

If one was interested only in quantifying the general foraging pattern of a species (e.g. Holmes and Robinson 1988), then lumping years together may not seriously hinder the goal of that research. Resolution would be sacrificed, however, if one was interested in factors that influence foraging behavior, especially if those elements varied over time. Had we drawn conclusions based upon the first year's data alone, even though we had >1,500 foraging observations, our impression of Prothonotary Warbler foraging behavior would have been substantially different than what we ultimately concluded. For example, females during the 1984 prenestling period foraged below 1 m 85.6% of the time; the 4-yr average was 67.4%. Similarly, females during the nestling period in 1984 took prey from leaves in 39.8% of all observed capture attempts. When 2 more years of data were added, this value was inflated to 61.8%. Thus, foraging data collected during a single year, regardless of sample size, may yield results not indicative of the range of activities exhibited by a population or species.

ACKNOWLEDGMENTS

Funding was provided by the following: The Association of Field Ornithologists (Bergstrom Award); The American Ornithologists' Union (Carnes Award); Sigma Xi, The Scientific Research Society; Arkansas Audubon Society Trust Fund; Department of Biological Sciences, Bowling Green State University; Department of Zoology, University of Arkansas (all to L. J. Petit); U.S. Fish and Wildlife Service; and, especially, B. E. and K. G. Reichhardt, and R. E. and J. M. Petit. Logistical support and equipment were donated by F. M. Stephen, University of Arkansas; the staff at Nathan Bedford Forrest State Historic Area, Tennessee; M. Gudlin, W. Phifer, and B. Hatcher, Tennessee Wildlife Resources Agency; W. J. Davis and R. Carlton, Lambuth College, Jackson, Tennessee; H. Webber, Lakeshore Methodist Assembly, Eva, Tennessee; and J. Gentry, The University Museum, University of Arkansas. P. H. Albers, T. Brush, C. E. Grue, K. V. Rosenberg, and D. W. Sparling made numerous suggestions for the improvement of previous drafts. This work is dedicated to the memory of Richard E. Petit.

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APPENDIX 1. Summary of foraging ecology of Prothonotary Warblers during prenestling seasons (see text), 1984–1987. Values represent percentages (rounded to nearest whole number); sample sizes are shown in parentheses below years.

	Male				Female			
Variable	1984 (923)	1985 (163)	1986 (167)	1987 (140)	1984 (346)	1985 (106)	1986 (65)	1987 (62)
Foraging method								
Glean	95	68	88	93	98	78	95	94
Hover	4	31	11	7	2	19	5	6
Hawk	1	1	1	0	0	3	0	0
Foraging height								
≤1 m	71	37	17	29	86	45	32	41
>1–3 m	16	23	10	15	10	25	14	29
>3–5 m	6	18	25	25	4	12	29	16
>5–7 m	2	8	26	13	0	9	14	3
>7 m	5	14	22	18	0	9	11	11
Perch diameter								
≤1 cm	42	51	72	50	49	61	80	52
>1–2.5 cm	31	35	19	37	29	23	10	22
>2.5–8 cm	9	7	5	7	8	8	2	5
>8–15 cm	10	5	3	4	8	4	3	12
>15 cm	8	2	1	2	6	4	5	9
Substrate								
Maple	10	6	11	7	10	8	3	6
Buttonbush	15	7	5	3	10	8	9	14
Vine	10	4	2	9	12	6	3	8
Willow	23	43	31	18	13	33	22	18
Elm	3	4	5	13	2	10	11	2
Hackberry	2	2	4	4	1	0	0	2
Herbaceous	4	1	1	1	4	1	0	0
Sweetgum	2	6	20	12	3	4	9	8
Birch	1	2	10	4	1	2	15	5
Dead branch	17	5	2	14	28	12	6	18
Snag	2	1	4	2	1	1	3	0
Misc. trees	9	15	5	11	9	5	15	13
Misc. shrubs	2	4	0	2	6	10	3	6
Horizontal location								
Inner	48	19	21	22	43	25	28	32
Middle	19	25	21	29	19	21	16	19
Outer	33	56	58	49	38	54	56	49
Substrate height								
≤1 m	39	20	8	28	55	31	23	29
>1–3 m	21	13	11	6	16	10	5	27
>3–5 m	5	12	10	10	6	13	3	6
>5–7 m	5	6	10	12	2	9	26	6
>7 m	30	49	61	44	21	37	43	30
Prey location								
Leaf	24	46	65	33	16	42	62	34
Branch	41	42	24	54	46	41	23	48
Trunk	19	10	9	11	14	10	14	16
Ground	16	1	2	1	24	4	1	2
Air	1	1	1	1	0	3	0	0

APPENDIX 2. Summary of foraging ecology of Prothonotary Warblers during nestling period (see text), 1984-1987. (No data were gathered in 1986.) Values represent percentages (rounded to nearest whole number) and sample sizes are shown in parentheses below years.

	Male			Female		
Variable	1984 (163)	1985 (254)	1987 (213)	1984 (109)	1985 (153)	1987 (114)
Foraging method						
Glean	74	78	81	73	77	80
Hover	17	20	18	17	22	17
Hawk	9	2	1	10	1	3
Foraging height						
≤1 m	17	18	8	48	35	17
>1-3 m	50	21	13	46	21	29
>3-5 m	20	18	26	6	21	17
>5-7 m	10	20	22	0	11	16
>7 m	3	23	31	0	12	21
Perch diameter						
≤1 cm	66	71	80	63	78	82
>1-2.5 cm	22	23	13	25	13	13
>2.5-8 cm	7	3	4	6	3	5
>8-15 cm	3	1	0	3	1	1
>15 cm	2	2	3	3	5	0
Substrate						
Maple	8	27	22	2	32	9
Buttonbush	3	4	1	10	6	4
Vine	5	4	2	4	5	4
Willow	48	19	8	26	19	8
Elm	7	6	5	4	4	1
Hackberry	1	6	11	0	4	8
Herbaceous	1	1	0	0	2	0
Sweetgum	4	5	22	9	2	24
Birch	1	1	5	0	1	2
Dead branch	1	4	2	9	9	8
Snag	7	1	1	12	1	2
Misc. trees	15	19	20	24	12	24
Misc. shrubs	0	3	1	0	3	6
Horizontal location						
Inner	20	12	10	23	18	5
Middle	44	31	13	50	33	22
Outer	36	57	77	27	49	73
Substrate height						
≤1 m	17	18	7	31	32	20
>1-3 m	15	7	4	24	10	4
>3-5 m	17	4	6	17	2	13
>5-7 m	24	7	14	19	5	11
>7 m	27	64	69	9	51	52
Prey location						
Leaf	58	76	82	40	64	80
Branch	24	14	14	35	26	16
Trunk	9	3	3	12	4	1
Ground	0	5	0	3	5	0
Air	9	2	1	10	1	3