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BEHAVIORAL PLASTICITY OF FORAGING MANEUVERS OF MIGRATORY WARBLERS: MULTIPLE SELECTION PERIODS FOR NICHES?

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Abstract. Foraging maneuvers used by eight migratory wood warbler species were studied during spring and fall migrations over two years. Four of these species were also studied for two years during breeding and winter seasons. Foraging maneuver patterns (patterns of the distribution of effort among foraging maneuvers) changed within and among seasons, and were most different during the colder periods of migration. Such changes may reflect responses to changes in the types of available insects or responses to thermoregulatory costs. Shifts may also occur because food is limited relative to energy demands. In particular, increased used of the energetically-expensive flight maneuvers of hovering and sallying and increases in the general diversity of maneuvers may reflect responses to food limitations. These indices suggest that food limitation can occur in several periods but may be particularly severe during early spring and late fall migration. Migration periods have received the least attention as a period of selection on the foraging niche of migratory species and deserve more attention. While foraging behavior of species differed statistically within and among seasons, the general ranking of the relative use of foraging maneuvers remained similar among seasons. This stability suggests that species were plastic only within limits set by their evolutionary histories. Such evolutionary conservatism deserves more attention in community and comparative studies.

Key Words: Foraging behavior; warblers; Illinois; migration.

Behavioral and morphological traits that affect foraging efficiency should be adapted in part to the foods available during periods when food limits survival or reproduction. Some authors argue that food is most limiting in winter and that foraging traits are adapted to winter foods (Fretwell 1968, 1972; Pulliam and Enders 1971; Alatalo and Alatalo 1979). Others argue that the breeding season is a more important influence on foraging traits because of the food demands of reproduction (see review in Martin 1987). Although migration seasons have received far less attention than breeding or winter, food limitation may exist during periods of migration when food demands are high and food availability can be low (Rappole and Warner 1976, 1980; Laursen 1979; Martin 1980; Morse 1980c). Thus, food limitation may exert selection on the foraging niche of species during several periods of the year (Bennett 1980, Morse 1980c, Rappole and Warner 1980, Cox 1985).

The types or locations of foods undoubtedly change within and among seasonal periods, and such changes may favor different foraging traits. Because morphology cannot change between seasons, changing conditions may favor shifts in foraging behavior (i.e., plasticity, *sensu* Morse 1980a, Greenberg, this volume). Indeed, foraging behavior can shift between breeding and winter seasons (Eaton 1953, MacArthur 1958, Moreau 1972, Lack 1976b, Bennett 1980, Keast 1980, Rabenold 1980, Hutto 1981b, Greenberg 1984a) and even among periods within these seasons (Pinkowski 1977, Greenberg 1981b, Martin 1985a). On the other hand, shifting behavior during spring and fall migration is unstudied, despite marked changes in food types and abundances (see Kendeigh 1979). Comparisons of the extent of behavioral shifts within and among all seasons may provide insight into periods when conditions are particularly stringent.

Morphology of a bird constrains the types of foraging maneuvers that can be used efficiently. Consequently, birds tend not to shift foraging maneuvers as readily as other behaviors (e.g., foraging height) that are not as closely tied to morphology (Hutto 1981b). Shifts in foraging maneuver patterns (patterns of the distribution of effort among foraging maneuvers), therefore, may reflect periods when environmental conditions are particularly demanding, such as when food is limiting. Indeed, increases in the diversity of foraging maneuvers used by a bird may reflect periods of increased food limitation; the diversity of food types taken by a predator should increase with decreasing food abundance according to optimal foraging theory (Schoener 1971b, Pyke et al. 1977, Pyke 1984) and different foraging maneuvers are assumed to allow acquisition of additional food types (Rabenold 1978).

Here, we examine behavioral plasticity of foraging maneuvers of migratory birds throughout their annual cycle, with particular emphasis on migration seasons. We examine plasticity of foraging of wood warblers within and among seasons: (1) to examine the degree that species shift their behaviors, (2) to examine differences in foraging plasticity among species, (3) to identify possible causes for shifting behaviors, and (4) to determine potential periods of selection on foraging niches of migrants. We emphasize warblers because they are abundant during migration and they include a diversity of relatively closely-related species that employ a diversity of foraging behaviors.

STUDY AREAS AND METHODS

The study site for work during spring and fall migration was Trelease Woods, a 22 ha woodlot northeast of Urbana, Illinois. The forest included mature deciduous tree species and numerous tree-fall gaps that provide patches of understory vegetation that are denser than nongap understory (see Martin and Karr 1986b, Blake and Hoppes 1986 for a more detailed description of the forest). The site for winter work was a young (ca. 25 years old) second-growth forest in Soberania National Park, Panama, where the vegetation was somewhat shorter than in Trelease Woods (see Martin 1985a, Martin and Karr 1986a for more details of study sites). The sites for summer work were early-shrub seral stages (from previous clear-cutting) in northern Ontario (ca. 49°N latitude). Most of the vegetation was deciduous, but some conifers were also present. The foliage was distributed at much shorter heights than on either the migration or winter sites (Martin, unpubl.). Thus, vertical foliage distributions and species of plants varied among the sites.

Foraging maneuvers and other behaviors were observed and recorded on a hand-held tape-recorder for later transcription. Individuals were followed for up to 10 maneuvers, although in practice most individuals could only be followed for one or two observations due to their mobility and obscuring by foliage. Foraging maneuvers we identified included: gleaning (foraging from a substrate from a perched position); hover-gleaning (foraging from a substrate while hovering); sallying (a continuous flight motion while snatching prey from a substrate); and hawking (a flight to snatch an insect in the air). During spring and fall migrations in 1979, only three of these maneuvers (gleaning, hovering, and hawking) were recognized; sallying was categorized as hovering at that time. Consequently, sally maneuvers are absent in figures for 1979 migration seasons.

Foraging behavior was studied in all sites from 1979–1981. Observations in the breeding seasons started in late May and continued into mid-July. Fall migration included late August through early November. Winter foraging behaviors were studied during January and March. Spring migration included mid-April to late May.

Each season was partitioned to allow examination of within-season changes in foraging behaviors. Winter samples were compared between January (middle of the winter season) and March (end of the winter season). Summer was divided into incubation, nestling and fledgling periods. Migration was partitioned into early and late periods; the median date that individuals of each species were observed or captured (see Martin and Karr 1986b for data) during each migration season was used as the cut-off date for grouping observations into early or late categories. A minimum sample size of 25 observations was deemed necessary to provide a representative sample of the foraging behavior. This sample size was derived by using the G-test (see below) to compare the foraging maneuver pattern when sample size was incremented by 5 observations until a sample size was reached where foraging maneuver patterns did not differ statistically. In some cases sample sizes were insufficient ($N < 25$) for one or the other half of a season and such data were not included. In a few cases, such as the Yellow-rumped Warbler (*Dendroica coronata*) during fall migration and Chestnut-sided Warbler (*Dendroica pensylvanica*) during spring migration in 1980, observations were obtained over a brief period that fell in the late or early part of the season, respectively; such data were only displayed for the appropriate seasonal period. The Shannon index of diversity ($H' = -\Sigma\, p_i \ln[p_i]$) was used to examine the degree to which species were generalized in their foraging. Diversity of foraging maneuvers was not calculated for spring and fall migrations in 1979 because only three of the four maneuvers classified in all other seasons were available for calculations. Differences in foraging within and between seasons were determined based on the log-linear, contingency table, G-test (Sokal and Rohlf 1981).

RESULTS

PLASTICITY DURING MIGRATION

Foraging behavior changed for all of eight warbler species within spring (Fig. 1) and fall (Fig. 2) migrations. Moreover, the changes were relatively consistent among species; most species increased gleaning and decreased hovering and sallying maneuvers from early to late spring (Fig. 1). The exception was the American Redstart (*Setophaga ruticilla*), which increased hawking late in the spring.

Patterns during fall migration were the mirror image of those during spring; species generally decreased gleaning and increased hovering from early to late fall (Fig. 2). Exceptions were the American Redstart, with a mirror image of its foraging maneuver pattern during spring migration, and the Bay-breasted Warbler (*Dendroica castanea*) during fall 1980.

The changes in foraging maneuver patterns also caused consistent shifts in the diversity of foraging maneuvers used by warblers; diversity was greater in early than late spring for all of five species (Fig. 1) and greater in late than early fall for five of six species (Fig. 2).

PLASTICITY DURING WINTER

Three of the four species studied during winter in Panama increased their degree of frugivory from early (January) to late (March–April) in the dry season; the exception was the Magnolia Warbler (*Dendroica magnolia*) which rarely eats fruits (Martin 1985a). The degree to which the other three species shifted to frugivory varied among species in the order: Chestnut-sided Warbler <

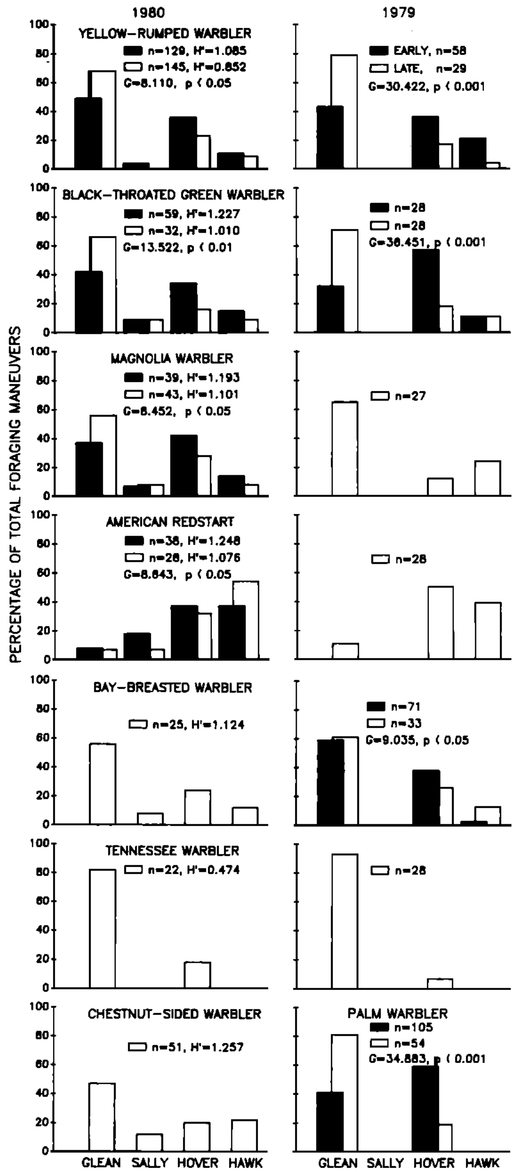

FIGURE 1. The percentage of total foraging maneuvers that was comprised by each type of maneuver during early (solid bars) and late spring (open bars) migrations 1980 and 1979 in Illinois. Only three behaviors were classified in 1979.

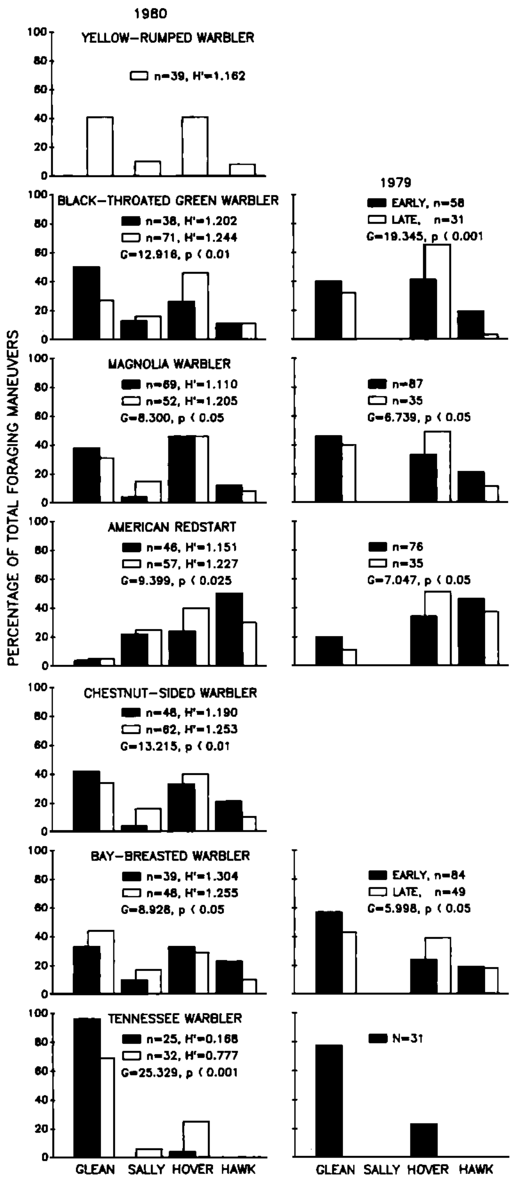

FIGURE 2. The percentage of total foraging maneuvers that was comprised by each type of maneuver during early (solid bars) and late fall (open bars) migrations 1980 and 1979 in Illinois. Only three behaviors were classified in 1979.

Bay-breasted Warbler < Tennessee Warbler (*Vermivora peregrina*) (Martin 1985a) as also found by Greenberg (1981b, 1984a). However, if fruits are considered a substrate rather than a maneuver, then our data indicate that foraging maneuvers did not change significantly over the winter in these four species (Fig. 3).

BREEDING SEASON

Of the 1980 data analyzed, Chestnut-sided Warblers exhibited a shift in foraging behavior from the incubation to late nestling-fledgling period ($G = 12.563$, $P < 0.005$), and a marginally significant ($G = 7.616$, $P < 0.06$) shift from incubation to nestling periods (Fig. 4). The net re-

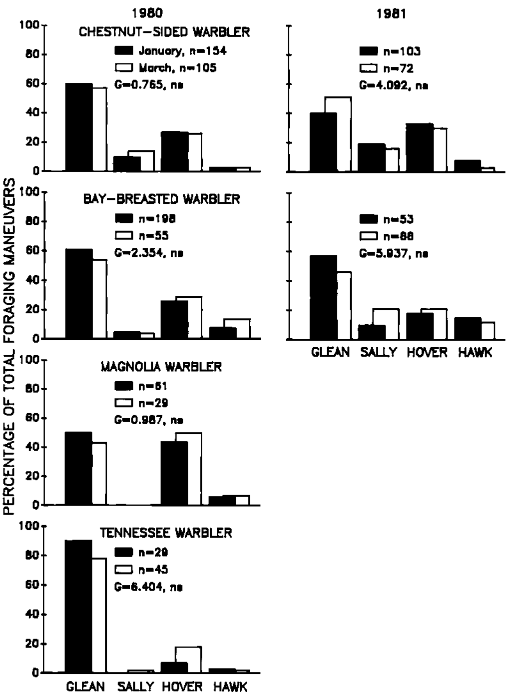

FIGURE 3. The percentage of total foraging maneuvers that was comprised by each type of maneuver during January (solid bars) and March (open bars) for winters in 1980 and 1981 in Panama.

sult was an increase in the diversity of foraging maneuvers due to increased hovering and sallying from incubation through fledgling periods (Fig. 4). Moreover, this pattern was exhibited by each of at least four color-banded individuals included in the 1980 sample (Martin, unpubl.).

Between-year Differences

Frequency and intensity of between-year changes in foraging maneuver patterns varied among species during migration; some species did not change between years (e.g., Yellow-rumped Warbler, Black-throated Green Warbler [*Dendroica virens*]), and others changed frequently (e.g., Bay-breasted Warbler, Magnolia Warbler) (Table 1, Figs. 1, 2). Between-year changes in foraging maneuver patterns also differed among species for breeding and winter seasons; Tennessee and Bay-breasted Warblers changed between years in both of these seasons, whereas Magnolia and Chestnut-sided Warblers did not change between years in either season (Table 1, Fig. 5). Thus, species differed in the relative stability of their foraging behavior during similar periods in different years.

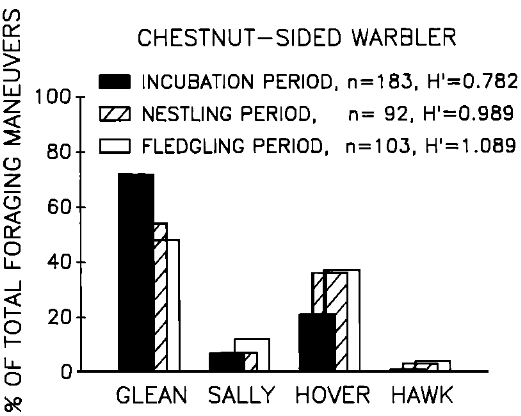

FIGURE 4. The percentage of total foraging maneuvers that was comprised by each type of maneuver during three periods of the breeding cycle of the Chestnut-sided Warbler in Ontario, Canada.

Between-seasons Differences

Foraging maneuver patterns were similar between breeding and wintering seasons; 10 of 14 comparisons showed no changes between winter and breeding seasons (Table 2, Fig. 5). Foraging maneuver patterns were generally most different during migration seasons (Table 2). Foraging during migration differed from breeding or winter seasons in 37 cases and did not differ in only 12 cases ($\chi^2 = 12.755$, $P < 0.001$). Moreover, foraging during migration differed from breeding or winter more frequently in early spring or late fall (17 of 19 cases, Table 2) than in late spring or early fall (20 of 30 cases) ($\chi^2 = 4.142$, $P < 0.05$). Similarly, the diversity measures of foraging maneuvers showed that foraging was usually most generalized (greatest H') during early spring and late fall migrations when comparing all seasons (Fig. 5).

DISCUSSION

Foraging Plasticity During Migration

All species shifted their foraging maneuver patterns to a variable degree during migration. Most species showed a consistent shift toward increased gleaning and decreased hovering and sallying as spring progressed and the opposite pattern during fall. In part, such shifts can be attributed to shifts in availabilities of insects. Foliage-clinging arthropods and the density of their substrate (leaves) increase through spring and decrease through fall (Kendeigh 1979, Graber and Graber 1983, Martin, pers. obs.). Consequently, more effort is devoted to gleaning foliage-clinging arthropods during late spring and

TABLE 1. SUMMARY OF *G*-TEST STATISTICS[a] FOR COMPARISONS OF DIFFERENCES IN FORAGING BEHAVIORS BETWEEN YEARS. HOVERING AND SALLYING BEHAVIORS WERE LUMPED FOR MIGRATION SEASONS IN 1980 TO COMPARE WITH MIGRATION SEASONS IN 1979 BECAUSE SALLYING BEHAVIORS WERE NOT SEPARATED FROM HOVERING IN 1979 OBSERVATIONS

	Breeding	Winter	Early spring	Late spring	Early fall	Late fall
Magnolia	4.4	1.6	21.6***	5.7	6.8*	2.9
Tennessee	9.4*	8.7*			29.0***	
Chestnut-sided	3.1	4.4				
Bay-breasted		8.2*		6.4*	12.3**	2.9
Yellow-rumped			3.8	3.7		
Black-throated Green			3.9	1.5	3.3	5.4
Redstart				0.8	14.2***	4.7

[a] * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

early fall (Figs. 1, 2). Moreover, ambient air temperatures are lower during early spring and late fall, which tends to reduce flying insect activity and causes reduced hawking and increased hovering behaviors (Holmes et al. 1978). The increased incidence of hovering and decreased incidence of hawking by American Redstarts during early spring and late fall potentially reflect such effects. Moreover, the increased hovering during early spring and late fall exhibited by several other species may also be partly explained by such effects.

All changes in foraging maneuvers, however, cannot be attributed to changes in food availabilities. Species such as Tennessee and Palm (*Vermivora palmarum*) Warblers used gleaning for 80–90% of their foraging maneuvers during periods of abundant food (Figs. 1, 2). Reductions in flying insect activity during cold periods should thus not greatly influence their foraging behavior. Yet, both of these species increased hovering and sallying in these cold periods during migration and these increases were not acomplished by reduced hawking maneuvers. Similarly, many of the other species, except American Redstart, decreased both hovering and sallying in the warm periods (late spring, early fall, Figs. 1, 2) when flying insects should be most abundant (Kendeigh 1979).

The consistent increase in flying maneuvers during cold periods may reflect thermoregulatory influences. Migratory birds stay in a warm environment most of their life and, as a result, lack the ability to acclimate (Kendeigh et al. 1977). Early spring and late fall represent some of the coldest temperatures and greatest thermoregulatory costs incurred by most migratory species. Temperatures ranged from 0–34°C from early to late spring and the converse in the fall on our Illinois sites (unpubl. data). Since flight metabolism is only about 25% efficient, 75% of the energy is produced as heat which is available for thermoregulation (Calder and King 1974). During cold periods when energy costs of thermoregulation are already high, it may be more efficient to hover and sally because of the increased heat produced by flying movements. Field observations provide some support for this argument. Birds often sat with their feathers fluffed until spotting a prey item that they then flew to eat during early spring and late fall, whereas they were much more active at hopping and walking in late spring and early fall.

Alternatively, the energetically expensive flight maneuvers may simply be used to increase food intake rates (Morse 1973, Bennett 1980) when food is scarce. This possibility is supported by the analyses of the foraging behavior of the Chestnut-sided Warbler during breeding; it increased the incidence of hovering and sallying during later stages of breeding, when food demands of reproduction are apparently greater (see review in Martin 1987). Such shifts cannot be attributed to temperatures, which were also greater (also see below).

In short, foraging maneuvers may vary with changes in available food types, changes in food demands relative to food availability, changes in thermoregulatory costs, or, most likely some combination of these factors.

DIVERSITY OF FORAGING MANEUVERS AND FOOD LIMITATIONS

Increases in the diversity of foraging maneuvers used by a species may reflect decreasing food availability relative to demand (Rabenold 1978), but they could also simply reflect responses to changes in the types of foods that are available. Consequently, comparisons among periods must be interpreted with caution. However, increases in the diversity of foraging maneuvers used by species were generally accomplished by increas-

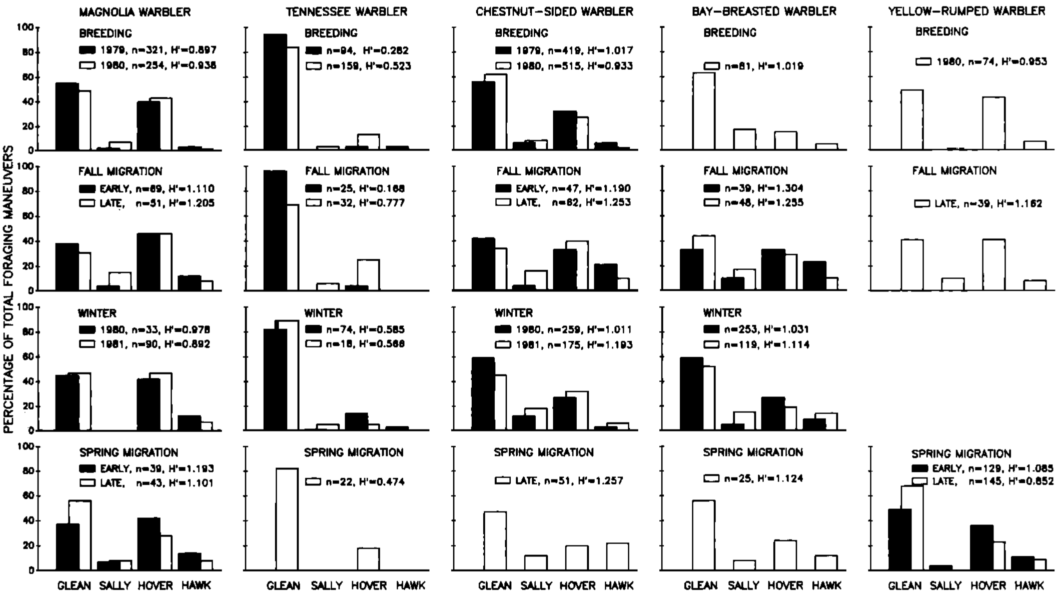

FIGURE 5. The percentage of total foraging maneuvers that was comprised by each type of maneuver during breeding season in Ontario, Canada, fall migration in Illinois, winter in Panama, and spring migration in Illinois. Breeding and winter data are for each of two years and migration data are for early and late in each season for 1980.

ing their use of energetically-expensive maneuvers, such as hovering and sallying. Moreover, increases in both foraging diversity and use of energetically-expensive maneuvers typically occurred when food was reduced relative to demand. For example, species were most generalized in their foraging during early spring and late fall migration periods (Fig. 5), when food abundance was low and energy demands of migration were high (Kendeigh 1979, Graber and Graber 1983). In addition, the increase in diversity of foraging maneuvers of the Chestnut-sided Warbler from incubation to fledgling periods (Fig. 3) also coincides with increasing energy demands of raising young (see Martin 1987 for a review). Thus, foraging diversity seems to provide a crude index to periods of food stress.

The fact that foraging diversity tends to be greatest during early spring and late fall migrations (Fig. 5) suggests that these periods may represent particularly severe periods of food limitation. Moreover, foraging patterns in the food-rich late spring and early fall were more similar to those in winter and breeding, but the patterns differed during the food-poor periods of early spring and late fall when diversities were also greatest. These observations, when taken together, suggest that food is indeed difficult to obtain during these periods.

Migration seasons are not the only periods of food limitation. A variety of correlative and experimental work, as well as the increasing diversity of foraging maneuvers during breeding (Fig. 4), indicates that food is commonly limiting during breeding (reviewed in Martin 1987). Thus, attempts to focus on any single season as the primary determinant of the foraging niche of migratory birds is likely to produce erroneous conclusions.

CONSERVATISM OF FORAGING MANEUVER PATTERNS

Although warblers exhibited statistically significant shifts in their foraging behavior over time, many shifts were basically matters of degree. The general ranking of the four behaviors remained similar among seasons and years, so that the general foraging maneuver pattern of a species was largely conserved (Fig. 5). This conservatism may be expected because foraging maneuvers are so closely tied to morphology (Hutto 1981b).

Studies of communities typically focus on documenting differences among species as a measure of resource partitioning (see Martin 1986, 1988a; Schoener 1986b for reviews). Determination of the conservative nature of traits is important to the way we examine communities. If traits are conservative, many differences among coexisting

TABLE 2. SUMMARY OF G-TEST STATISTICS[a] FOR COMPARISONS OF DIFFERENCES IN FORAGING BEHAVIOR BETWEEN SEASONS. ALL MIGRATION DATA ARE FROM 1980.

	Early spring	Late spring	Early falll	Late fall	Winter 1980	Winter 1981
		Magnolia Warbler				
Breeding 1979	8.4*	14.3**	10.0*	20.8***	7.2	3.2
Breeding 1980	9.9*	15.2**	13.3**	13.4**	13.2**	7.7
Winter 1980	11.0*	6.0	2.7	18.3***		
Winter 1981	11.9**	8.9*	4.2	18.1***		
		Chestnut-sided Warbler				
Breeding 1979		15.3**	11.3*	12.1**	3.6	7.5
Breeding 1980		23.4***	24.1***	19.4***	1.1	9.2*
Winter 1980		18.7***	22.8***	13.9**		
Winter 1981		13.4**	18.6***	3.8		
		Bay-breasted Warbler				
Breeding 1980		8.8*	30.8***	9.6*	11.7**	6.1
Winter 1980		1.4	16.1**	9.2*		
Winter 1981		3.1	11.3*	3.6		
		Tennessee Warbler				
Breeding 1979		13.7**	1.2	28.6***	8.9*	4.6
Breeding 1980		1.9	6.9	7.9*	2.1	4.3
Winter 1980		1.9	8.4*	7.9*		
Winter 1981		11.0*	3.3	17.2***		

[a] * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

species may be simply due to differences in their evolutionary histories, rather than the result of interactive processes (Wiens 1983, Martin 1986). Consequently, communities may be noninteractive accumulations of species responding to resources as a function of their individual evolutionary histories (Grinnellian niche approach, *sensu* James et al. 1984). Alternatively, if traits are conservative and communities are structured by interactions, then resource partitioning among coexisting species may be achieved by selection for resource partitioning (permissible combinations, *sensu* Connell 1980; Martin 1988b, c). If traits are more plastic, then individuals of a species may partition resources by modifying their behavior relative to other coexisting species (see Martin 1986). Clearly, we cannot fully understand community dynamics until we understand the dynamics of individuals of the species that make up the community.

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