INTERSEXUAL AND TEMPORAL 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*) over four breeding seasons to determine if this species exhibited sex-specific or temporal variation in foraging behavior. Significant differences between sexes during the prenestling period were found for foraging height and substrate height (foraging method, plant species/substrate, perch diameter, horizontal location from trunk, and prey location were not significantly different). During the nestling period, this divergence between sexes was evident for foraging height, substrate height, substrate/tree species, and prey location. Additionally, male warblers significantly altered their behavior for all seven foraging variables between the two periods, whereas females exhibited changes similar to those of males for five of the foraging variables. This parallel shift suggests a strong behavioral response by both sexes to proximate factors (such as vegetation structure, and prey abundance and distribution) that varied throughout the breeding season. Sex-specific foraging behavior during the prenestling period was best explained by differences in reproductive responsibilities rather than by the theory of intersexual competition for limited resources. During the nestling period, neither hypothesis by itself explained foraging divergences adequately. However, when integrated with the temporal responses of the warblers to changes in prey availability, reproductive responsibilities seemed to be of primary importance in explaining intersexual niche partitioning during the nestling period. We emphasize the importance of considering both intersexual and intraseasonal variation when quantifying a species' foraging ecology. *Received 29 September 1988, accepted 16 August 1989.*

SEX-SPECIFIC spatial and behavioral differences in exploiting food resources have been documented for woodpeckers (e.g. Selander 1966, Kisiel 1972, Grubb 1975, Jenkins 1979), emberizids (Morse 1968, Robbins 1971, Williamson 1971, Franzreb 1983, Holmes 1986), fringillids (e.g. Ebenman and Nilsson 1982), and sittids (e.g. McEllin 1979). Two hypotheses have been advanced to explain intersexual partitioning of foraging niches. One is reduction in competition for food resources (Selander 1966, Robbins 1971) and a second correlates other sex-related behaviors during the breeding season (e.g. females forage closer to the nest, whereas males forage higher near singing posts [Morse 1968, Williamson 1971]).

Most studies of foraging behavior during the breeding season did not consider temporal variation in niche characteristics; instead, they regarded the entire breeding season as a homogeneous unit (e.g. Ligon 1968, Morse 1968, Williams 1975, Hooper and Lennartz 1981, Franzreb 1983). Due to seasonal changes in habitats (e.g. Whitmore 1979), variation in prey abundance or distribution (Custer and Pitelka 1978, Jamieson et al. 1982, Craig 1984, Holmes and Schultz 1988), and changes in reproductive responsibilities, important information may be lost if foraging behavior is pooled over a prolonged period. For example, foraging behavior of American Redstarts (*Setophaga ruticilla*) varies between the nestling and prenestling stages of the breeding season (Sherry 1979). Yet, despite valuable insight into factors influencing avian foraging ecology that intraseasonal variation may yield, this aspect of bird foraging behavior has been largely neglected (but see Root 1967, Morse 1968, Williamson 1971, Robinson 1986).

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During four breeding seasons, we observed the foraging behavior of male and female Prothonotary Warblers (*Protonotaria citrea*). Prothonotary Warblers are long-distance migrants that arrive in Tennessee during early to mid-April. These cavity-nesting wood-warblers select nest sites 1–5 m above ground always in close proximity to water (Petit 1989). Most warblers we studied nested in nest boxes (1–2 m above ground or water) placed along a river (Petit et al. 1987, Petit 1989). Here we document the partitioning of breeding territories during foraging bouts. We divided our data set into two time periods when changing proximate conditions might place contrasting demands on foraging. Measures of niche breadth and overlap between sexes and between time periods were used to discuss intersexual microhabitat partitioning with respect to predictions of niche theory.

STUDY AREA AND METHODS

We studied Prothonotary Warblers in riverine habitat along a 30-km stretch of the Tennessee River (Kentucky Lake) near New Johnsonville, Benton, and Humphreys counties, Tennessee. The lake is ca. 2.4 km in width and is bordered by gently rolling, often steep, wooded terrain. The riverine habitat, limited to narrow (10–75 m) bands along the river, is partially flooded in spring and summer, and is dominated by willow (*Salix* sp.), American elm (*Ulmus americana*), river birch (*Betula nigra*), hackberry (*Celtis occidentalis*), sweetgum (*Liquidambar styraciflua*), maples (*Acer* spp.), and buttonbush (*Cephalanthus occidentalis*). Canopy height ranges from 6–20 m ($\bar{x} \approx$ 12 m), and there is relatively sparse understory. All trees and shrubs begin to leaf by early April, and most leaves are completely developed by early May. The river is dotted with numerous small (0.5–8 ha) islands that are partially flooded in the spring and summer months. The vegetation there is similar to that of the shoreline.

We observed Prothonotary Warblers on islands and along the shoreline during the four breeding seasons between 1984–1987. Foraging observations were divided into prenestling and nestling periods which corresponded to different adult activities. The prenestling period represented a time of territory establishment, pair formation, nest building, and incubation. Observations during this stage were made from 21 April to 3 May 1984, 17 April to 9 May 1985, 11 April to 8 May 1986, and 18 April to 9 May 1987. Records during the nestling interval included only those for warbler pairs that were feeding nestlings. Observations during the nestling phase were made from 11 June to 23 July 1984, 18 May to 14 July 1985,

and 1 June to 18 July 1987. We did not record foraging data on adults feeding nestlings in 1986.

The seven variables recorded for each observation of an actively foraging bird are as follows:

1. *Foraging method*—glean, hover, hawk (for descriptions, see Robinson and Holmes 1984, D. Petit et al. 1990);
2. *Foraging height*—for analysis, grouped into the following categories: ≤1.0 m, >1.0–3.0 m, >3.0–5.0 m, >5.0–7.0 m, >7.0 m;
3. *Perch diameter*—≤1.0 cm, >1.0–2.5 cm, >2.5–8.0 cm, >8.0–15.0 cm, >15.0 cm;
4. *Substrate*—plant species (maple, buttonbush, vine, willow, elm, hackberry, herbaceous plants, sweetgum, birch, miscellaneous bushes, miscellaneous trees) or substrate (dead branch on ground, snag) toward which individual directed foraging motion;
5. *Substrate height*—same as foraging height (2);
6. *Horizontal location from trunk*—inner ⅓ (including trunk), middle ⅓, outer ⅓;
7. *Prey location*—leaf, branch, trunk, ground, air.

Sample sizes differed slightly in some analyses because of our inability to accurately estimate all variables for some observations. Although we did not restrict the time of sampling foraging behavior of Prothonotary Warblers, most (>75%) of our data were collected before 1200.

Each day, observations were collected on individuals at ≥1-min intervals for up to 10 observations/individual. Because individuals were often lost from sight for several minutes, observation periods on an individual often lasted up to 0.5 h. We ceased recording foraging data when the focal bird was not seen for more than several minutes or engaged in a behavior other than foraging. Because Prothonotary Warblers make ca. 4–12 attempts/min at capturing prey while foraging actively, our records do not reflect consecutive foraging movements but regular sampling out of strings of 100 or more foraging maneuvers. Although the ≥1-min interval between records may have allowed adequate time for an individual to perform statistically independent maneuvers (cf. Wiens et al. 1970), taking sequential observations from the same bird and subjecting those data to statistical analyses may lead to pseudoreplication (Hurlbert 1984). However, multiple observations per individual apparently are better for detection of uncommon foraging behavior as compared with single observations of individuals (Wagner 1981, Morrison 1984, Morrison and With 1987, Holmes and Robinson 1988). To resolve this dilemma, we present graphically results that reflect all foraging acts observed, but we based statistical analyses upon only one observation (the first) per individual each day (e.g. Holmes and Robinson 1988). (Individual identity was based on unique combinations of colored leg bands or affinity to a certain territory.) This produced

only one observation per bird each year for >80% of the individuals, and we believe that we have adequately met the assumption of independence of samples required for statistical inference.

Because our "populations" of interest were males and females during each time period regardless of year, we pooled all 4 years of data for analysis. Annual variation in Prothonotary Warbler foraging ecology is presented elsewhere (L. Petit et al. 1990).

Log-likelihood ratio (G) tests (Zar 1974) were used to test for significant differences in foraging behavior between the sexes and within each sex between periods. When possible, adjacent or biologically meaningful cells in contingency tables were collapsed to ensure that <20% of the cells had expected values of <5 (Siegel 1956). Significant differences in mean foraging heights were assessed with t-tests.

Niche breadth of each foraging variable (all observations included) was calculated as: $1/B = \Sigma p_i^2$, where B was the niche breadth for a given variable and p_i was the proportion of observations where the birds were exploiting resource category i (Levins 1968). We compensated for the varying number of categories for each foraging variable by standardizing each B so that it represented the fraction of the largest possible niche breadth (Reynolds and Meslow 1984). To assess the degree of resource overlap between sexes, we used Schoener's (1968) index of niche overlap: $O_{xy} = 1 - 0.5 |p_{xi} - p_{yi}|$, where p_{xi} and p_{yi} were the proportions of a given foraging behavior (i) utilized by females (x) and males (y), respectively. Values of O_{xy} range from 0 to 1, where 1 represents complete overlap between the sexes for a given variable, and 0 indicates complete separation. We made four sets of comparisons: (1) males vs. females during the prenestling period, (2) males vs. females during the nestling period, (3) males, prenestling vs. nestling period, and (4) females, prenestling vs. nestling period.

Arthropod abundance.—We assessed relative arthropod abundance only in 1985 and 1987. Data from those 2 yr, along with sampling in 1988 and 1989, suggest that relative arthropod densities follow a similar seasonal trend from year to year on our study areas (but see below). Thus, the data reflect typical spring and summer temporal changes in arthropod abundances. Only 1984 was atypical, due to a severe flood in early May. The effect was to delay emergences of insects by 2–3 weeks. Our subjective impression was that once the floodwaters had receded, normal numbers of insects occupied the bottomland forests. We can summarize our arthropod sampling for 1985 and 1987–1989 to provide quantitative information on the interseasonal changes in arthropod numbers. These changes can be related to concurrent alterations in the foraging behavior of the warblers.

Every 2 weeks (a "count"), usually from late April to mid-July, we counted visually arthropods on leaves 1.5–3 m above ground. We searched 20,000 cm² of leaf area (top and bottom) from up to six different tree species in each sampling plot (5-m radius circle). The number of leaves searched for each tree species was proportional to its density within the plot and inversely related to its average leaf area. Sixteen plots, all over water or within 30 m of the river's edge, were counted over a 2–3-day period. All arthropods were identified to order. In addition, for each sample plot, 20 sweeps of an insect net were made at each of four locations. In 1985, data were collected in a slightly different—but comparable—fashion. This methodological difference, however, should not be detrimental to the present analysis because of our standardization of data within years (see below).

Arthropod data for each 2-week period (all 16 plots summed) are presented as percent deviations from that year's average number of individuals per count. In this way, we controlled for between-year differences in absolute abundances of arthropods. Taxonomic groups are analyzed separately. Data are presented only for Diptera (flies), Ephemeroptera (mayflies), Arachnida (spiders), and Lepidoptera larvae (moths and butterflies), because those are the main prey items of Prothonotary Warblers throughout the breeding season (L. Petit unpubl.).

RESULTS

A total of 2,978 observations were collected on foraging "prenestling" male (1,393 observations), "prenestling" female (579), "nestling" male (630), and "nestling" female (376) adult Prothonotary Warblers. For statistical analyses, we used only one observation per individual each day, which resulted in sample sizes of 223 (males; $n = 147$ different individuals) and 101 (females; $n = 79$ individuals) during the prenestling phase, and 130 (males; $n = 87$ individuals) and 109 (females; $n = 83$ individuals) during the nestling period.

Prenestling period: males vs. females.—During spring, before full leaf, male and female warblers differed significantly in 2 of the 7 foraging variables. Males ($\bar{x} \pm SD = 3.0 \pm 3.3$ m) foraged higher than females ($\bar{x} = 1.5 \pm 1.9$ m; $t = 4.3$, $df = 321$, $P < 0.001$). Females spent two thirds of their foraging time below 1 m; males spent only about half of the time below 1 m ($G = 20.8$, $df = 3$, $P < 0.001$; Fig. 1). Females used shorter trees and shrubs than did males ($G = 11.6$, $df = 4$, $P < 0.05$; Fig. 2). Males most frequently foraged in trees >7 m tall; females often used shrubs and trees <3 m tall. Intermediate-sized trees (>3–7 m) were uncommon and were used <20% of the time by each sex.

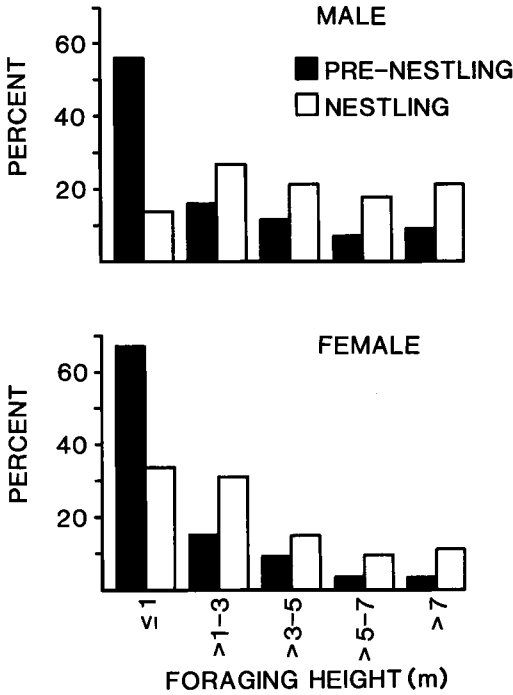The remaining five foraging variables measured did not differ significantly between male

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Fig. 1. Percentage use of foraging-height intervals by adult Prothonotary Warblers during prenestling and nestling periods (see text), 1984–1987.
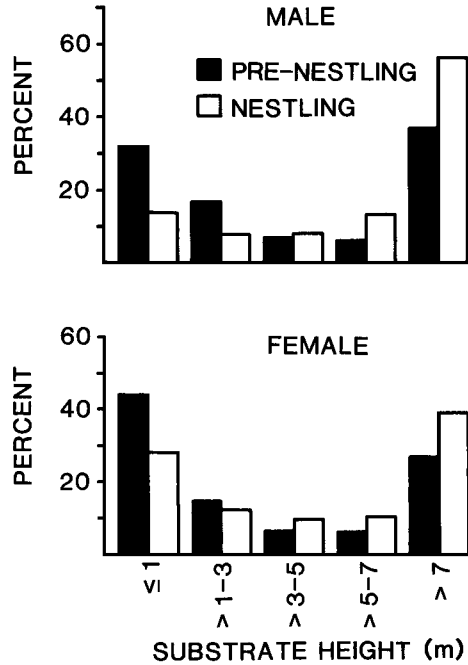

Fig. 2. Percentage use of plants (substrates) of different heights by adult Prothonotary Warblers during prenestling and nestling periods (see text), 1984–1987.

and female warblers. During the prenestling period, both sexes captured nearly all prey by gleaning arthropods from substrates ($G = 1.2$, df = 1, $P > 0.20$; Fig. 3). Small- (≤1.0 cm) and intermediate-sized (>1.0–2.6 cm) branches were used as perch substrates ca. 50% of the time ($G = 4.9$, df = 4, $P > 0.30$; Fig. 4). Use of substrate also did not vary between sexes during the prenestling period ($G = 12.2$, df = 9, $P > 0.20$; Fig. 5). Both males and females used a wide variety of plants but concentrated on willows, buttonbushes, maples, and dead fallen branches. Both sexes foraged more often in the inner one third and outer one third of trees and shrubs than in the middle one third ($G = 0.6$, df = 2, $P > 0.70$; Fig. 6). Use of inner parts of trees and shrubs was related to the birds' gleaning from trunks during the early part of the breeding season. Use of distal regions of trees reflected typical foraging on emerging leaves and small twigs. Both sexes attempted to capture most prey on branches, but they also located prey often on emerging leaves, trunks, and ground ($G = 3.0$, df = 3, $P > 0.30$; Fig. 7).

Nestling period: males vs. females.—Foraging be-

havior during the nestling period differed significantly between sexes for four variables. Nearly two thirds of foraging maneuvers by females ($\bar{x} = 2.7 \pm 3.0$ m) were at 3 m or lower, whereas males ($\bar{x} = 4.8 \pm 3.5$ m; $t = 5.0$, df = 234, $P < 0.001$) spent only 40% of the foraging time at this level ($G = 23.7$, df = 3, $P < 0.001$; Fig. 1). Male and female warblers feeding nestlings differed significantly in use of substrates ($G = 26.2$, df = 9, $P < 0.01$; Fig. 5). Males used willows and maples more frequently than females used them, but females foraged more often on buttonbushes and fallen dead branches than males did. Females searched for prey in trees and shrubs smaller than those used by males ($G = 25.2$, df = 4, $P < 0.001$; Fig. 2). During the nestling period, both sexes foraged most often on leaves, but males used relatively more leaves and less branches than females did ($G = 14.4$, df = 3, $P < 0.01$; Fig. 7).

Sexes displayed similar behavior in their methods of prey capture ($G = 7.2$, df = 1, $P > 0.20$; Fig. 3). Gleaning during the summer period accounted for >75% of all foraging maneuvers. Both sexes most frequently used perches ≤1.0 cm ($G = 0.2$, df = 2, $P > 0.90$; Fig.
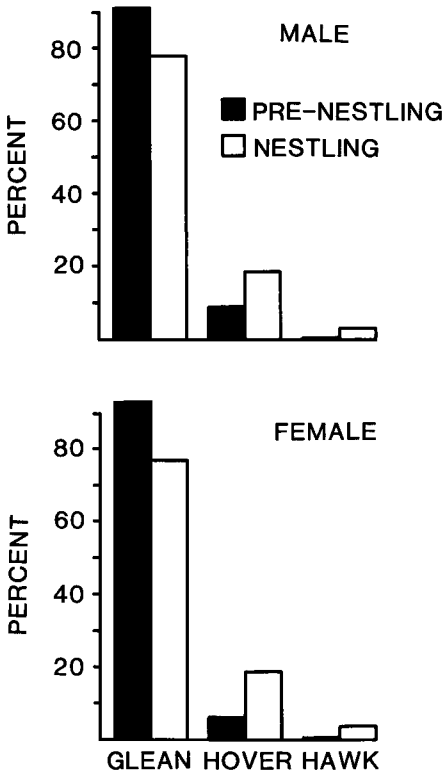
Fig. 3. Percentage use of foraging methods by adult Prothonotary Warblers during prenestling and nestling periods (see text), 1984–1987.
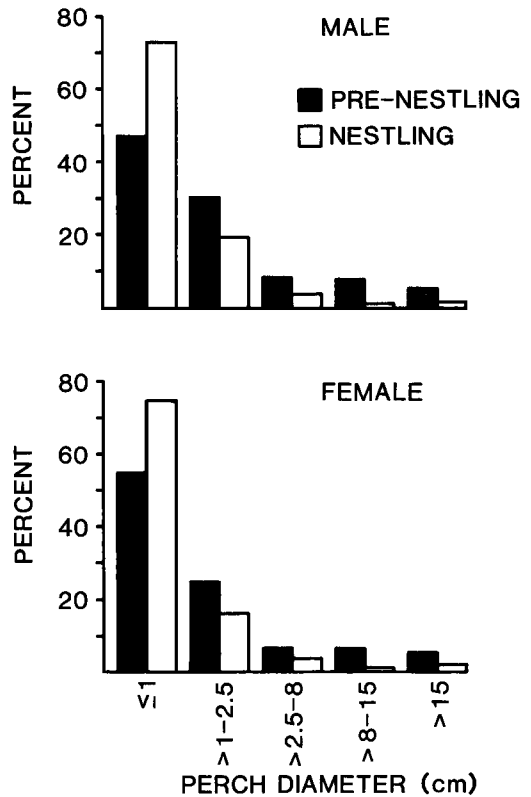

Fig. 4. Percentage use of perches of different diameters by adult Prothonotary Warblers during prenestling and nestling periods (see text), 1984–1987.

4) and used middle and outer parts of bushes and trees during the nestling period ($G = 1.4$, df = 4, $P > 0.40$; Fig. 6).

Foraging height, substrate type, substrate height, and prey location differed significantly between the sexes for one or both periods. The divergence in substrate type and, correspondingly, substrate height may be an indirect result of the heights at which male and female Prothonotary Warblers foraged, and not a direct outcome of ecological constraints placed on them. For example, males, which searched for food at greater heights, did not have access to lower substrates, such as shrubs and fallen branches. Similarly, females, which foraged lower than males, had limited foraging opportunities in the upper portions of larger trees. During the prenestling period, males and females separated on the basis of height, independent of substrate type (see above). To determine if males and females partitioned the use of substrates during the nestling period (in-

dependent of their height differences), we held foraging height interval constant and applied G-tests to contingency tables of sex × substrate for each of three height intervals separately (the ≤1 m and >1–3 m intervals were pooled because of small sample sizes). There were no significant sex-specific differences in use of substrates at any of the foraging-height intervals (≤3 m: $G = 5.8$, df = 6, $P > 0.40$; >3–7 m: $G = 1.4$, df = 3, $P > 0.70$; >7 m: $G = 0.3$, df = 3, $P > 0.90$). Conversely, it is possible that substrate influenced the height at which birds foraged during the nestling period. A similar analysis was performed, except that substrate (willow, maple, and sweetgum) was held constant, and the distribution of heights for each sex was of interest. There were no intersexual differences in the vertical use of maple ($G = 1.2$, df = 2, $P > 0.50$), willow ($G = 0.4$, df = 1, $P > 0.50$), or sweetgum ($G = 0.5$, df = 1, $P > 0.40$), although in each case there was a trend for females to forage lower than males.
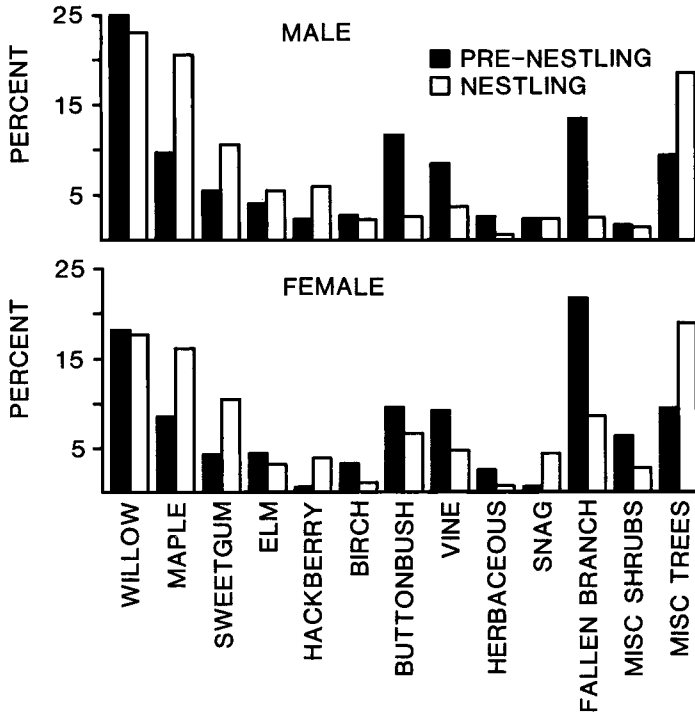
Fig. 5. Percentage use of substrates by foraging adult Prothonotary Warblers during prenestling and nestling periods (see text), 1984–1987.

These same analyses were applied to explain the divergence between sexes in prey location (i.e. because of varied opportunities encountered at different heights, males and females could differ in behavior simply because of their disproportionate exploitation of those height intervals). "Prenestling" male and female warblers partitioned the vertical component of the habitat independent of changes in prey location (see above). We compared locations from which the sexes attempted to capture prey during the nestling period with height held constant. Male and female warblers differed in their use of prey locations for only 1 of the 4 comparisons across foraging height intervals; females took prey from branches more often than males did when foraging below 1 m ($\leq$1 m: $G = 16.0$, df = 2, $P < 0.001$; >1–3 m: $G = 0.1$, df = 2, $P > 0.90$; >3–7 m: $G = 0.5$, df = 2, $P > 0.80$; >7 m: $G = 0.5$, df = 1, $P > 0.40$). Again, these results show no systematic partitioning of prey locations across height intervals. When, however, the vertical distribution of the sexes was analyzed separately for each of two categories of prey location (sample sizes were too small for other categories), there was a clear trend for males and females to forage at different heights even when capturing prey from the same type of microsubstrate (leaf: $G = 10.2$, df = 3, $P < 0.05$; branch: $G = 14.2$, df = 2, $P < 0.01$). We suggest that the heights at which male and female warblers foraged affected the proportion of time each sex searched for prey on leaves and branches.

Differences between prenestling and nestling periods.—Throughout the breeding cycle, male Prothonotary Warblers significantly altered foraging tactics for all 7 variables. During the prenestling stage, males spent <28% of their time foraging above 3 m, but males feeding nestlings searched for food 60% of the time above that height ($G = 33.5$, df = 3, $P < 0.001$; Fig. 1). On average, males feeding nestlings searched for food nearly 2 m higher than during the prenestling stage ($t = 4.9$, df = 348, $P < 0.001$). Compared with "prenestling" males, "nestling" males reduced use of branches, trunks, and ground, and they increased their maneuvers for prey on leaves and in the air ($G = 55.1$, df = 3, $P < 0.001$; Fig. 7). Males also changed the tree species upon which they for-
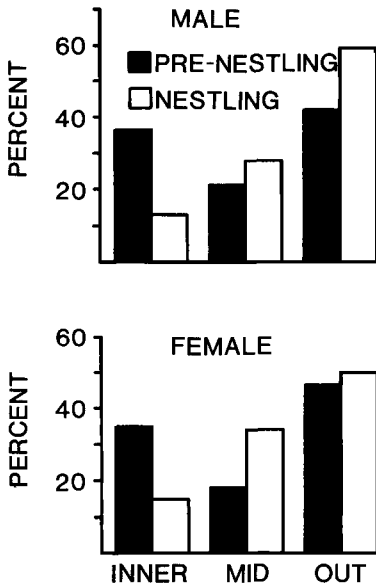
Fig. 6. Percentage use of horizontal tree and shrub axis (inner, middle, outer one third) by adult Prothonotary Warblers during prenestling and nestling periods (see text), 1984–1987.
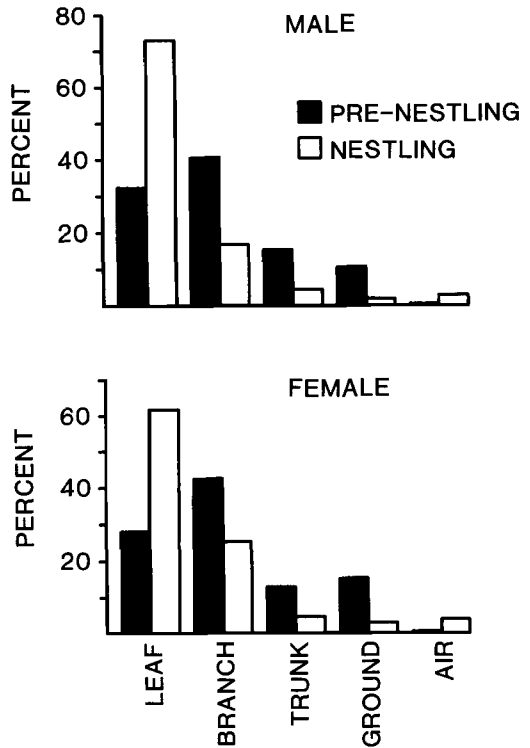

Fig. 7. Percentage use of prey locations by adult Prothonotary Warblers during prenestling and nestling periods (see text), 1984–1987.

aged ($G = 37.2$, df = 6, $P < 0.001$; Fig. 5). After full leaf, males devoted $>40\%$ of foraging bouts to searching in willows and maples, and reduced use of buttonbushes, vines, and fallen branches. They also shifted to taller trees ($G = 19.8$, df = 3, $P < 0.001$; Fig. 2). Although they still used gleaning as the most frequent foraging maneuver, males hovered and hawked more often as the season progressed ($G = 9.3$, df = 1, $P < 0.01$; Fig. 3). "Nestling" males perched on smaller diameter substrates more than did males earlier in the season ($G = 20.9$, df = 3, $P < 0.001$; Fig. 4). This reflected a preference for perching on twigs and nearly complete elimination of trunks as perch sites. During late spring and summer, males spent less time foraging in the inner portion of trees and shrubs, and more time in the outer two thirds of the flora ($G = 22.0$, df = 2, $P < 0.001$; Fig. 6).

As the season progressed, females significantly changed their foraging behavior for 4 of the 7 variables. Like male warblers, females foraged at greater heights while feeding young, yet they only occasionally searched above 5 m ($G = 12.5$, df = 3, $P < 0.01$; Fig. 1). On average, females during the nestling period foraged 1.2 m higher than females during the prenestling period ($t = 3.3$, df = 207, $P < 0.01$). Females

feeding nestlings increased their use of arthropods on leaves and in flight, while they diminished search time on the ground, branches, and tree trunks ($G = 15.3$, df = 3, $P < 0.01$; Fig. 7). They also perched on smaller diameter branches and twigs during the nestling period ($G = 6.0$, df = 2, $P = 0.05$; Fig. 4) and spent more time hovering and hawking insects ($G = 5.5$, df = 1, $P < 0.05$; Fig. 3). Although females increased their foraging activity on sweetgum, maples, and other trees, and reduced their use of vines, buttonbushes, shrubs, and fallen branches during the nestling period, the change was not significant ($G = 8.0$, df = 6, $P > 0.20$; Fig. 5). Female Prothonotary Warblers selected similar sized trees and shrubs during the prenestling and nestling periods ($G = 2.4$, df = 3, $P > 0.40$; Fig. 2). Females shifted their foraging patterns from the inner one third of trees to the center and outer portions, but this difference was not quite statistically significant ($G = 5.6$, df = 2, $P = 0.06$; Fig. 6).

Niche breadth.—"Prenestling" male and fe-

TABLE 1. Standardized niche-breadth values for male and female Prothonotary Warblers during the prenestling and nestling periods (see text), 1984–1987.

Period	Foraging method	Height	Perch diameter	Substrate	Substrate height	Distance to trunk	Prey location
Prenestling							
Males	0.099	0.425	0.499	0.561	0.633	0.901	0.565
Females	0.073	0.260	0.414	0.586	0.575	0.843	0.578
Nestling							
Males	0.280	0.956	0.186	0.466	0.429	0.632	0.189
Females	0.300	0.747	0.172	0.672	0.681	0.761	0.303

male warblers generally had similar standardized niche breadths for each of the seven variables (difference [$\bar{x} \pm$ SD] = 14.9 ± 13.4%). Males had wider niche breadths for 5 of the 7 variables (Table 1). Birds feeding young had wider niche breadths (mean difference = 22.6 ± 13.0%). In contrast to "prenestling" birds, niche widths of females were larger than those of males in 5 of 7 cases during the nestling period. However, neither of the above two comparisons was significantly different (Wilcoxon matched-pairs signed-ranks test; prenestling: $T = 3$, $P > 0.10$; nestling: $T = 7$, $P > 0.50$).

Comparing prenestling and nestling periods, male and female warblers generally changed niche breadth in the same "direction" for a given variable (5 of 7 cases). Both sexes expanded use of foraging method and height, and contracted niche breadths for perch diameter, prey location, and distance from trunk. "Nestling" females increased (and males decreased) diversity of use for both feeding substrates and substrate heights as compared with birds during the prenestling period.

Niche overlap.—"Prenestling" male and female warblers demonstrated a high degree of overlap for all foraging variables (Table 2). Most (5 of 7) of the overlap indices decreased from the prenestling period (mean overlap [O_{xy}] = 0.915 ± 0.044) to the nestling period (mean overlap [O_{xy}] = 0.881 ± 0.085), although this

trend was not statistically significant (Wilcoxon matched-pairs signed-ranks test, $T = 7$, $P > 0.50$). Predictably, niche overlap values usually were lowest for those variables that were statistically distinguishable between the sexes.

Arthropod abundance.—All arthropod groups had initially low relative abundances in April, peaked between mid-May and late June, and either declined or remained relatively constant thereafter (Fig. 8). Emergences of mayflies and, to a lesser degree, dipterans were very distinctive and pronounced. On the other hand, those of lepidopteran larvae and spiders exhibited gradual increases and declines with more prolonged durations.

DISCUSSION

Intersexual niche partitioning may be the result of several factors. We considered two possibilities that may explain the sex-specific foraging patterns of male and female Prothonotary Warblers. First, birds forage at locations which coincide with an individual's reproductive duties during the breeding cycle. Second, birds forage in a way to reduce intersexual competition for food resources.

Reproductive responsibilities.—Sex-specific foraging behavior has been associated with activities during the breeding season. For example, females stay closer to nests and males stay near-

TABLE 2. Niche overlap values for male and female Prothonotary Warblers during prenestling and nestling periods (see text), 1984–1987.

Period	Foraging method	Height	Perch diameter	Substrate	Substrate height	Distance to trunk	Prey location
Prenestling	0.975	0.890	0.924	0.853	0.877	0.957	0.932
Nestling	0.988	0.759	0.972	0.847	0.799	0.916	0.884

DIPTERA   EPHEMEROPTERA

LEPIDOPTERA
LARVAE   ARACHNIDA

% DEVIATION FROM YEARLY AVERAGE

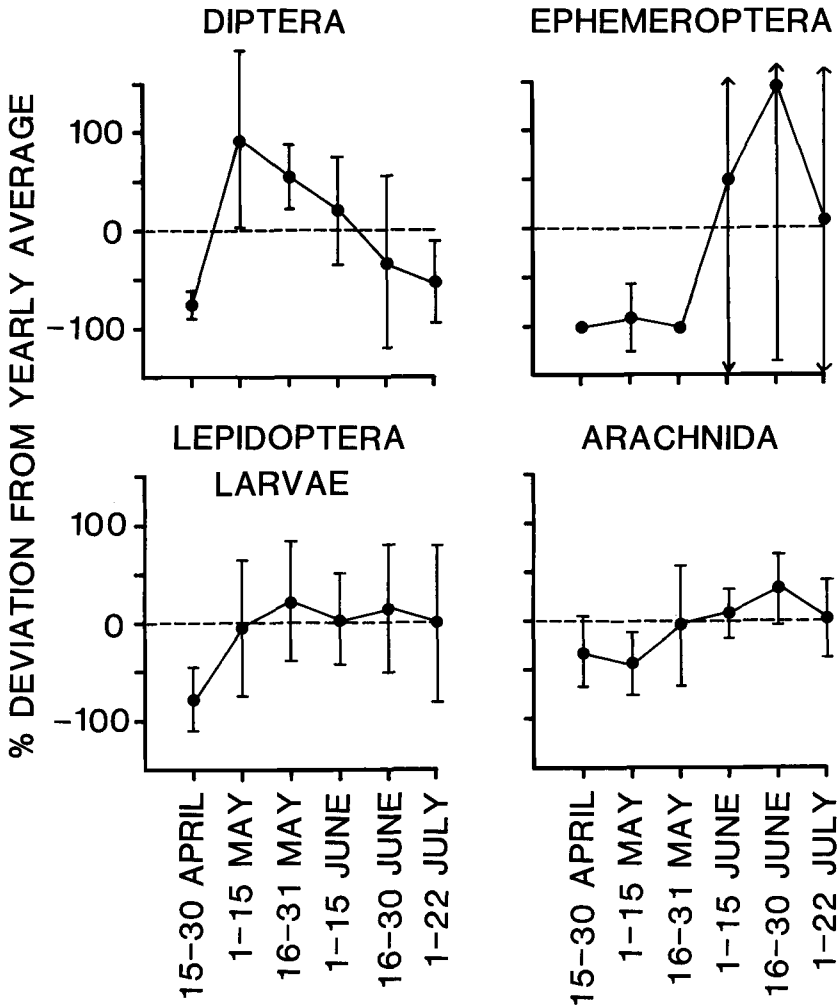15-30 APRIL   1-15 MAY   16-31 MAY   1-15 JUNE   16-30 JUNE   1-22 JULY

Fig. 8.   Relative abundances (represented by percent deviations from average for each year) of arthropods sampled along the Tennessee River in 1985 and 1987–1989. Vertical bars represent ±1 SD. These four taxa represent the most common prey items eaten by Prothonotary Warblers.

er to singing posts (Morse 1968, Franzreb 1983). Prothonotary Warblers partitioned their habitat vertically and, as predicted by the reproductive responsibilities theory, males foraged higher than females. During both periods, males maintained territorial vigilance from relatively high perches. It is unclear, however, whether or not height preferences were related totally to sex-specific behaviors associated with the reproductive cycle. First, males foraged at greater heights during the nestling phase than during territorial acquisition and courtship. This was counter to the idea that males forage near their singing posts, which were high relative to nest heights during the prenestling period. Activity during the nestling phase was concentrated at the relatively low nest site. During the prenest-ling period, males selected potential nest cavities (1–2.5 m high), placed nesting material in some of them, and courted females that foraged close to the ground. This made up <20% of the males' time (L. Petit unpubl.). Although it appears that foraging sites of males were influenced to some extent by the presence of females and the need to locate nest sites, the reproductive responsibilities theory does not account fully for the presence of males at such relatively low heights during the prenestling period. Second, female Prothonotary Warblers foraged lower when building nests. Material for nests

is found near the ground, and gathering nesting material may have influenced foraging heights of females during this time. Females foraged farther (on a vertical scale) from the nest (mean nest height ≈ 1.5 m) during the nestling period, thereby potentially increasing energetic costs. In addition, males foraged farther (on a vertical scale) from the nest while feeding nestlings even though the sexes shared equally in feeding duties (L. Petit unpubl.). The proposed advantage to foraging near centers of sex-specific activities is that time and energy costs are reduced (Morse 1968). Although that did not appear to be the case during the nestling period, variation in abundance and distribution of prey may make it more efficient energetically to forage in areas of high prey abundance (e.g. higher in trees), even though those areas are farther from the nest (see below).

There were some sex-specific preferences for substrate, substrate height, and prey location, and those differences appeared to be influenced by the height at which each sex foraged. In general, sex-specific height preferences may have limited the opportunities for both sexes with respect to other foraging variables (cf. Robinson and Holmes 1984, Holmes 1986). This still does not explain the preference of males and females for certain height intervals while foraging. Reproductive responsibilities appear to have influenced foraging height and may be the primary cause of intersexual niche partitioning, but this hypothesis by itself cannot explain all facets of sex-specific foraging ecology that we observed.

Reduction of intersexual competition.—Intersexual habitat partitioning is often accompanied by sex-specific variation in morphology (Selander 1966, Wallace 1974, Austin 1976, Williams 1980). A 5–10% difference in morphological characteristics is typical of sexually dimorphic species, although this divergence is frequently greater (Amadon 1959). In Prothonotary Warblers, we found males were slightly larger statistically for culmen length, tarsus length, wing chord (all <5% difference), and primary length (≈6% difference, $n > 300$ for each sex; L. Petit unpubl.). Because the differences in body parts were small, sexual dimorphism does not appear to be a pertinent factor driving the divergence of foraging behavior. One function of the observed sex-specific foraging patterns may be a reduction in competi-

tion between mates. Because competition is difficult to demonstrate without controlled experimental manipulations (Wiens 1983), one must often rely on indirect evidence to assess ecological principles in nature.

Under conditions of limited resources, individuals of a population are predicted to "compress" niches (MacArthur and Wilson 1967, Schoener 1974). Similarly, Selander (1966) suggested that intersexual niche partitioning should occur during periods when resources become limiting. Although the food supply was greater during the nestling than the prenestling period of our study (Fig. 8), it is generally believed that adults must increase their rate of prey capture severalfold to meet the increased demand of growing nestlings (e.g. Walsberg 1983, Holmes et al. 1986). If we assume a more demanding (i.e. competitive) situation for adults that feed young (as compared with adults during the prenestling period), then competition theory predicts both compressed niches and decreased resource overlap between sexes (Selander 1966, Schoener 1974). Niche breadth decreased in only 8 of 14 comparisons (57%) from prenestling to nestling. Although niche overlap decreased for 5 of the 7 foraging variables (71%) as the season progressed, most differences were slight (range = 0.006–0.131). Ricklefs and Lau (1980) demonstrated that overlap indices must differ by at least 0.1–0.2 to be statistically distinct. Thus, our results are equivocal with respect to competition theory. In addition, when we controlled for sex-specific foraging heights (see Results), sexes did not systematically partition microhabitat, which would be expected if intersexual competition was of primary importance. There is little support for the idea that sexes partition habitat so as to prevent depletion of resources on a microhabitat scale (cf. Charnov 1976).

Resource abundance and distribution.—Seasonal shifts in foraging behavior have been attributed to changes in habitat structure and prey distribution (e.g. Ligon 1973, Austin 1976, Winkler 1979, Morrison and With 1987). However, few investigators have considered modification of avian foraging behavior *within* a season (but see Root 1967, Sherry 1979, Robinson 1986). We found in Prothonotary Warblers that both leafing of vegetation and emergence of insects accounted for at least some of the parallel shifts in male and female foraging behavior during
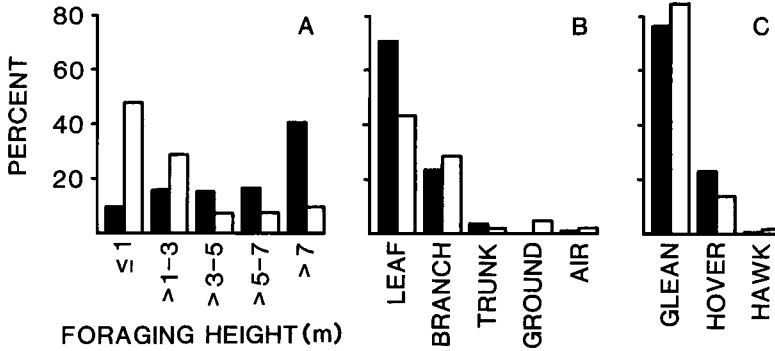
Fig. 9. Percentage use of (A) foraging heights, (B) prey locations, and (C) foraging methods by male (solid bars) and female (open bars) Prothonotary Warblers not feeding nestlings during the "nestling" period (see text), 1984–1987.

the breeding season. The contracted summer niche breadths were related to decreased use of larger trunks and branches, and increased use of small branches and twigs in the outer regions of tree and shrub crowns where there are more leaves and more food items. Foraging height niche breadths for both sexes expanded during the nestling period because of the escalated use of taller tree species by males. During the nestling period, Prothonotary Warblers hovered frequently to capture lepidopteran larvae on the bottom side of leaves. Larvae were substantially more abundant during the nestling period than during the prenestling period (Fig. 8). Emergences of mayflies and mosquitos during the nestling periods of all years (Fig. 8) required more diversified foraging maneuvers. These latter two observations suggest a direct relationship between prey abundance and foraging behavior (also see Holmes and Schultz 1988). Williamson (1971) reported a similar trend in foraging techniques for Red-eyed Vireos (*Vireo olivaceus*) and attributed it to the types and numbers of arthropods present. Alternatively, Root (1967) showed that the foraging behavior of Blue-gray Gnatcatchers (*Polioptila caerulea*) was more closely related to reproductive duties than to characteristics of the prey base. We have little data on birds in the nestling period that did not feed nestlings (often as a result of nest predation). Our observations on males ($n = 101$) and females ($n = 59$), as well as numerous casual observations over 6 yr, indicate that the abundance and distribution of arthropods were the factors of primary influence on the foraging ecology during the nestling

period (Fig. 9). Birds that did not feed young during the summer foraged in ways more similar to adults that feed nestlings than to prenestling adults.

We believe that the full leafing of foliage and elevated numbers of arthropods on those leaves can be linked causally to the significant temporal shifts in foraging ecology of the warblers. The reproductive responsibilities theory failed to explain the divergences from centers of activity (i.e. nest sites) during the nestling phase for the same reasons. There should be an inverse relationship between foraging efficiency and distance from centers of activity related to reproductive duties only if environmental factors remain relatively constant as distances from those centers increase (Schoener 1971). Changes in the benefits accrued at increasing distances alter that simple, direct relationship. We suggest that a substantial increase in the arthropod prey created more profitable foraging in the canopies of trees as compared with fallen branches, small shrubs, tree trunks, and the ground exploited by warblers during the prenestling period. The temporal shift in foraging behavior may have been especially critical to parent birds that fed nestlings. Although both male and female warblers altered their behavior in a parallel fashion, they maintained distinct height preferences, apparently in relation to their respective reproductive duties. Those height differences presented males and females with distinct opportunities to exploit their foraging environment and may have been the primary cause of other observed aspects of intersexual niche partitioning.

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