GEOGRAPHIC VARIATION IN FORAGING ECOLOGY OF NORTH AMERICAN INSECTIVOROUS BIRDS

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Abstract. There is little information on geographic variation in foraging ecology of North American insectivorous birds during the breeding season. We summarized foraging data for 22 species of arboreal Passeriformes. Four to 11 ($\bar{X} = 5.6$) populations per species were compared using foraging technique (i.e., glean, hover, and hawk) and prey location (i.e., branch, trunk, leaf, ground, and air) to characterize foraging niches. Detrended correspondence analysis and an index of ecological overlap were employed to quantify interpopulational foraging plasticity (variability). Of 11 species that had data for both foraging technique and prey location, the Blue-gray Gnatcatcher, Ash-throated Flycatcher, and Warbling Vireo had the highest levels of plasticity, whereas the Yellow-rumped Warbler, White-breasted Nuthatch, and Red-eyed Vireo were relatively stereotyped. The Solitary Vireo, Black-throated Green Warbler, Acadian Flycatcher, and Yellow Warbler exhibited high degrees of foraging plasticity. In contrast, the Brown Creeper, Pine Warbler, White-breasted Nuthatch, Red-breasted Nuthatch, and Mountain Chickadee revealed substantial stereotypy in foraging techniques. Bark gleaners showed less geographic variation than leaf gleaners and leaf hoverers. Those differences may be related to the differential accessibility of arthropods on the two types of substrates. We suggest that behavioral plasticity exhibited by many species is due to simple functional responses associated with local environmental conditions (e.g., vegetation structure).

Key Words: Detrended correspondence analysis; foraging behavior; foraging niche; foraging plasticity; geographic variation; guilds.

Studies of foraging behavior have provided important insights into many aspects of avian ecology, including intersexual relationships (e.g., Kilham 1965, Morse 1968, Franzreb 1983a), temporal variation in behavior (e.g., Kessel 1976, Holmes et al. 1978, Hutto 1981b), guild structure (e.g., Willson 1974, Pearson 1977a, Holmes et al. 1979b), morphological constraints imposed on species (e.g., Selander 1966, Ricklefs and Cox 1977, Miles and Ricklefs 1984), and factors affecting bird community structure and composition (e.g., Morse 1968, Holmes et al. 1979b, Holmes and Recher 1986a). Most of these studies recorded species' foraging behavior over one to several years and drew conclusions pertaining to the ecology of the species. Although numerous authors (e.g., Sabo 1980, Sabo and Holmes 1983, Petit et al. 1985, Emlen et al. 1986) have assumed that individual species occupy similar foraging niches across study areas, this assumption remains largely untested.

Several studies have compared the foraging niches of species inhabiting two distinct habitats (e.g., James 1979, Maurer and Whitmore 1981, Sabo and Holmes 1983), tree species (e.g., Franzreb 1978, Szaro and Balda 1979), or communities (e.g., Crowell 1962, Morse 1971a, Rabenold 1978). Most authors found significant differences, showing that many species were capable of responding to changes in the external environment. Sabo and Holmes (1983) called for study of avian foraging niches across multiple sites, thereby allowing for more definitive examination of niche theory. With the exception of Morse (1971a, 1973), we know of no published studies that have quantitatively compared foraging niches among more than two populations of a species in North America.

The profusion of studies of foraging behavior and the concomitant development of foraging theory have spawned predictions about how individuals should forage under certain prescribed conditions. In addition, terminology has been introduced that categorizes the behavorial and temporal aspects of species' niche shapes. Morse (1971a, b) defined specialists as individuals, populations, or species of birds that exploit a narrow range of available resources. Resource utilization commonly is used in reference to food, foraging area, or habitat preference (Morse 1971b, Pianka 1983). Conversely, generalists are birds that use many of the resources available to them.

Morse (1971a, b) also introduced terminology describing the temporal or interpopulational consistency of niche shape. (Niche shape is used here in the sense of Hutchinson's [1957] "hypervolume.") Stereotypy refers to an individual, population, or species that uses a certain subset of resources with high predictability. Alternatively, birds that exhibit plasticity use resource types with little regularity, varying their use of prey types, behavior, or habitat in response to environmental stimuli.

Based on those concepts, ecological theoreticians have postulated a number of hypotheses regarding how animals should alter their niche shape when they encounter various combinations of resource availabilities and habitat types

(e.g., MacArthur 1965, Emlen 1966, MacArthur and Pianka 1966, Charnov 1976a). However, despite more than 200 published reports on the foraging ecology of North American insectivorous birds, no attempt has been made to integrate those results into a comprehensive analysis of geographic variation of foraging behavior. Compounding the difficulties of such an investigation are substantial differences among investigators in describing, quantifying, and analyzing foraging behavior. Considering the volume of literature, we believe that such an investigation is long overdue, and may provide insight into factors that influence shapes of foraging niches. The objectives of this paper are to assess the degree of interpopulational variability (plasticity) of foraging behavior in some insectivorous birds and relate any plasticity to the natural history of the species.

METHODS

THE DATA SET

Data were taken from 27 published and unpublished scientific papers and dissertations (see below) which met the following criteria: (1) observations of foraging behavior were gathered during the breeding season, i.e., the period between the time of arrival on breeding territories and the end of nesting. To minimize temporal variation, when possible we restricted use of data to those collected during incubation and nestling stages of the breeding cycle; (2) the foraging behavior documented could be classified into three "technique" or five "prey location" categories (see below); (3) species were observed in forests, woodlands, or second growth woodlands (in the Temperate Zone) with canopies >4 m tall (most were >8 m tall); (4) species were passerines that typically did not forage from the ground and that devoted (as a species) >33% of their foraging maneuvers to techniques other than hawking (= flycatching; see below). This criterion emphasized species that frequently had direct foraging interaction with vegetation; and (5) data on ≥4 populations were available for each species. Some studies (e.g., Rabenold 1978, James 1979, Landres 1980) provided data on more than one population per species. We subjectively chose four as the minimum number of studies needed to judge a species' behavioral variability.

To determine if differences in behavioral plasticity existed among groups with distinct foraging modes, each species was placed into a trophic group or guild (*sensu* Root 1967) based upon the predominant foraging behavior of the populations we surveyed: (1) glean—leaf, (2) glean—bark, (3) hover—leaf, and (4) hawk.

FORAGING BEHAVIOR

A variety of methods and terminology permeates the foraging ecology literature and, therefore, a synthesis of studies necessarily will be ambiguous unless data are standardized. Documentation of foraging behavior in most studies, including those used in this paper, followed one of four techniques: (1) one observation

was made per bird, usually taken when the individual was first sighted (e.g., Franzreb 1983a, 1984); (2) multiple, consecutive records were taken on each bird sighted, and there may (e.g., Williamson 1971, Rabenold 1978) or may not (e.g., James 1976, Eckhardt 1979, Holmes et al. 1979b) have been a limit placed on total number of foraging maneuvers recorded for an individual or total time an individual was watched on any given day; (3) multiple observations were recorded at given time intervals, usually with a maximum number allowed per bird (e.g., Landres 1980, Morrison 1984a); and (4) a stopwatch was used to measure time devoted to a given foraging behavior (e.g., MacArthur 1958; Morse 1967b, 1968). Because data used in this study were collected under such varied manners, it was not possible to categorically describe how data were recorded and we refer the reader to the original papers. Also, although there may be statistical biases associated with some of those techniques of gathering data (e.g., see Wagner 1981a, Morrison 1984a), we assumed that this potential problem was minimal and each investigator accurately quantified behavior of the population(s) under study.

The schemes into which behaviors were classified also varied among studies. In our analyses, we were concerned mainly with two measures of passerine foraging ecology, the technique used to attack prey and the location of attacked prey. Although other behaviors (e.g., foraging rates, distances travelled, height) may be important in quantifying species' niche characteristics, they often are not recorded by researchers or are peripheral to the scope of this study. Terminology used to describe passerine foraging behavior is often ambiguous and often designed so as to accentuate species' differences in studies of guild-community ecology. We used the simplest divisions that we deemed adequate to describe foraging ecology of arboreal passerines. Our definitions are taken largely from James (1976), Eckhardt (1979), and Holmes et al. (1979b).

Foraging technique was partitioned into three mutually exclusive categories: (1) glean, a maneuver directed toward a prey item on a substrate (or, rarely, in the air) while the bird was perched or hopping, also included such maneuvers as probe (Holmes et al. 1979b, Landres 1980, Franzreb 1983a), peck (Williamson 1971, Sabo 1980), pounce (Eckhardt 1979), and hang (Morse 1968, Rabenold 1978, Greenberg 1987b); (2) hover, a maneuver in which prey located on a substrate is attacked by a nonperching (i.e., hovering or flying) bird, which some authors (e.g., Rabenold 1978, Landres 1980, Sabo 1980) have termed sally and hawk; and (3) hawk, a behavior in which both insect and bird are in flight, which is sometimes termed flycatching (e.g., Sabo 1980), sallying (e.g., Eckhardt 1979, Hutto 1981b), and chase (Morse 1967b).

Prey location (i.e., the location of the arthropod prey when a bird made an attempt to procure it) was apportioned into five mutually exclusive categories: (1) branch, which included all surfaces covered by bark, except trunk; (2) trunk; (3) leaf, including petioles and flowers; (4) ground; and (5) air.

Most data could be adapted to our classification scheme. However, in several instances, frequencies within categories in the original paper did not equal 100%, or an extra division (e.g., "other") was given

that did not conform to our categories. In the former case, we changed the values relative to one another, so that the total equalled approximately 100%. For the latter, we distributed the anomalous observations equally across those categories in which there was a possibility that they belonged. The error we introduced into estimates of foraging behavior was negligible using this method because we manipulated percentages only when the unassigned observations were ≤10% of all records gathered for that study.

ANALYSES

Species were divided into two groups based upon the amount of information that was available: (1) Group A, species for which observations had been made in all eight (i.e., technique and prey location) foraging categories; and (2) Group B, species that were represented by ≥4 studies for the technique variable only. Groups were not mutually exclusive (e.g., all Group A species were also included in Group B analyses), but were necessary due to the varied amounts of data that were available from individual studies. These studies were: Airola and Barrett 1985 (Groups A and B), Bennett 1980 (AB), Eckhardt 1979 (B), Ficken et al. 1968 (B), Franzreb 1983a (AB), Franzreb 1984 (B), Holmes et al. 1979b (AB), Hutto 1981b (B), James 1976 (AB), James 1979 (AB), Landres 1980 (AB), MacArthur 1958 (AB), Maurer and Whitmore 1981 (AB), McEllin 1979 (AB), Morrison et al. 1987b (B), M. L. Morrison et al., unpubl. data (AB), Morse 1967b (AB), Morse 1968 (AB), Morse 1973 (AB), Morse 1974a (B), D. R. Petit et al., unpubl. data (AB), Rabenold 1978 (AB), Rogers 1985 (B), Root 1967 (AB), Sabo 1980 (AB), Sherry 1979 (AB), and Williamson 1971 (AB).

We used three techniques to assess the degree of behavioral plasticity-stereotypy exhibited by different arboreal passerines: (1) detrended correspondence analysis (DCA)-interval method, (2) DCA-standard deviation method, and (3) overlap method. Because all three types of analyses have minor biases associated with them (when applied to quantifying niche breadths), we developed a scheme to rank species' behavioral plasticity based on a combination of the three methods.

DCA-interval method

Detrended correspondence analysis (Hill 1979, Hill and Gauch 1980) was used to evaluate the degree of behavioral plasticity both within and between species. DCA is an improved version of reciprocal averaging and may be superior to other ordination procedures (e.g., principal components analysis) in characterizing relationships in ecological data sets (e.g., Sabo 1980, Gauch 1982a). For both groups A and B, species from each study (a "species-sample") were ordinated as separate samples along with all other species-samples from that group. Scores of the species-samples on each DCA axis were used to describe quantitatively each species-sample's position on the derived "foraging behavior" gradient and its relationship (distance) to all other samples of a given species. Ecological interpretation of axes was determined from correlations between axis scores and original variables. Following Johnson (1977) and Rotenberry and Wiens (1980b), we divided each DCA axis into four divisions of equal length. Next, the dis-

tribution of behavior along the derived resource gradients was estimated by counting the proportion of samples for each species that fell into each interval. Species behavioral variability (plasticity) was defined using the niche breadth equation of Levins (1968):

$$B = 1/\sum p_i^2,$$

where p_i is the proportion of samples that were contained in the ith interval. Niche breadth values (B) ranged from 1, if all samples fell within one interval, to 4, the number of intervals available.

Several biases are inherent in this method. One shortcoming of the niche breadth measure is that the maximum B (B_{max}) for any data set depends on the number of samples in that set, especially with small (e.g., <10) sample sizes. To correct for this bias, we divided all niche breadth values (B) by their maximum possible values (B_{max}) to produce a relative measure of variability. B and B_{max} were highly correlated (Pearson's r's > 0.90) for all axes in all analyses.

Another source of potential error with using this technique is that adjacent divisions along a multivariate axis are usually more similar in "ecological space" than are intervals separated by some distance (e.g., Gauch 1982a). Therefore, in disjunct distributions along these axes, the "space" (distance) is not acknowledged and the distribution is treated as continuous (see, for example, Rotenberry and Wiens 1980b:Fig. 5). Because of small sample sizes, the discontinuous distribution of several species on axes in our analyses may be artifactual. Therefore, both the distribution of species-samples across intervals and the relationships among intervals may be important in describing species' behavioral niche breadths. Our second technique (DCA-standard deviation) took into account these concerns (see below).

To assess species' overall niche breadths, we calculated species' responses across all niche dimensions simultaneously. The orthogonality of DCA axes allowed us to use the product of the first two axes as a measure of overall niche variability because the axes are independent (May 1975). Because the niche breadth values were scaled relative to the maximum possible niche breadth for that species, potential overall niche breadth ranged from 0.06 (0.25 × 0.25) to 1.0 (1.0 × 1.0). We also performed ordinations on the 11 Group A species based on separate analyses of prey location and foraging technique. The purpose of this was to determine if one variable showed greater variability along the derived gradients than the other.

DCA-standard deviation method

Species-samples' scores on the DCA axes were used to calculate a standard deviation for each species on each axis. Large standard deviations indicated a wide range of foraging behaviors between studies, while small standard deviations represented relatively stereotyped behavior. The standard deviation of sample scores is proportional to the projection of a confidence ellipse onto that axis (Noon 1981a). Thus, our technique is mathematically and biologically comparable to plotting the commonly used confidence ellipses (e.g., Green 1974, Smith 1977).

TABLE 1. SPECIES USED IN THIS STUDY, ALONG WITH THEIR PREDOMINANT FORAGING MODE

Taxon	Foraging mode
Family Tyrannidae	
Acadian Flycatcher, *Empidonax virescens*	Hover—leaf
Least Flycatcher, *E. minimus*	Hover—leaf
Dusky Flycatcher, *E. oberholseri*	Hawk
Ash-throated Flycatcher, *Myiarchus cinerascens*	Hawk
Family Paridae	
Mountain Chickadee, *Parus gambeli*	Glean—leaf
Family Sittidae	
White-breasted Nuthatch, *Sitta carolinensis*	Glean—bark
Red-breasted Nuthatch, *Sitta canadensis*	Glean—bark
Family Certhiidae	
Brown Creeper, *Certhia americana*	Glean—bark
Family Muscicapidae	
Golden-crowned Kinglet, *Regulus satrapa*	Glean—leaf
Blue-gray Gnatcatcher, *Polioptila caerulea*	Glean—leaf
Family Vireonidae	
Solitary Vireo, *Vireo solitarius*	Glean—bark
Yellow-throated Vireo, *V. flavifrons*	Glean—bark
Red-eyed Vireo, *V. olivaceus*	Hover—leaf
Warbling Vireo, *V. gilvus*	Glean—leaf
Family Emberizidae	
Black-throated Green Warbler, *Dendroica virens*	Glean—leaf
Yellow Warbler, *D. petechia*	Glean—leaf
Yellow-rumped Warbler, *D. coronata*	Glean—leaf
Magnolia Warbler, *D. magnolia*	Glean—leaf
Blackburnian Warbler, *D. fusca*	Glean—leaf
Pine Warbler, *D. pinus*	Glean—bark
Northern Parula, *Parula americana*	Glean—leaf
American Redstart, *Setophaga ruticilla*	Hover—leaf

Overlap method

Because the positions of species-samples along derived gradients are determined, to some extent, by their relationships to other species-samples in the data set, we used a simple index of overlap to evaluate within-species variability in foraging behavior. This measure of overlap (O), based on Lotka-Volterra principles (MacArthur 1972, Hurlbert 1978), was formulated by Pianka (1973):

$$O = \frac{\sum (x_i y_i)}{[\sum x_i^2 \cdot \sum y_i^2]^{1/2}},$$

where x_i and y_i are proportions of behavioral observations for populations x and y in the ith resource category. For our analysis, eight resource states, those of technique (3) and prey location (5), were recognized. This symmetrical measure of overlap ranges from 0 (no overlap) to 1 (total overlap) and was computed for all pairwise combinations of species-samples within a species. Mean overlap values were used to assess degree of behavioral plasticity within a species. Comparatively large overlap values were interpreted as stereo-

typed behavior, while small overlap values depicted species with high degrees of behavioral plasticity.

RESULTS

We located 123 species-samples of foraging behavior representing 22 species of arboreal passerines (Table 1). More than one-third were wood-warblers (Parulinae); Tyrannidae, Vireonidae, Muscicapidae, Sittidae, Paridae, and Certhiidae were also represented.

GROUP A SPECIES

DCA-interval method

Only 11 of the 22 species had ≥ 4 samples for all eight foraging categories. The 59 species-samples were ordinated using DCA and the distribution of each species was plotted across four equally-spaced divisions along the first two DCA axes (Fig. 1). Only axes I (eigenvalue = 0.43) and II (0.10) were used because of their disproportionately large eigenvalues as compared to axes
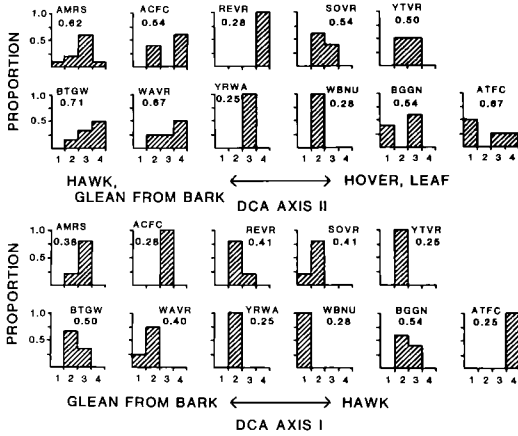
FIGURE 1. Distribution of (Group A) species' sample scores across four equally spaced intervals on DCA (detrended correspondence analysis) axes I and II. The ordination is based on three technique and five prey location categories for each sample (i.e., Group A species). The number in each graph is a measure of niche breadth (B/B_{max}; see text for description) along that axis. See Table 2 for species' acronyms.

III (0.05) and IV (0.02) (see Hill 1979). Axis I represented a gradient from gleaning from branches and trunks to hawking flying insects. Axis II separated the hawkers and branch gleaners from the species that hover and take prey from leaves. Most species exhibited stereotyped use of one or both foraging niche axes (Fig. 1). On axis I, only the Black-throated Green Warbler and Blue-gray Gnatcatcher had niche breadth measures >0.50, while 8 of the 11 species exceeded this value on axis II. The Red-eyed Vireo, Yellow-rumped Warbler, and White-breasted Nuthatch were highly stereotyped on both axes.

The White-breasted Nuthatch and Yellow-rumped Warbler showed the lowest overall foraging variability (i.e., product of axes I and II) with the DCA-interval method. In contrast, the Black-throated Green Warbler, Blue-gray Gnatcatcher, and Warbling Vireo demonstrated relatively high plasticity (Table 2). Most species, however, demonstrated a moderate amount of restriction in their foraging niches.

Based on separate ordinations, the magnitude of the overall niche breadth scores for technique ($\bar{X} = 0.28$, median = 0.25) was not significantly different (Mann-Whitney U-test, P > 0.20) from that of prey location ($\bar{X} = 0.22$, median = 0.22).

DCA-standard deviation method

The DCA-standard deviation method produced results somewhat similar (Spearman's r_s = 0.55, P < 0.10) to those of the previous tech-

nique. However, the DCA-standard deviation method recognized the discontinuous distributions of the Blue-gray Gnatcatcher, Ash-throated Flycatcher, and Acadian Flycatcher on DCA axis II and ranked those species as the three most behaviorally diverse (Table 2). Clearly, the Red-eyed Vireo, White-breasted Nuthatch, and Yellow-rumped Warbler still were the most stereotyped species in Group A.

In separate ordinations, neither technique ($\bar{X}$ overall niche breadth = 672, median = 588) nor prey location ($\bar{X} = 811$, median = 365) was consistently larger than the other (Mann-Whitney U-test, P > 0.20).

Overlap method

The overlap method produced results comparable to the DCA-interval method ($r_s = 0.59$, P < 0.10), but diverged more from the DCA-standard deviation results ($r_s = 0.36$, P > 0.10). The overlap method seemed to rank species as a compromise between the other two indices (Table 2). The Blue-gray Gnatcatcher and Ash-throated Flycatcher were (as for the standard deviation method) the two most behaviorally plastic species, and the Warbling Vireo showed the third highest level of diversity (as for the interval method). As before, the Red-eyed Vireo, White-breasted Nuthatch, and Yellow-rumped Warbler showed the least geographic variability. In concurrence with previous results, technique ($\bar{X}$ overlap = 0.85, median = 0.75) was no more variable than prey location ($\bar{X}$ overlap = 0.84, median = 0.86) when separate analyses were performed (Mann-Whitney U-test, P > 0.20).

We determined an overall rank of behavioral plasticity for each species by averaging its ranks from the three analyses. We concluded that, for Group A species, the Blue-gray Gnatcatcher, Ash-throated Flycatcher, and Warbling Vireo showed the most geographic variability in foraging behavior, while the Red-eyed Vireo, White-breasted Nuthatch, and Yellow-rumped Warbler had relatively narrow foraging niches (Table 2). We used this same averaging procedure for both prey location and technique separately, and found that the Yellow-throated Vireo, Ash-throated Flycatcher, and Acadian Flycatcher took prey from a variety of substrates, whereas the Solitary Vireo, Acadian Flycatcher, and Blue-gray Gnatcatcher used a diversity of techniques. For both variables, the White-breasted Nuthatch, Red-eyed Vireo, and Yellow-rumped Warbler were highly stereotyped. Both measures were positively correlated with overall niche plasticity (technique: $r_s = 0.70$, P < 0.05; prey location: $r_s = 0.59$, P < 0.10) and between themselves ($r_s = 0.59$, P < 0.10).

TABLE 2. COMPARISON OF THREE METHODS USED TO EVALUATE BEHAVIORAL PLASTICITY OF SPECIES WITH ≥4 SAMPLES OF BOTH FORAGING TECHNIQUE AND PREY LOCATION (GROUP A). DCA REFERS TO DETRENDED CORRESPONDENCE ANALYSIS. SEE TEXT FOR DETAILS OF THE DIFFERENT METHODS

Species	Acronym	DCA-interval	DCA-standard deviation	Overlap	Overall average rank
Blue-gray Gnatcatcher	BGGN	0.36 (1)[a]	2240 (1)	0.717 (1)	1.3 (1)
Ash-throated Flycatcher	ATFC	0.17 (6)	1464 (2)	0.760 (2)	3.3 (2)
Warbling Vireo	WAVR	0.27 (3)	395 (7)	0.773 (3)	4.3 (3)
Acadian Flycatcher	ACFC	0.15 (7)	827 (3)	0.775 (4)	4.7 (4)
Black-throated Green Warbler	BTGW	0.36 (1)	559 (6)	0.914 (8)	5.0 (5)
American Redstart	AMRS	0.24 (4)	748 (5)	0.876 (7)	5.3 (6)
Solitary Vireo	SOVR	0.22 (5)	288 (8)	0.781 (5)	6.0 (7)[b]
Yellow-throated Vireo	YTVR	0.13 (8)	793 (4)	0.787 (6)	6.0 (7)[b]
Red-eyed Vireo	REVR	0.12 (9)	113 (9)	0.971 (10)	9.3 (9)
White-breasted Nuthatch	WBNU	0.08 (10)	105 (10)	0.949 (9)	9.7 (10)
Yellow-rumped Warbler	YRWA	0.06 (11)	102 (11)	0.973 (11)	11.0 (11)

[a] Rank; 1 = most variable foraging behavior (i.e., plastic); 11 = least variable foraging behavior (i.e., stereotyped).
[b] Tied with ≥1 other species.

Behavioral plasticity and guild membership

Most Group A species took prey from leaves (leaf gleaners, N = 4; leaf hoverers, N = 3), but there were three bark gleaners and one flycatcher (Table 1). Although bark gleaners tended to be more stereotyped than leaf gleaners, the difference was not significant (Mann-Whitney U-test, P > 0.20). However, when average percent use of bark for each species was correlated with overall foraging plasticity, the use of branches and trunks was positively related to foraging stereotypy (r_s = 0.68, P < 0.05, Fig. 2).

GROUP B

Group B was comprised of 22 species that were represented by ≥4 samples of the technique variable. The 123 species-samples were analyzed in a way comparable to that of Group A species.

DCA-interval method

DCA axis I (eigenvalue = 0.528) separated samples dominated by gleaning from those characterized by high percentages of hawking (Fig. 3). The Black-throated Green Warbler, Blue-gray Gnatcatcher, Solitary Vireo, and American Redstart showed wide distributions along axis I, while 10 species were found in only one interval. Axis II (eigenvalue = 0.096) placed the hoverers and the hawkers at opposite ends of the gradient. The Black-throated Green Warbler, Solitary Vireo, Acadian Flycatcher, Yellow Warbler, and Golden-crowned Kinglet demonstrated high variability along this axis, whereas many others were highly stereotyped. Overall, the Solitary Vireo, Black-throated Green Warbler, and Acadian Flycatcher showed substantial geographic variation in capture methods, whereas the Brown Creeper, Mountain Chickadee, Pine Warbler, Blackburn-

ian Warbler, White-breasted Nuthatch, and Red-breasted Nuthatch did not (Table 3).

DCA-standard deviation method

This technique produced species' niche breadths that were highly correlated with those of the interval method (r_s = 0.89, P < 0.01). Considering both axes, the Solitary Vireo, Black-throated Green Warbler, Ash-throated Flycatcher, Acadian Flycatcher, and Yellow Warbler were highly diverse in their foraging repertoires, while the Mountain Chickadee, Red-breasted Nuthatch, White-breasted Nuthatch, Brown Creeper, and Pine Warbler were not (Table 3).

Overlap method

Average species' overlap values corroborated results obtained for species in Group B, as they were highly correlated with both the DCA-standard deviation (r_s = 0.89, P < 0.01) and DCA-interval (r_s = 0.87, P < 0.01) methods. The only major difference was that the Blue-gray Gnatcatcher showed the least overlap (i.e., greatest variation) between different populations, when it ranked no better than eighth previously (Table 3).

Consolidating results from the three analyses showed that foraging behavior of the Solitary Vireo, Black-throated Green Warbler, and Acadian Flycatcher varied the most from area to area. In contrast, the Brown Creeper, Pine Warbler, White-breasted Nuthatch, Red-breasted Nuthatch, and Mountain Chickadee were highly predictable (Table 3).

Behavioral plasticity and guild membership

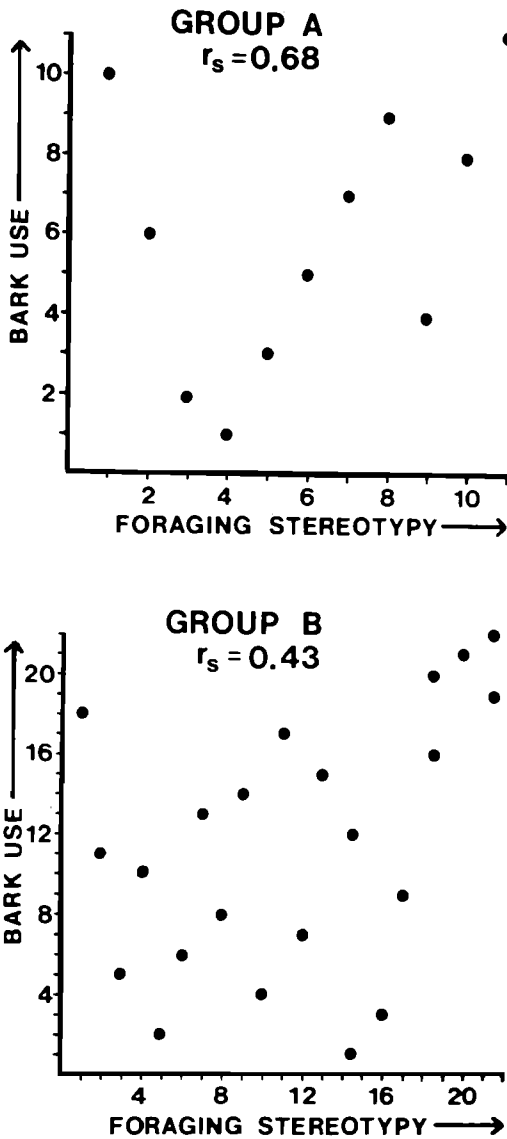Group B was comprised of 6 bark gleaners, 10 leaf gleaners, 4 leaf hoverers, and 2 species that

FIGURE 2. Relationship between foraging plasticity and use of bark (twig, branch, trunk) for both Group A (foraging technique and prey location) and Group B (foraging technique only) species. Numbers on all axes represent ranks for individual species.

hawk insects (Table 1). There were no significant differences in foraging plasticity among bark gleaners, leaf gleaners, and hoverers (Kruskal-Wallis one-way analysis of variance, $P > 0.10$). However, as a group, species that take prey from leaves exhibited significantly more behavioral plasticity than did bark gleaners (Mann-Whitney U-test, $P < 0.10$). In support of this claim, there was a significant positive relationship between

use of bark and foraging stereotypy ($r_s = 0.43$, $P < 0.05$, Fig. 2).

DISCUSSION

Although each species occupied a recognizable foraging niche, there was considerable variation among populations of many species. Bark gleaners appeared to be more stereotyped than birds that take prey from foliage, in that bark foragers almost always gleaned prey. This trend may have been created by our consolidation of foraging techniques, such that the variety of maneuvers by bark gleaners was lumped under gleaning for our analysis. However, we grouped several foraging modes under each of the three main foraging techniques, so a bias towards the bark gleaners seems unlikely. Foliage insects often were taken by both gleaning and hovering. The stereotyped behavior of many bark gleaners may be due to the types of arthropods found on bark, which may be generally less mobile and thus more accessible, than those inhabiting foliage. Jackson (1979) found that ants, spiders, and hemipterans were the most commonly found arthropods on tree trunks in Mississippi. More importantly, though, may be the differences in accessibility of arthropods on bark vs. leaf surfaces. Species that glean from bark can usually perch on the same substrate (e.g., branch or twig) as their prey items. In contrast, arthropods on leaves (especially leaves with relatively long petioles) are less easily gleaned because they are farther from the bird's perch (Holmes and Robinson 1981). In those cases, techniques such as hovering must be employed.

Several previously held beliefs on species foraging diversity and plasticity were not supported by our analyses. Morse (1967b, 1971a) and Sabo and Holmes (1983) considered the Black-throated Green Warbler to be behaviorally stereotyped; however, our examination of 11 populations demonstrated high levels of plasticity. This was surprising because most populations were studied in similar geographical locations and habitat types. In fact, even comparing records from the same study area, but in different years, revealed substantial plasticity (e.g., compare Holmes et al. 1979b with Bennett 1980), suggesting that Black-throated Green Warblers may not only respond to changes in vegetation structure and bird community composition, but also to annual variation in resource availability and distribution.

Although American Redstarts have been reported to be highly plastic (e.g., Holmes et al. 1978, Sherry 1979, Maurer and Whitmore 1981), we found them no more opportunistic, on an interpopulational scale, than many other species. This does not preclude, however, the possibility
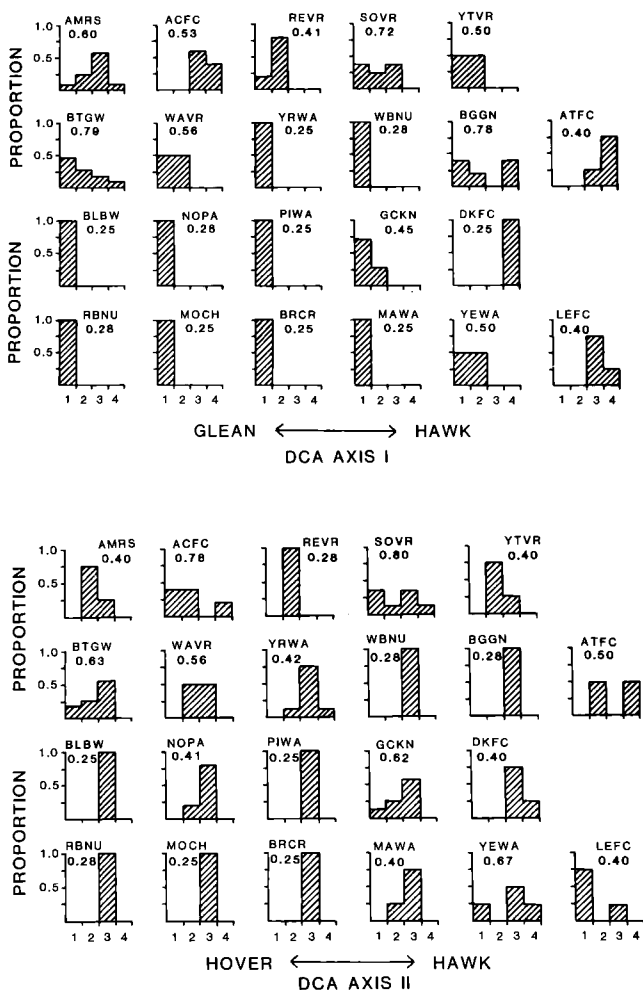
FIGURE 3. Distribution of (Group B) species' sample scores across four equally spaced intervals on DCA (detrended correspondence analysis) axes I and II. The ordination is based on three technique categories for each sample (i.e., Group B species). The number in each graph is a measure of niche breadth (B/B_{max}; see text for description) along that axis. See Table 3 for species' acronyms.

that within-site plasticity is different than the foraging variation measured among populations. Because the terms plasticity and stereotypy are relative, researchers should use this terminology only in comparing with specific populations or species.

The substantial intraspecific behavioral plasticity and interspecific differences in the degree of plasticity detected in this study may be due to a multitude of factors, such as: (1) differences in methods, abilities, and biases of the various data gatherers; (2) nonrandom samples of some (or all) species' populations; and (3) genuine ecological responses by species to the proximate and ultimate constraints imposed on them.

Whether the diverse array of techniques that have been used in the past to quantify passerine foraging ecology biases our results is not known. We believe that the various methods and observers did not obscure the general picture because sample sizes in each study (when reported) were sufficiently large to overcome the error introduced by different sampling techniques (e.g., Petit et al., this volume). We cannot assess observer-expectancy bias (Balph and Balph 1983, Balph and Romesburg 1986), but assume that it was equal across studies. In addition, we safeguarded against the possibility of one aberrant study greatly influencing results by considering a minimum of four populations of any species.

TABLE 3. COMPARISON OF THREE METHODS USED TO EVALUATE BEHAVIORAL PLASTICITY OF SPECIES WITH ≥4 SAMPLES OF FORAGING TECHNIQUE (GROUP B). DCA REFERS TO DETRENDED CORRESPONDENCE ANALYSIS. SEE TEXT FOR DETAILS OF THE DIFFERENT METHODS

Species	Acronym	Method			
		DCA-interval	DCA-standard deviation	Overlap	Overall average rank
Solitary Vireo	SOVR	0.58 (1)[a]	1780 (1)	0.652 (2)	1
Black-throated Green Warbler	BTGW	0.50 (2)	1298 (3)	0.725 (3)	2
Acadian Flycatcher	ACFC	0.42 (3)	1090 (5)	0.751 (4)	3
Yellow Warbler	YEWA	0.33 (4)	1255 (4)	0.778 (5)	4
Ash-throated Flycatcher	ATFC	0.20 (9)[b]	1339 (2)	0.797 (7)	5
Blue-gray Gnatcatcher	BGGN	0.22 (8)	725 (10)	0.626 (1)	6
Golden-crowned Kinglet	GCKN	0.28 (6)	906 (6)	0.810 (8)	7
American Redstart	AMRS	0.24 (7)	880 (8)	0.781 (6)	8
Warbling Vireo	WAVR	0.31 (5)	763 (9)	0.837 (9)	9
Least Flycatcher	LEFC	0.16 (11)	890 (7)	0.878 (10)	10
Yellow-throated Vireo	YTVR	0.20 (9)[b]	286 (11)	0.981 (16)	11
Red-eyed Vireo	REVR	0.12 (12)[b]	210 (15)	0.939 (12)	12
Yellow-rumped Warbler	YRWA	0.11 (14)	245 (12)	0.973 (15)	13
Dusky Flycatcher	DKFC	0.10 (15)[b]	173 (16)	0.929 (11)	14[b]
Magnolia Warbler	MAWA	0.10 (15)[b]	225 (14)	0.967 (13)	14[b]
Northern Parula	NOPA	0.12 (12)[b]	115 (17)	0.984 (17)	16
Blackburnian Warbler	BLBW	0.06 (19)[b]	232 (13)	0.969 (14)	17
Mountain Chickadee	MOCH	0.06 (19)[b]	42 (18)	0.992 (18)	18[b]
Red-breasted Nuthatch	RBNU	0.08 (17)	24 (19)	0.998 (19)	18[b]
White-breasted Nuthatch	WBNU	0.08 (18)	20 (20)	0.998 (20)	20
Pine Warbler	PIWA	0.06 (19)[b]	1 (22)	0.999 (21)	21[b]
Brown Creeper	BRCR	0.06 (19)[b]	2 (21)	0.999 (22)	21[b]

[a] Rank: 1 = most variable foraging behavior (i.e., plastic); 21 = least variable foraging behavior (i.e., stereotyped).
[b] Tied with ≥1 other species.

Examination of DCA ordination plots revealed few outliers and there was no relationship (r_s = 0.05, P > 0.80) between behavioral plasticity and the number of populations used in analyses of Group A species. Nevertheless, because of these concerns, we encourage more interpopulational comparisons conducted by the same research team using one technique to quantify behavior.

This study has demonstrated that data recorded on 4–12 groups of individuals cannot be considered to depict precisely the behavior of each population of that species. If we used species-samples for analysis that were in a restricted geographic area, such that they did not represent a species' full range of behaviors, but used other species' data from a diverse set of areas, then our interspecific comparisons may have erred because of nonrandom sampling of those populations. We can address this indirectly by comparing behavioral plasticity and average distances between study plots for each species. If behavioral variability was positively related to geographic distances between populations, then measures of behavioral plasticity may be incomplete for some species. We measured the distances between all study sites for all 11 Group A species and then averaged the distances for

each species. We found no significant relationship between behavioral plasticity and average distance between study sites (r_s = −0.04, P > 0.80). These results suggest that our measures of species' behavioral plasticity were not noticeably biased due to the populations sampled.

We suggest that the observed trends of behavioral flexibility are real—an outcome of past and present selective pressures imposed on each species—and represent simple functional responses to their environments. Holmes and Robinson (1981), Robinson and Holmes (1982), and D. R. Petit (unpubl.) have demonstrated that foliage-gleaning birds alter their foraging behavior in apparent response to variation in vegetation structure and composition. The ability to modify foraging behavior may allow species to occupy a diverse array of habitat types that are geographically distant (e.g., Morse 1971b, Cody 1974, S. L. Collins 1983).

That insectivorous passerines exhibit extensive interpopulational variation in foraging behavior has several ramifications. First, researchers should restrict conclusions to study sites and species on which the data were gathered. Because many species vary their behavior from area to area, we do not accept the concept "adaptive

syndromes" (Eckhardt 1979), which attempts to categorize insectivorous birds into groups that exhibit very specific behavioral foraging responses to their environment. Strict delineation of foraging niches at the species (vs. population) level can be misleading and counterproductive to elucidation of ecological trends.

Second, in the design of some ecological studies, species are divided into guilds or trophic groups based on published reports or the general knowledge of researchers. As a result, conclusions are determined to some extent by the classification of each species. Blake (1983), for example, categorized the trophic characteristics of birds breeding in forest tracts in Illinois, then conducted analyses based on those groups. Of the eight species that are common to both Blake (1983) and our study, three were classified differently. Blake (1983) even used a cautious approach by only considering broad-based trophic groups. Likewise, James and Boecklen (1983) divided a Maryland bird community into foraging guilds and then tested very specific ecological theories based on those classifications. One-third

(2 of 6) of the species used in both James and Boecklen (1983) and our study were categorized differently. Thus, avian ecologists should consider the extensive variation that exists among different populations of the same species and the consequences of assuming that foraging niches remain constant geographically. Similarly, use of the guild concept in environmental impact assessment (e.g., Severinghaus 1981) will have limited value if species do not occupy similar foraging niches in different geographic regions or habitats.

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