

COMPARATIVE DIETARY ECOLOGY OF SYMPATRIC, INSECTIVOROUS NEOTROPICAL FLYCATCHERS (TYRANNIDAE)¹

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Abstract. This study compares and contrasts diets, based on 2834 prey individuals from 126 stomachs, of 16 insectivorous, aerially foraging Neotropical flycatcher species (Tyrannidae) that are seasonally sympatric in the humid Caribbean lowlands of Costa Rica. Dietary parameters examined are prey type, diversity (breadth) of prey types, heterogeneity of prey types among individuals of a species, "patchiness" of morphologically indistinguishable prey within individual stomachs, and number of prey items per stomach.

An *R*-type factor analysis of prey taxa in flycatchers' stomachs delimited four interpretable factors (axes) based on differences in prey detectability, location, escape behavior, and substrate where caught. A *Q*-type cluster of flycatcher species, based on factor scores from the analysis of prey variables, tended to juxtapose congeners. Noncongeners that clustered closely included a pair of species (*Todirostrum sylvia* and *Oncostoma cinereigulare*) that tend to replace each other geographically. Some flycatchers failed to cluster with any other species. "Saturation curves" of prey-type diversity against number of stomachs sampled showed (1) adequate sampling effort for most species with 4–10 stomachs, and (2) species differences in breadth of prey types eaten. The flycatchers that did not cluster with any other species on the basis of prey taxa had the largest and smallest diet breadths of all species studied. Two species are exceptional and consistent specialists: the Ruddy-tailed Flycatcher (*Terenotriccus erythrurus*) ate 94% Homoptera (largely Fulgoroidea), and the Long-tailed Flycatcher (*Colonia colonus*) ate 67% stingless bees (*Trigona* species). Flycatcher species that had the most "patchy" diets (i.e., many individuals of the same prey species within a stomach) tend to hawk flying prey and/or reside in open country or forest canopy. *Colonia colonus* had extremely patchy stomach contents, but unlike other flycatchers that hawk flying prey, it had an exceptionally homogeneous diet. "Patch feeders," compared with other flycatchers, tended to have many more items per stomach, suggesting the selection of many, relatively small prey per unit time. Significant variation in numbers of items per stomach, even among congeners, suggested differences in feeding rate and perhaps prey size.

Comparison of species with respect to these dietary parameters helps identify a "food resource" for each species. The identification of the food resource (1) helps interpretation of foraging behavior of the predators, (2) facilitates discussion of prey-type and prey-size selection, (3) delineates potential ecological and evolutionary routes of species interactions, and (4) focuses attention on the nature of the food supply available to each species. The assumption that species with patchy and heterogeneous diets feed opportunistically on relatively ephemeral prey permits the following conclusions: (1) many tropical flycatchers are not opportunistic, (2) many guilds, including tropical ones, are composed of species with a variable degree of opportunism, (3) migrants are more opportunistic while wintering (in Caribbean Costa Rica) than syntopic year-round residents, and (4) open-country and canopy flycatchers tend to be more opportunistic than forest-interior species. Variation in flycatcher diets with respect to all parameters examined necessitates multiple explanatory hypotheses, and warrants a pluralistic approach to questions of community structure in these birds.

Key words: birds; community structure; diet; flycatchers; insects; migration; opportunism; patchiness; specialization; species-interactions; stomach contents; tropics; Tyrannidae.

INTRODUCTION

Many ecologists have sought evidence that competition structures communities from the way species partition resources (Mac Arthur 1958, 1972, Cody 1974, Schoener 1974, Diamond 1978). Measurements of food type and size are necessary to quantify overlap along a food dimension. With overlaps along other dimensions (e.g., temporal, habitat) one could then investigate how other species influence the position and shape

of a particular species' "niche" in the niche hypervolume (Hutchinson 1957). Accordingly, recent studies of diets in multispecies assemblages have typically quantified breadth and overlap in use of food resources to examine questions about the niche (Holmes and Pitelka 1968, Orians and Horn 1969, Hespenheide 1971b, 1973, 1975a, Baker and Baker 1973, Beaver and Baldwin 1975, Brown 1975, Pianka 1975, Herrera and Hiraldo 1976, Ulfstrand 1977, Laursen 1978, Wiens and Rotenberry 1979, Toft 1980).

Other ecologists have expressed dissatisfaction both with the pancompetitive view of nature that has arisen from niche theory and with the way empiricists test the theory (e.g., Connell 1975, 1978, Wiens 1977, Birch

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TABLE 1. Species names, species codes, body mass, prey-capture methods, habitats, strata, and migratory status of 16 flycatcher species in the Caribbean lowlands, Costa Rica. Species characterizations are based on T. W. Sherry (1982, *personal observations*), and Slud (1964).

| Species | Code | Body mass (g) | Prey-capture method* | Habitat† | Stratum‡ | Migratory status§ |
|-----------------------------------|------|---------------|----------------------|----------|----------|-------------------|
| <i>Contopus cinereus</i> | CC | 12.3 | HP | O | ALM | R |
| <i>Contopus virens</i> | CV | 14.0 | H | OESF | ALMH | M |
| <i>Contopus borealis</i> | CB | 31.6 | H | OE | A H | M |
| <i>Colonia colonus</i> | CCO | 15.6 | H | OE | A MH | R |
| <i>Terenotriccus erythrurus</i> | TE | 7.2 | PS | SF | LM | R |
| <i>Myiobius sulphureipygius</i> | MS | 12.0 | HPS | SF | LM | R |
| <i>Myiornis atricapillus</i> | MA | 5.3 | S | F | MH | R |
| <i>Todirostrum sylvia</i> | TS | 7.5 | S | S | L | R |
| <i>Todirostrum cinereum</i> | TC | 6.2 | S | OE | LM | R |
| <i>Todirostrum nigriiceps</i> | TN | 6.2 | S | ES | H | R |
| <i>Oncostoma cinereigulare</i> | OC | 7.2 | S | ES | LM | R |
| <i>Rhynchocyclus brevirostris</i> | RB | 22.9 | S | SF | M | R |
| <i>Platyrinchus coronatus</i> | PC | 8.8 | S | F | L | R |
| <i>Tolmomyias assimilis</i> | TOA | 14.5 | S | F | H | R |
| <i>Tolmomyias sulfurescens</i> | TOS | 14.7 | S | OES | H | R |
| <i>Empidonax virescens</i> | EV | 13.4 | H S | SF | LM | M |

* H = aerial hawk, P = flutter pursuit, S = upward strike (and some downward strikes in the case of hawking species). See Fitzpatrick (1980a) for definition of terms.

† O = open habitats (pastures, towns), E = forest edge, S = second-growth vegetation, F = primary rainforest.

‡ A = airspace, L = low, M = middle, H = high (canopy or above).

§ M = migrant, R = year-round resident.

1979, Huston 1979, Lawton and Strong 1981). For example, if the conditions in which resources are in short supply occur infrequently, then the ecological context of competition-related adaptations will frequently remain obscure (Wiens 1977, Boag and Grant 1981). Moreover, Wiens and others have drawn attention to assemblages of opportunistic species for which environmental heterogeneity and unpredictability apparently preclude competitive "fine-tuning" (thus niche segregation) among locally co-occurring species (Wiens 1977, Rabenold 1978, Wiens and Rotenberry 1979, 1981a, b, Rotenberry 1980). In particular, species diets in such communities overlap highly at any one time and place and fluctuate over time, because of opportunistic exploitation of ephemeral resources (Fenton and Morris 1976, Fenton et al. 1977, Wiens 1977, Wiens and Rotenberry 1979, Bell 1980, Fenton and Thomas 1980, Rotenberry 1980, Fenton 1982).

An important disagreement among ecologists clearly centers on the factors that determine diets of coexisting predators. The purpose of the present study was to quantify a variety of dietary parameters of sympatric predators, then to evaluate those factors most strongly influencing prey selection, dietary diversification, and potential processes—including species interactions—structuring communities of predators. Species-rich terrestrial communities in the humid tropics have been viewed as experiencing relatively small-amplitude fluctuations in the physical environment, and biotic interactions ought to predominate among factors structuring such communities (Dobzhansky 1950,

Mac Arthur 1969, 1972, Diamond 1978). Tropical communities are thus a standard against which to compare other terrestrial communities with respect to the extent and kinds of biotic interactions (or the lack thereof). The present study of an insectivorous flycatcher assemblage in the humid lowlands of Costa Rica represents an attempt to provide such a yardstick.

Biologists have quantified animal diets in diverse ways. Breadth, overlap, and fluctuation of the diet in space and time are prominent among the parameters examined (see references cited above). Comparison of food selected with food available is also frequent and informative (e.g., Morse 1971a, Herrera and Hiraldo 1976, Toft 1980, Schluter 1982, Sherry, *in press*). To make such comparisons in a meaningful way for the present study would have been almost impossible technologically, considering the range of habitats involved (including all foraging heights and substrates in rainforest), the range of resource taxa, and the variation in prey dispersion patterns (see Discussion). Instead, I quantified a variety of dietary parameters which, in combination with knowledge of particular arthropod taxa (e.g., spatio-temporal distribution and antipredator behavior), help delineate for each species what resources are consumable relative to all those available. I term this the "food resource": some subset of all resources that is effectively available owing to psychological, morphological, behavioral, or habitat constraints, among others, on the predator. Because prey characteristics reflect the processes by which predators search for, recognize, pursue, and handle prey, both

foraging behavior and morphology of predators are intimately associated with diets. Functional analyses of foraging behavior and of relevant morphological characteristics in the flycatchers under study (Sherry 1982) thus help interpret diets and vice versa.

In the present study, then, I compared and contrasted 16 sympatric Neotropical flycatcher species with respect to five dietary parameters: prey type (to portray similarity of the predators), diversity of prey types (to measure diet breadth), patchiness of prey morpho-species within stomachs (to assess prey dispersion), population dietary heterogeneity (to quantify reliability of prey taxa), and number of items per stomach (to estimate prey energetic content). Based on these dietary parameters and information in the literature, I discuss four general questions. (1) How do the species differ with respect to all dietary parameters, and how are the parameters interrelated? (2) What is the food resource of each species? (3) Can insectivorous vertebrates such as flycatchers be classified as opportunists or generalists, as some authors have suggested, and if not, why not? (4) How are diets related to ecological or evolutionary processes that structure communities? In addition to these general questions, I address several more specific questions. (1) How many stomachs are needed to be representative, and how representative for a species are diets from the populations under study? (2) How are the diets of the flycatchers under study influenced by predator body size and foraging techniques? (3) Do diets of migratory flycatchers differ from those of residents? (4) How do flycatcher diets reflect habitat differences in arthropod abundance or variability? (5) How are flycatcher diets influenced by characteristics of arthropods or arthropod assemblages?

New World flycatchers (Tyrannidae) are convenient for study. They comprise one of the largest passerine (perching bird) families in the world, represent $\approx 10\%$ of the land bird species throughout the Neotropics, and occupy diverse adaptive zones as a result of extensive radiation during the Tertiary isolation of South America (Keast 1972, Fitzpatrick 1978, Traylor and Fitzpatrick 1981). Numerous species are available per community (and many communities available) to test hypotheses. Many tyrannids are migratory; hence one can study them over a wide range of latitudes; one can also study year-round residents and migrants exploiting the same tropical regions (Fitzpatrick 1980b). Recent quantitative studies of foraging behavior (Davies 1977, Eckhardt 1979, Fitzpatrick 1980a, 1981, Sherry 1982) and of morphology (Hespenheide 1971b, Fitzpatrick 1978, Traylor and Fitzpatrick 1981, Sherry 1982) have enhanced understanding of flycatcher ecology and vice versa.

STUDY COMMUNITY

The community of tyrannids considered here was chosen to contain few enough species to study each in

detail, yet enough species to suggest patterns among the ecological and evolutionary influences on diets. I arbitrarily but operationally defined the community under study: Tyrannidae which are primarily ($\geq 90\%$; see Schoener 1968) insectivorous, catch prey while in flight, and inhabit lowland sites in the Caribbean sector of Costa Rica (Table 1). These species tend to be small-bodied (< 15 g), but vary with respect to prey-capture method, habitat, foraging stratum within vegetation, and status as migrant or resident (Table 1). Three additional tyrannids (*Onychorhynchus mexicanus*, *Aphanotriccus capitalis*, and *Empidonax flaviventris*) meet the criteria for inclusion in the present study, but fewer than three specimens were available to quantify their diet (see Sherry 1982, and below). A variety of tyrannids in the Sarapiqui lowlands were excluded from study: *Ornithion* primarily gleans prey from foliage (Fitzpatrick 1980a); *Zimmerius* (= *Tyranniscus*), *Camptostoma*, *Elaenia*, *Mionectes*, *Phylloscartes* (= *Capsiempis*), *Attila*, *Rhytipterna*, *Myiarchus*, *Pitangus*, *Megarhynchus*, *Myiozetetes*, *Conopias*, *Myiodynastes*, and *Tyrannus* regularly consume fruit or small vertebrates (Slud 1964, Fitzpatrick 1980a, and T. W. Sherry, personal observations; generic names follow Traylor 1977). A few other birds (e.g., *Parulidae* and *Galbulidae*) in Caribbean Costa Rica feed much like Tyrannidae (T. W. Sherry, personal observation), but their inclusion would not likely alter the conclusions reached in the present study.

STUDY AREA

I collected birds for dietary analysis in the Caribbean lowlands, Costa Rica, primarily in the vicinity of Puerto Viejo de Sarapiqui (henceforth "Puerto Viejo"). Puerto Viejo lies in the northeastern part of the country at the base of the Cordillera Central. Collectively, the flycatchers came from sites between 50 and 150 m elevation, and from virtually all habitats in the region: primary rainforest, riparian rainforest, secondary growth of various ages and physiognomy, swamp forest, and open pasture. At Estación Finca La Selva (an Organization for Tropical Studies field station) 3 km southeast of Puerto Viejo, mean monthly temperatures vary little over an annual cycle. Total rainfall averages ≈ 4000 mm annually (Stiles and Wolf 1979, G. S. Hartshorn, personal communication), and rainfall averages well in excess of 100 mm/mo, although it is seasonal, with lowest values between February and April and peaks in July and December (Stiles 1980). Holdridge et al. (1971) and Frankie et al. (1974) have described the vegetation, and Slud (1960) has described the avifauna at Finca La Selva.

A few birds were collected in the Sixaola region of Costa Rica, in the lowlands and foothills between Puerto Viejo de Limón and the Panamanian border. This region is slightly drier than the Sarapiqui lowlands (Tosi 1969), but faunistically quite similar. Birds of the entire

Caribbean coast of Costa Rica are primarily South American in their affinities (Slud 1964), and the Sarapiqui region in particular lies within the most species-rich "dispersal center" for vertebrates in Central America (Müller 1973).

METHODS

Data collection

Birds were collected from 1976 to 1978 using shotgun and mist nets between 0600 and noon. High feeding rates of the birds during the early hours of the day usually guaranteed full stomachs for analysis. To control for seasonally changing prey availability, I collected only between September and December. For most if not all of the species this time period corresponds with a relatively wet pre-breeding period (Stiles 1980), which spans late molt (T. W. Sherry, *personal observation*) and then subsistence. The subsistence period is a "lean season" for many kinds of rainforest birds (Fogden 1972, Stiles 1980). In Central America, arthropod abundance is relatively low during the late rainy period (September–December; reviewed by Karr 1976). A period of food scarcity would test the ability of the birds to harvest arthropods.

Even though diets in at least some of these species change seasonally, the change is insufficient to obscure species-specific combinations and characteristics of prey taxa. More specifically, breeding-season diets cluster more closely with conspecific lean-season diets, based on prey taxa, than with lean-season diets of any other flycatcher species (Sherry, *in press*). This result implies that the stomachs considered in the present study are representative for at least the year-round resident populations under study, and therefore permit meaningful comparison of the flycatchers with respect to prey taxa.

Upon collecting a bird, I removed the stomach immediately and preserved it in 95% ethanol to preclude continued digestion of the contents (see Van Koersveld 1950). In the laboratory each stomach sample was washed into a small Petri dish (5 cm diameter) and systematically scanned under 10 \times , then 20 \times magnification, using a dissecting microscope, to obtain all identifiable arthropod remains. The minimal number of arthropods present per stomach was determined after association of as many parts as possible of each prey individual (e.g., pairing spider poison claws, beetle head with thorax with elytra, etc.). Most arthropods of a size eaten by tyrannids have well-sclerotized parts that persist undigested in the stomach: spider poison claws, mouthparts of Lepidoptera larvae and Orthoptera, heads or hind tarsi and femora of Homoptera, elytra of Coleoptera, heads or thoracic segments of Hemiptera and Hymenoptera, wings and mouthparts of Odonata, and anal forceps of Dermaptera. Adult Lepidoptera and Diptera, which I generally recognized from wings and heads, probably remain recognizable in stomachs for shorter periods than other prey types.

Since absolute proportions of different prey taxa were not required in this study, I made no attempt to apply correction factors to stomach contents (cf. Hartley 1948, Mook and Marshall 1965, Custer and Pitelka 1975). Because variable disappearance rates among prey taxa must affect all flycatcher species, I assume that differences of stomach contents reflect real differences in the taxa eaten.

Several procedures in the present study minimized the problem of differential digestion rates of prey taxa: (1) the common phylogenetic history of tyrannids presumably standardizes digestive morphology; (2) diets limited to arthropods minimize the range of digestion times (e.g., compared with seeds, nectar, and fruit); and (3) collection of birds during peak feeding activity tended to standardize the stage of digestion among different stomachs. Collection of specimens over several years and in habitats often separated by many kilometres (never more than two individuals per species were collected per day in a particular area) insured that results were not biased by any peculiar set of local ecological circumstances.

Diet analysis

Multivariate analyses of prey types and predator relationships.—I first expressed the diet of each species (all stomachs pooled) as percent use of each of 15 prey categories (Table 2). These percentages were then transformed to natural logarithms to normalize the distributions of prey frequencies across species (see Bryant 1973), after first adding "1" to each percentage to avoid taking the logarithm of zero. I did not add "0.1" or "0.01" to percentages, even though the addition of a smaller number affects the results (J. R. Karr, *personal communication*), because I did not want to exaggerate small differences of small percentages. From the species-by-prey-taxa (16 rows by 15 columns) matrix I calculated a correlation matrix for each prey taxon with every other one (thus a 15 by 15 matrix). I then executed two *R*-type analyses (Sneath and Sokal 1973): factor analysis of variables and cluster analysis of variables (see below). Factor analysis of variables (BMDP4M—all multivariate statistics were computed using University of California at Los Angeles BMD Biomedical Computer Programs, P-series, 1979) served (1) to identify fewer independent "factors" (i.e., linear combinations of one or more original, potentially intercorrelated prey variables); and (2) to suggest "meaningful dimensions" within the data set (Cooley and Lohnes 1971). In the present study, I used common characteristics of prey variables correlated with each significant factor to suggest "meaningful" dimensions: i.e., those that reflect how different flycatcher species locate or capture prey. I used varimax rotation, which generally facilitates interpretation of factors by causing high factor loadings to tend towards "1" and low loadings to tend towards "0" (Harman 1967, Cooley and Lohnes 1971). I only considered those factors to be

significant whose eigenvalues were greater than unity, and I report only those factor loadings >0.45 (Aspey and Blankenship 1977).

Factor scores of each bird species (i.e., position of each species in multidimensional space defined by significant varimax factors) enabled me to compare diet composition of the 16 bird species. Euclidian distances calculated from factor scores (a *Q*-type analysis; Sneath and Sokal 1973) were used to cluster bird species (BMDP2M, average linkage to cluster centroids). Such comparison of bird species was intended to be a first step to examine their dietary relationships (see Discussion).

Cluster analysis of variables (BMDP1M, average linkage), just like factor analysis of variables, examines the relationships of different prey variables using the correlation matrix of each prey variable with every other one. I used cluster analysis of variables as a recipe to pool "significantly correlated" prey variables. Since all correlations (from which variables were clustered) were based on 16 flycatcher species, the critical correlation coefficient, for 14 degrees of freedom and the .05 level of significance, was used as the significance criterion for pairwise correlations. In the one case of three variables clustering at a correlation coefficient greater than this value, I checked the three possible pairwise correlations, to ensure that each met the above pairwise criterion. The cluster analysis thus identified fewer categories of correlated prey variables (i.e., clusters) than the original 15 variables. Analyses of population dietary diversity and population dietary heterogeneity (see below) were based on these new clusters of original variables. These new prey variables have the advantage that they are not intercorrelated in different flycatchers' stomachs, as were most of the original 15 prey variables.

Diet specialization.—Each stomach contains the remains of food eaten over some previous (unknown) time span, and as such does not necessarily represent what an individual or a population typically eats. I used a method described and justified by Pielou (1975) and applied to stomach-content data by Hurtubia (1973) both to estimate the diversity of items eaten by a population of flycatchers (i.e., population dietary diversity) and to assess sample size adequacy. Specifically, one takes the stomachs in random order and calculates the diversity of prey items in stomach 1, then in stomachs 1 plus 2 (contents pooled), and so on to the total number of stomachs in the sample. One uses the Brillouin diversity index (H) at each step, in part because each stomach contains a potentially nonrandom collection of prey (Pielou 1975):

$$H = (1/N) \cdot \ln(N!/(n_1! \cdot n_2! \cdot \dots \cdot n_t!)),$$

where there are n_1, n_2, \dots, n_t prey items in each of t different prey categories, with N total prey items per collection. If enough stomachs are available from a particular predator species, the "saturation curve" re-

TABLE 2. Sorted, varimax rotated, factor loadings for 15 prey taxa (two ant categories; see text) in stomachs of 16 flycatcher species from the Caribbean Lowlands of Costa Rica. Data pooled from all (at least 3) individuals per species. Loadings <0.45 are not reported. See text for factor interpretation.

| Prey taxon | Factor 1 | Factor 2 | Factor 3 | Factor 4 |
|------------------------------|----------|----------|----------|----------|
| Formicidae, flying | -0.91 | | | |
| Arachnida | 0.82 | | | |
| Lepidoptera larvae | 0.79 | | | |
| Apoidea | -0.77 | | | |
| Cercopoidea | 0.76 | -0.49 | | |
| Odonata | -0.75 | | | |
| Orthoptera | 0.74 | | | 0.49 |
| Hemiptera | | 0.85 | | |
| Coleoptera | | 0.78 | | 0.53 |
| Fulgoroidea | 0.49 | -0.77 | | |
| Formicidae, nonflying | | 0.69 | 0.53 | |
| Diptera | | | 0.87 | |
| Parasitoids* | | | 0.84 | |
| Dermoptera | | | | 0.78 |
| Lepidoptera adults | | | | 0.60 |
| Eigenvalue | 4.72 | 2.87 | 2.36 | 1.95 |
| Percent variation | 32.5 | 19.6 | 17.2 | 10.0 |
| Cumulative percent variation | 32.5 | 52.1 | 69.3 | 79.3 |

* Hymenoptera.

sulting from this analysis reaches a plateau at t stomachs, when additional stomachs add little dietary information for the species. All diversity values in the plateau of the saturation curve, i.e., all values for $t \geq 1$ where t was determined subjectively, were used to calculate mean prey-type diversity of the bird species. Population dietary diversity (assumed here to represent diet breadth) includes both evenness and richness diversity components (Pielou 1975).

Heterogeneity of stomach samples.—Species for which more stomachs are required to reach a diversity plateau clearly have more heterogeneous diets than other species. I quantified this population dietary heterogeneity (PDH) using the G statistic (Sokal and Rohlf 1969). This statistic is often used in lieu of chi-square to test the hypothesis that observations in each of C cases (columns) are distributed independently among each of R discrete classes (rows). Greater independence of the observations in each of the cases (stomachs of a species, in this case) among the classes (prey taxa), i.e., a more heterogeneous distribution among the classes, will increase G from a value of zero when all cases have identical frequencies among all classes. Since G increases with the number of cases and classes, I calculated PDH as $G/(df)$, where $df =$ degrees of freedom = the product $(R - 1) \cdot (C - 1)$ appropriate to each flycatcher species.

"Patchiness" of morphospecies in stomachs.—Real arthropod species are often aggregated in nature (e.g., a reproductive swarm of ants or termites), and such prey patches must often account for the occurrence of

several individuals of the same prey species in a predator's stomach. I adopted Lloyd's index for spatial aggregation (C) to quantify patchiness of morphospecies (i.e., morphologically identical prey, assumed to represent one species) within flycatcher stomachs:

$$C = m^*/\lambda,$$

$$m^* = 1/N \cdot \sum_{i=1}^k n_i \cdot (n_i - 1),$$

where m^* = "mean crowding," λ = mean patch size (a patch is any group of identical morphospecies in a flycatcher stomach), n_i = size of patch i (n_i ranged from 1 to 34 in the flycatchers studied here), k = total number of patches, and N = total number of prey = $\sum_{i=1}^k n_i$. For example, if a stomach contained three unique morphospecies, two individuals of a fourth morphospecies, and five individuals of a fifth morphospecies, then

$$C = [(1/10) \cdot (2 + 20)]/2 = 1.1.$$

I calculated C for each stomach, and compared flycatcher species using the mean value. Lloyd's patchiness index, like most others, is essentially a variance/mean ratio (Vandermeer 1981), and any such index would have served to compare the flycatchers studied here.

Misclassification of morphospecies into "patches" is a potential problem with fragmentary arthropods such as occur in stomachs. The most likely sources of error, none of which is believed to have been important numerically, are as follows. (1) Arthropod groups which were typically recognized from fragments such as poison claws and mouthparts (e.g., Arachnida, Lepidoptera larvae, Orthoptera) could have been overclassified as unique items, since I tended to treat all specimens as unique unless there were compelling reasons to do otherwise. I think this was not a problem, since available evidence (T. W. Sherry, *personal observations*) suggests the flycatcher species studied encountered these particular arthropod taxa singly. (2) Some sexually dimorphic arthropods that could have been encountered together would usually have been classified as separate morphospecies. (3) Individuals of common arthropod species may have been assigned to the same patches even though the individuals were encountered separately, but after the bird had caught intervening taxa. Spatial patchiness involving nonidentical prey species may be important to a bird, but is not quantifiable with stomach contents alone.

RESULTS

Dietary parameters based on pooled stomach contents

Factor analysis.—Four significant factors, each one an axis statistically independent of all the others, ac-

counted for 79% of the scatter of points in multivariate "space" (Table 2). Each point represented a prey variable whose position in the 16-space depended on the use each of the 16 flycatcher species made of that prey type. No one factor accounted for an overwhelming amount of scatter in the data (factor 1 accounted for about three times the variance for which factor 4 accounted; Table 2).

Three of the four factors are readily interpretable from knowledge of arthropod behavior and distribution. Factor 1 resulted from the tendency for one group of birds to consume Arachnida, Lepidoptera larvae, Orthoptera, cercopoid Homoptera, and fulgoroid Homoptera (described by high positive correlations with, or "loadings on," factor 1); and a second group of birds, by contrast, to consume flying Formicidae (ants), Apoidea, and Odonata (with high negative loadings on factor 1—Table 2). Arthropods of the first group tend to be found within vegetation. Arachnida, Lepidoptera larvae, and Orthoptera, in particular, tend often to be relatively immobile, relying on defenses other than flight. These arthropods might evade predators through such defenses as crypsis, distastefulness, or mimicry. Crypsis within vegetation is an important defense of many cercopoid and fulgoroid Homoptera (T. W. Sherry, *personal observations*), although these two taxa have additional defenses (see below). Arthropods eaten by the second group of birds tend to be more active, susceptible to capture while flying outside of vegetation. Thus the first factor appears to distinguish less active prey that searching predators encounter within vegetation, from flying prey that hawking predators capture in the airspace.

Factor 2 resulted from the tendency for Hemiptera, Coleoptera, and nonflying Formicidae (high positive loadings) to co-occur in stomachs of a third group of flycatchers, whereas Fulgoroidea and Coccoidea (negative loadings) tended to co-occur in stomachs of yet another group of flycatchers (Table 2). The first three prey taxa tend to be relatively conspicuous (many species in all three taxa can often be seen walking within vegetation) and often hard bodied. The other two (homopteran) taxa are often inconspicuous, but they also share the ability to jump from vegetation at the approach of a disturbance (no Cicadidae, Aphididae, Psyllidae or other non-jumping Homoptera were recorded in any flycatcher stomachs). Factor 2 thus appears to distinguish relatively conspicuous arthropods that drop or walk (occasionally fly) from a disturbance (T. W. Sherry, *personal observation*) from arthropods that attempt to evade approaching predators with sudden jumps.

Factor 3 suggests that yet another group of birds that can find or capture Diptera also finds or captures parasitoid Hymenoptera and nonflying Formicidae (Table 2). Two hypotheses to explain this grouping of taxa concern the evasiveness (using flight) characteristic of some Hymenoptera and Diptera, and the concentra-

tion of all three taxa at extrafloral nectaries (see Discussion). Interpretation of factor 4 is not obvious. The two taxa with highest loadings on factor 4 (Dermaptera and Lepidoptera adults) were found infrequently in flycatcher stomachs (Appendix).

Factor scores give the coordinates of each flycatcher species in four-dimensional "factor space" (Table 3). Foraging behavior of these flycatchers (Table 1) helps interpretation of factors themselves. The observation that hawking species (CC, CV, CB, and CCO) all had negative scores on factor 1 whereas small-bodied upward-strikers that capture prey from vegetation (MA, TS, OC, and PC) had high positive scores (Tables 1 and 3) corroborates the interpretation of factor 1 above: arthropods that are positively loaded on factor 1 were taken by flycatchers that take prey in vegetation while negatively loaded arthropods were taken by flycatchers that forage in the airspace.

Two understory pursuers (TE and MS) had the largest negative scores on factor 2 because they consumed more jumping Homoptera (negatively loaded on this factor) and fewer Hemiptera, Coleoptera, and nonflying Formicidae (positively loaded on this factor) than other flycatcher species (Tables 1 and 3; and Appendix). These data suggest that acrobatic pursuit behavior serves to capture Homoptera after they have jumped from the vegetation (see Discussion). Although TE and MS had similar scores on factor 2, their scores on factors 1, 3, and 4 were quite different (Table 3), an observation which relates to large dietary differences of these two species with respect to most dietary parameters (see below).

The two species with highest positive scores on factor 2 were TOA and TOS (Table 3), which are relatively large-bodied, stereotyped upward-strikers (Table 1). The two other species with next highest scores on this factor (RB and EV—Table 3) are also relatively large-bodied species which upward-strike at least part of the time (Table 1). Thus factor 2 distinguishes between flycatcher species that simply snatch prey off vegetation from species that acrobatically pursue evasive prey types in flight. In combination with the different prey types positively and negatively correlated with this factor (Table 2), the behavioral differences confirm that different flycatcher species use contrasting foraging behaviors to capture differentially evasive prey. Coleoptera, Hemiptera, and Formicidae do have defenses against foraging birds, including running and/or dropping from an approaching predator, and sitting on inaccessible substrates. The upward-strokes used by some of these flycatchers may be particularly effective against such prey behaviors, as discussed below.

The two species with highest positive scores on factor 3 were two congeneric *Todirostrum* species (TC and TN—Table 3). These species are tiny-bodied, stereotyped upward-strikers in canopy and open vegetation (Table 1). The flycatcher with the next highest score on this factor (MS—Table 3) is quite different behav-

TABLE 3. Factor scores for 16 flycatcher species indicating species positions in "factor space" based on 15 prey variables (ants subdivided into flying vs. nonflying individuals; see text).

| Bird species | Factor | | | |
|--------------|--------|-------|-------|-------|
| | 1 | 2 | 3 | 4 |
| CC | -1.22 | 0.48 | 0.08 | 0.73 |
| CV | -0.76 | 0.06 | 0.50 | 1.06 |
| CB | -2.25 | -0.24 | -0.87 | -0.58 |
| CCO | -1.04 | -0.18 | -1.30 | -0.14 |
| TE | 0.24 | -2.55 | -0.62 | -1.85 |
| MS | -0.55 | -1.38 | 0.92 | 1.82 |
| MA | 1.14 | -0.39 | -0.61 | 0.37 |
| TS | 1.23 | -0.08 | 0.09 | -0.12 |
| TC | -0.17 | -0.26 | 2.02 | -0.88 |
| TN | 0.12 | 0.18 | 1.71 | -0.40 |
| OC | 1.34 | -0.06 | -0.23 | -0.29 |
| RB | 0.66 | 0.61 | -1.88 | 0.62 |
| PC | 1.09 | -0.03 | 0.01 | 0.83 |
| TOA | 0.23 | 1.33 | 0.32 | -0.80 |
| TOS | -0.24 | 1.88 | -0.04 | -1.48 |
| EV | 0.17 | 0.60 | -0.09 | 1.11 |

iorally from TC and TN, and species with the most negative scores on factor 3 are also diverse in terms of foraging behavior. Much the same observation holds for species with greatest positive and negative scores on factor 4. Thus foraging tactics do not correspond clearly with prey-taxa differences associated with factors 3 and 4, and I conclude that (1) flycatchers with similar tactics can diverge dietarily in some respects, and (2) flycatchers with different tactics can converge dietarily. The nature and possible causes of prey-type specializations are discussed in more detail below.

Flycatchers clustered by prey taxa.—Cluster analysis of the Euclidian distances between flycatcher species (based on factor scores, Table 3) provides a two-dimensional representation of flycatcher dietary relationships (Fig. 1). In most cases congeners clustered most closely together (TC with TN, TOA with TOS, and CV with CC). CB clustered with CCO rather than with CV and CC, probably because the two former species tended to occupy more similar habitats and strata than the latter (Table 1) and as a consequence may have encountered relatively similar prey. Four noncongeners (PC, MA, OC, and TS) clustered as closely dietarily as any congeners (Fig. 1), an observation that may be related to habitat segregation in these species (Table 1 and Discussion). Both MS and TE clustered alone (Fig. 1), and thus their dietary affinities with other flycatchers, based on prey taxa alone, remain ambiguous. Other analyses presented below suggest explanations for this ambiguity, and clarify other kinds of relationships involving these species.

The factor analysis for which results were just presented (Tables 2 and 3) was based almost exclusively on prey taxa. However, one behavioral measure was used in the analysis to distinguish two distinctive prey

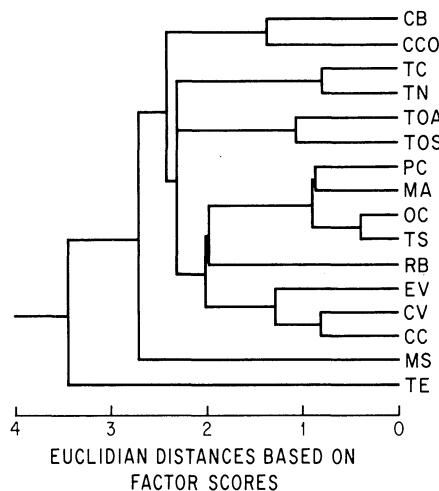


FIG. 1. Diet-based cluster analysis of 16 insectivorous flycatcher species inhabiting the Caribbean lowlands, Costa Rica. Species were clustered using their factor scores (Table 3).

groups within one prey taxon. Specifically, I used frequencies of aerial vs. nonaerial foraging tactics to determine for each flycatcher species whether flying (reproductive) or nonflying (primarily worker) Formicidae were eaten (Table 4). In several cases the foraging tactics suggested that a flycatcher could have eaten both reproductive and worker formicids (e.g., CC and CV; Table 4), but most species tended to eat one or the other group of ants. The necessity to make this distinction and to enter a behavioral parameter into the analysis resulted from an initial factor analysis in which factor scores indicated an artificially close relationship of CB with TOA and TOS (see Sherry 1982). These three species eat more ants than any others (Table 4), but behavioral and other information (e.g., Table 1) indicated that CB specializes on reproductive ants, which are a very different resource from the worker ants eaten by *Tolmomyias* species. Because different species relationships can clearly result from the way prey taxa are recognized, dietary relationships portrayed in Fig. 1 must still be considered approximate. Different relationships could result, for example, when finer distinctions within large prey taxa (e.g., Coleoptera and Diptera) are recognized (see Greene and Jaksic 1983); when the distinction between flying and nonflying arthropods is made in taxa other than Formicidae; or when prey size is taken into account (Hespenheide 1975a; T. W. Sherry and H. A. Hespenheide, personal observation).

The factor analysis, in summary, reduced the original 15 variables to four axes or factors, which differentiated the flycatchers on the basis of prey detectability, prey location (vegetation vs. airspace), and prey catchability. How prey taxa correspond with resources from a bird's perspective is an important question. For the Formicidae, for example, it was necessary to know

how the prey were captured. Cluster analysis of flycatcher species gave intuitively satisfactory results, e.g., close clustering of most congeners. Interesting dietary similarities of noncongeners were suggested, but relationships of some species (TE and MS) to the others remained ambiguous when only prey types were considered.

Dietary parameters based on contents of individual stomachs

In the foregoing analyses, the diet of each flycatcher species was treated as one composite stomach, with data pooled from all (at least three) individuals per species. However, individual stomachs contain information about the food resources effectively available to an individual, and I argue below that this information helps delineate what prey are available to the population. The following analyses concern information to be obtained from individual stomachs.

Prey-type diversity.—The issue of what constitutes a prey "taxon" or variable persists when individual stomachs are compared. The factor analysis above showed that the 15 original variables (taxa) do not all occur independently in the flycatchers' stomachs. One is compelled to treat variables such as Fulgoroidea and Cercopoidea, which predictably co-occurred in stom-

TABLE 4. Division of Formicidae (ants) into those caught flying (reproductives) vs. those not flying (mostly workers), as estimated from foraging tactics.

| Species | Ants in diet* | | Aerial† foraging tactics | | Estimated no. of ants | |
|---------|---------------|-----|--------------------------|-----|-----------------------|------------|
| | % | n | % | n | Fly-ing | Non-flying |
| CC | 18.4 | 174 | 87.0 | 77 | 23 | 9 |
| CV | 11.3 | 266 | 71.4 | 570 | 24 | 6 |
| CB | 34.0 | 100 | 87.0 | 23 | 34‡ | 0 |
| CCO | 6.1 | 359 | 95.2 | 167 | 21 | 1 |
| TE | 0.0 | 64 | ... | ... | ... | ... |
| MS | 2.2 | 137 | 55.0 | 101 | 2 | 1 |
| MA | 3.0 | 201 | 3.0 | 66 | 0 | 6 |
| TS | 2.5 | 122 | 0.0 | 20 | 0 | 3 |
| TC | 6.4 | 281 | 4.8 | 84 | 1 | 17 |
| TN | 7.8 | 154 | 0.0 | 37 | 0 | 12 |
| OC | 2.0 | 98 | 5.6 | 36 | 0 | 2 |
| RB | 0.0 | 41 | ... | ... | ... | ... |
| PC | 1.0 | 205 | 1.2 | 81 | 0 | 2 |
| TOA | 19.0 | 258 | 9.4 | 32 | 5 | 44 |
| TOS | 28.7 | 157 | 9.4§ | ... | 4 | 41 |
| EV | 8.2 | 110 | 12.5 | 32 | 1 | 8 |

* The discrepancy between these totals and those of Table 5 results from the exclusion in these data of Hymenoptera whose identity could not be established from the stomach contents.

† These tactics include hawks and pursuits (see Sherry 1982 for definitions and source of data).

‡ All these individuals (from one stomach) were *Odontomachus* (Formicidae) queens, probably from one swarm.

§ Without foraging data specifically for TOS, I assumed that it forages the same as its congener TOA (see Slud 1964).

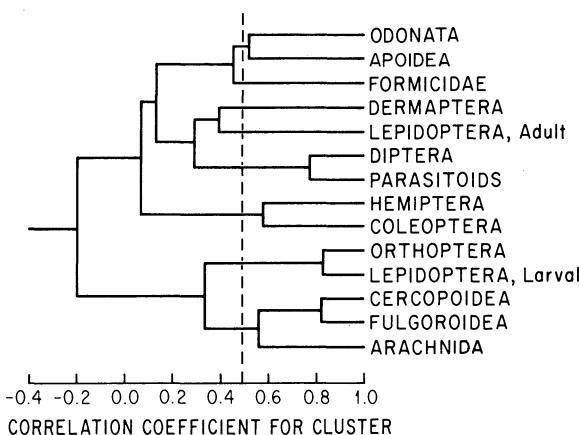


FIG. 2. Cluster analysis of 15 arthropod taxa in stomachs of 16 flycatcher species inhabiting the Caribbean lowlands, Costa Rica. Data pooled from all (at least 3) individuals per species. Dashed line is critical positive correlation coefficient ($P = .05$, 14 df) appropriate for comparisons of prey taxa based on 16 flycatcher species.

achs, as one new prey variable which is itself independent of other such new variables. Cluster analysis of variables suggested eight new ones (comprising one, two, or three original ones) based on the correlations between original variables: Odonata with Apoidea, Formicidae, Dermaptera, Lepidoptera adults, Diptera with parasitoid Hymenoptera, Hemiptera with Coleoptera, Orthoptera with Lepidoptera larvae, and Cercopoidea with both Fulgoroidea and Arachnida (Fig. 2). Ants (Formicidae) were not subdivided in this anal-

ysis because flying (winged) vs. nonflying (mostly worker) ants could not often be distinguished in individual stomachs. Compare the similarity of these clusters with the relationships that factor analysis suggested among the prey variables (Table 2, Fig. 2).

For most species, stomachs adequately disclosed the range of the prey types eaten by the local population, since the diversity of the pooled prey sample tended to reach a plateau (Fig. 3). In most species, however, each stomach was indeed a sample insofar as it generally contained only some of the prey types eaten by the entire population. The saturation curves (Fig. 3) demonstrate two important differences among the flycatcher species studied: (1) prey-type diversity differed considerably, and (2) the number of stomachs needed to sample adequately the diet of a population differed as well (contrast TE, CCO with TN, MA, CV). The same qualitative conclusions were obtained from saturation curves based on the original 15 prey variables (T. W. Sherry, personal observation).

These conclusions do not depend on the particular order in which stomachs were pooled to give successive points along a saturation curve. To show this, I produced different saturation curves for each species by taking real stomachs at random (sampling with replacement, so that the same stomach could appear repeatedly or not at all in any one saturation curve). I produced "n" curves per species, each curve having n points (based on as many randomly drawn stomachs), where n = the number of stomachs for that species. Thus the mean diversity and standard error for each position along the saturation curve were based on a

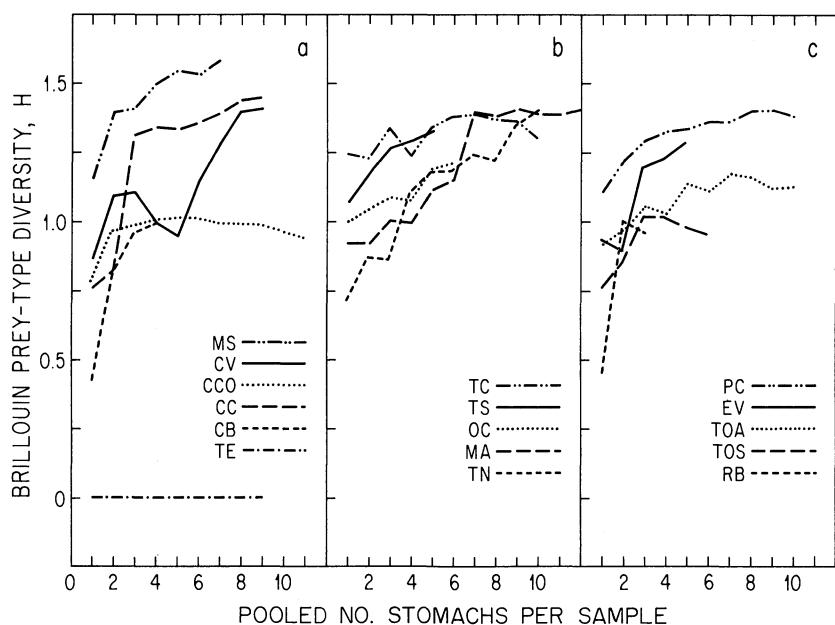


FIG. 3. Saturation curves of Brillouin population dietary diversity, H (used to approximate diet breadth) as a function of sample size (number of stomachs examined). The 16 species are roughly grouped by foraging technique. (See Table 1 for bird species codes and foraging techniques.)

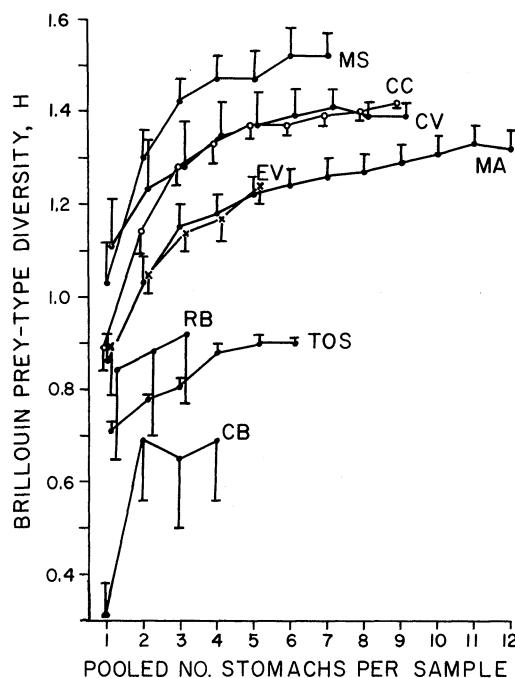


FIG. 4. Simulations of multiple saturation curves (mean \pm 1 se) for selected species, based on randomly drawn stomachs (i.e., sampling with replacement), to illustrate the repeatability and asymptotic tendency of such curves (see Fig. 3 and section on Dietary parameters based on individual stomachs).

number of saturation curves equal to the number of real stomachs available. Plots of means of random saturation curves for selected species (Fig. 4) reinforce conclusions drawn from Fig. 3. For example, the similarity of CV and CC after nine stomachs (Fig. 3) is real (Fig. 4). MA approached an asymptote within about

seven stomachs, and TOS within four, along their respective saturation curves (Fig. 4). Too few stomachs of CB, RB, and EV were available to estimate an asymptote (Figs. 3 and 4). In general, the simulated curves began to plateau after six stomachs, although the curves for some species (TS, TE, CCO, PC, TOA; T. W. Sherry, personal observation) were stable after four or fewer positions along a curve.

Species-differences in diet diversity did not result simply from differences in habitat. For example, TE and MS represent the two extreme prey-type diversities (Fig. 3) even though they used similar foraging behavior in identical habitats and foraging strata (Table 1). The five small-bodied upward-strikers (MA, TS, TC, TN, OC) had nearly identical prey-type diversities (Fig. 3) although they occupied different foraging strata and/or different habitats (Table 1). These latter species are closely related phylogenetically (Traylor 1977) and I subsequently refer to them as "euscarthmine" flycatchers (see Fitzpatrick 1978).

Diet diversity differences also did not result from differences in prey-capture technique alone. Hawking, upward-striking, and pursuing species all showed large differences in prey-type diversity. For example, CCO and CB, which fed on social Hymenoptera, had lower diet diversities than the more catholic CV and CC (Fig. 3). PC had a higher diet diversity than most larger bodied upward-strikers (Fig. 3), but a diet diversity quite comparable with that of the euscarthmine upward-strikers.

The extremely high diet diversity of MS and low diversity of TE probably explain the cluster-analysis result mentioned above (Fig. 1). Both of these species clustered far from any other species. In general, how does one interpret Euclidian distances (or diet "overlaps") between a generalist and a specialist? A relatively great Euclidian distance could represent the dietary

TABLE 5. Percentages of stomach patches (i.e., one or more individuals per morphospecies) in logarithmic size classes for 16 species of flycatchers in the Caribbean lowlands, Costa Rica.

| Bird species | Patch size | | | | | | Mean patch size (no. prey per patch) | Sample sizes | |
|--------------|------------|------|------|------|-------|-----|--------------------------------------|--------------|----------------|
| | 1 | 2-3 | 4-7 | 8-15 | 16-31 | >32 | | No. stomachs | Total no. prey |
| CC | 69.8 | 20.8 | 6.6 | 2.8 | ... | ... | 1.74 | 9 | 184 |
| CV | 80.2 | 14.6 | 4.3 | 0.9 | ... | ... | 1.39 | 9 | 294 |
| CB | 53.9 | 23.1 | 11.5 | 3.9 | 7.7 | ... | 3.92 | 4 | 102 |
| CCO | 79.0 | 9.7 | 2.4 | 3.2 | 4.8 | 0.8 | 2.94 | 11 | 364 |
| TE | 81.0 | 19.0 | ... | ... | ... | ... | 1.20 | 9 | 65 |
| MS | 90.2 | 7.1 | 1.8 | ... | 0.9 | ... | 1.37 | 7 | 153 |
| MA | 95.6 | 3.3 | 0.6 | 0.6 | ... | ... | 1.13 | 12 | 205 |
| TS | 95.0 | 4.2 | 0.8 | ... | ... | ... | 1.08 | 5 | 128 |
| TC | 83.6 | 8.5 | 5.8 | 2.1 | ... | ... | 1.53 | 10 | 289 |
| TN | 84.7 | 12.1 | 3.2 | ... | ... | ... | 1.27 | 10 | 157 |
| OC | 95.7 | 4.3 | ... | ... | ... | ... | 1.07 | 6 | 98 |
| RB | 86.1 | 13.9 | ... | ... | ... | ... | 1.19 | 3 | 43 |
| PC | 93.9 | 6.1 | ... | ... | ... | ... | 1.08 | 10 | 212 |
| TOA | 89.0 | 8.7 | 1.8 | 0.5 | ... | ... | 1.20 | 10 | 263 |
| TOS | 79.1 | 16.5 | 3.5 | 0.9 | ... | ... | 1.42 | 6 | 163 |
| EV | 91.8 | 5.1 | 3.1 | ... | ... | ... | 1.18 | 5 | 114 |

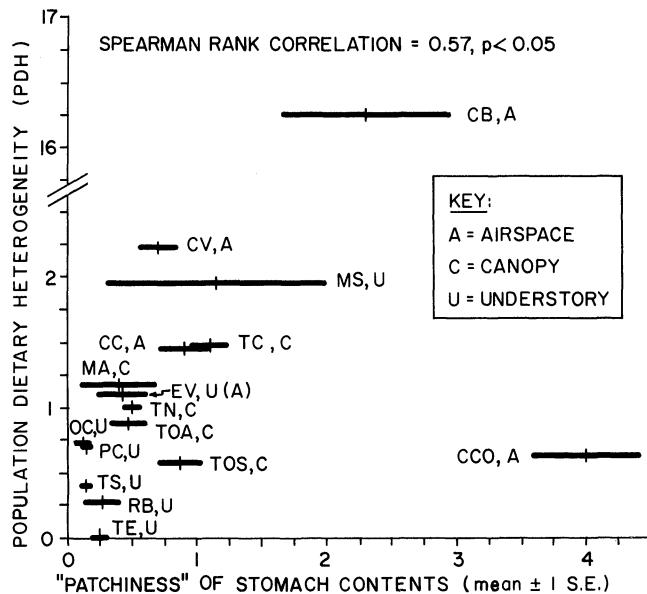


FIG. 5. The relationship between population dietary heterogeneity (PDH measured as G/df , of the array of stomachs vs. prey taxa) and dietary patchiness (aggregation of morphospecies measured as Lloyd's C) in stomachs of 16 insectivorous flycatchers inhabiting the Caribbean lowlands, Costa Rica. Habitat classifications are based on Table 1.

difference between (1) a generalist and any of a variety of different specialists, or (2) two species of equal diet breadth but very different prey preferences. I conclude that the large prey differences of TE and MS from the other flycatchers resulted from the extremes in diet breadth, since both TE and MS consumed many of the same groups of prey that other flycatchers consumed (Appendix).

Diet heterogeneity and patchiness

One or two stomachs adequately represented diet diversity of a population in some species (e.g., TE, CCO) whereas >10 stomachs would be necessary in other species (e.g., TN and CV; Fig. 3). Thus, population dietary heterogeneity (PDH) varied considerably among the species studied. I explore now the relationship of PDH to dietary patchiness (i.e., degree of morphospecies aggregation within stomachs) and to diet breadth.

The majority of "patches" in all 16 flycatcher species comprised just one prey individual per morphospecies (Table 5), i.e., were unique in a stomach. Many flycatcher species, particularly hawks (CC, CV, CB, and CCO), consumed more than one individual arthropod per morphospecies in the feeding time span represented by the contents of one stomach. Approximately 8% and 5% of the patches of CB and CCO, respectively, contained between 16 and 31 individuals per morphospecies (Table 5), suggesting these two species were either feeding within true clumps (=patches) of prey species, or were selectively feeding on particular prey that a bird repeatedly encountered (see Discussion). If

patches of prey in stomachs represented aggregations of ephemeral prey on which flycatchers fed opportunistically, one might predict that species with more patchy diets would also have more heterogeneous diets. This prediction was supported by the data (Fig. 5), although certain species (especially CCO) did not fit the relationship (see Discussion).

An important determinant of PDH was the habitat where a flycatcher foraged. I tested the null hypothesis that feeders in (1) the airspace, (2) canopy and open country vegetation, and (3) understory vegetation (Fig. 5) have equal PDH values. With all 16 species, PDH values were heterogeneous ($H = 3.93, P < .1$, Kruskal-Wallis k -sample test), and with the exclusion of CCO (an outlier; see Discussion), the PDH values were highly significantly heterogeneous ($H = 16.27, P < .005$). Thus I reject the null hypothesis and conclude that PDH values are ranked in the order airspace > canopy and open-country > forest-interior species. Two exceptions to the pattern help prove the rule: I classified EV as a forest interior species, even though its high PDH is consistent with (1) its frequent use of hawking behavior in the airspace (Willis 1966a), (2) its prey types, which align it with hawks (Fig. 1), and (3) its migratory status (see below). Similarly, MS is an understory species whose PDH and diet breadth appear to be elevated by the habit of following mixed-species bird flocks, as discussed below.

Diet breadth appears to account for a substantial amount of the variation in PDH (Fig. 6). However, certain species do not fit the relationship closely. Stomachs of CB contained clumped prey similar to those of

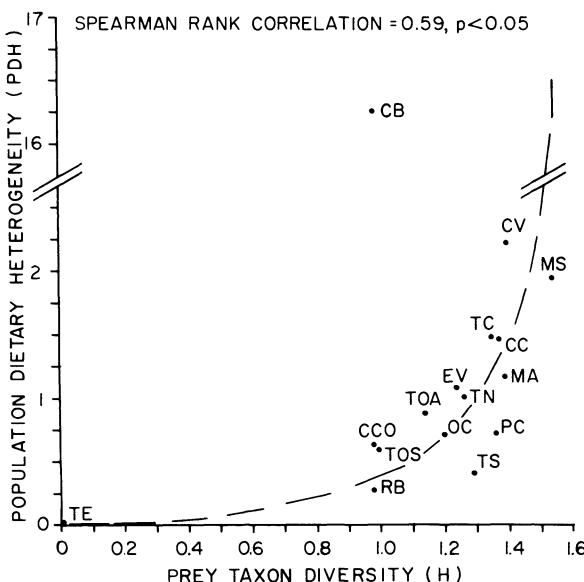


FIG. 6. The relationship between population dietary heterogeneity (PDH) and prey-type diversity (used to approximate diet breadth) of 16 insectivorous flycatchers inhabiting the Caribbean lowlands, Costa Rica. (Curve drawn by eye.)

CCO (Table 5; Figs. 1 and 4), yet different CB individuals appear to have fed on different types of clumped prey. The large number of prey individuals per clump may help account for the low diet diversity, and the different prey types for the high heterogeneity among CB stomachs (Fig. 6). Another exception to the relationship between PDH and prey-type diversity was the tendency for PC and TS to have broad yet homogeneous diets (Fig. 6); thus each individual in these two species tended to eat the same broad array of arthropods as every other individual.

Migratory birds are opportunistic insofar as they exploit seasonally abundant, often ephemeral resources during the breeding period (see Discussion). Homogeneous diets are expected of species exploiting an environment opportunistically; thus one might expect migrants to have higher PDH's, even while residing in the tropics, than year-round residents. The null hypothesis that migrant and resident species had equal mean PDH was rejected ($P < .05$, Mann-Whitney U test). Based on very small sample sizes, diets of two other Sarapiquí flycatchers not included in the above analyses tentatively support the hypothesis that migrants feed more opportunistically than syntopic year-round residents. Two stomachs of the migratory *Empidonax flaviventris* contained very heterogeneous prey taxa (PDH = 4.71), whereas two stomachs of the resident *Aphanotriccus capitalis* (which forages much like the migratory *Empidonax* spp. and occupies similar habitats; Slud 1964) were much more homogeneous (PDH = 0.85; T. W. Sherry, personal observation). The migrant-resident difference in PDH did not result en-

tirely from the tendency for migrant flycatchers to winter in more open or disturbed habitats than residents (Fitzpatrick 1980b, but cf. Hespenheide 1980): In most cases year-round residents that foraged similarly in the same habitats had more homogeneous diets. For example, *Aphanotriccus capitalis* had a lower PDH than *Empidonax flaviventris*, certainly lower than EV; and both CCO and CC had lower PDH than CV and CB (Fig. 5).

No other dietary differences between residents and migrants were noted. In particular, some residents specialized dietarily more, and others less than migrants (Fig. 6).

Number of prey items per stomach

The number of prey items per stomach illustrates additional ways that diets can differ between species. Three species-pairs clustered closely on the basis of prey types but had different mean numbers of prey items per stomach (Figs. 1 and 6): TN vs. TC (Student's t statistic = 3.33, $P < .05$), OC vs. TS ($t = 1.89$, $.10 > P > .05$), and CC vs. CV ($t = 3.67$, $P < .01$). The similarity of prey taxa within these species-pairs reduces the probability that differential digestion rates of arthropod taxa can account for the different mean numbers of items per stomach. Two of the most obvious alternative hypotheses (different prey sizes or energy contents, and different energy demand on the birds) are discussed below. The consistently few items found in TE stomachs was striking (Fig. 7), and also has more than one possible explanation (see Discussion).

The mean number of items per stomach was positively, but not significantly, correlated with the loga-

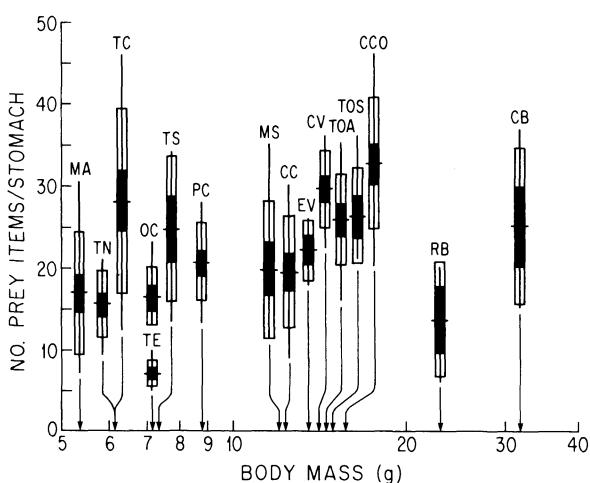


FIG. 7. Number of items per stomach of 16 insectivorous flycatchers inhabiting the Caribbean lowlands, Costa Rica. For each species, the mean number of items, 1 SE (solid bar), 1 SD (open bar), and range are indicated. Note logarithmic axis for flycatcher body mass.

rithm of flycatcher body mass (Fig. 7; $r = .33$, $P > .05$), and positively correlated with patchiness of the prey morphospecies (Spearman rank correlation = 0.56, $P < .05$; patchiness is shown in Fig. 5).

DISCUSSION

Before discussing species dietary similarities and differences, one should ask how representative the prey data are for a species. The number of stomachs needed to represent the diet of a population depends (at least) on the number of items per stomach, the diversity of prey types, and the heterogeneity of stomach samples from different individuals of a population. All these parameters varied among the species studied (Figs. 3–6). For the degree of resolution in prey types achieved here, one or two stomachs represented the range of prey types eaten by TE and CCO, whereas more than 9–10 stomachs would be needed to record the full diversity of prey types that TN and MA eat (Fig. 3). The homogeneity of TE diets was surprising because stomachs with few items should provide poor statistical estimates of a larger population (available prey) from which the items were taken.

Unfortunately, few data exist with which to examine how representative the Sarapiqui diets are for a species. The predictable (Sarapiqui) specialization by TE on Homoptera, exemplified by nine stomachs collected in a variety of locations over several months in different years, is corroborated by stomachs from the Osa Peninsula, on the Pacific coast of Costa Rica (H. A. Hespenheide, personal communication); from Brazil (Schubart et al. 1965); and from Surinam (Haverschmidt 1968), all of which contained only Homoptera. Similarly, fragmentary evidence suggests that Diptera constitute a dietary common denominator in the genus *Todirostrum*. Both TN and TC ate many Diptera and TS ate some (see six taxa under Diptera in Appendix). Haverschmidt (1968) lists Diptera in the diet of every species of *Todirostrum* he examined: TC, *T. chrysocrotaphum*, *T. maculatum*, and *T. fumifrons*. Moreover, two Neotropical Tyrannidae (TC and *Nesotriccus ridgwayi*) for which I had stomach samples from breeding and nonbreeding periods fed on similar prey in these two seasons (Sherry, *in press*). I tentatively conclude that diets of the resident flycatcher populations studied are representative for the species, at least with respect to broad prey taxa eaten, but more data are needed to resolve this issue.

How and why do species differ in their diets?

Prey type.—Do sympatric flycatcher species consistently eat different prey taxa? Three kinds of evidence strongly affirm that this is so, even within genera (e.g., *Todirostrum* and *Contopus*): (1) marked differences in the prey taxa comprising pooled samples by species (Tables 2–4, Fig. 1, and Appendix), (2) considerable homogeneity in the diets of many species (Figs. 3 and 4) whose prey taxa differ, and (3) strong relationships

TABLE 6. "Food resource" of 16 species of insectivorous, Neotropical flycatchers inhabiting humid, lowland Costa Rican habitats. The food resource identifies the lowest common denominator of prey characteristics (e.g., prey type, diversity, heterogeneity, and degree of clumping) as reflected by stomach contents. See Discussion for hypotheses to explain why the birds recognize such prey types as a resource.

| Species | Food resource |
|----------|---|
| CC, CV | A variety of aggregated, probably ephemeral flying prey (including many social Hymenoptera) |
| CB | Mostly aggregated, probably ephemeral social Hymenoptera (ants and bees) |
| CCO | Predictable patches of flying stingless bees, <i>Trigona</i> species, perhaps near bee nests |
| TE | Mostly fulgoroid, and some cercopoid, Homoptera that jump to evade vertebrate predators |
| MS | A wide variety of active insects, many of which were fleeing from members of mixed-species bird flocks |
| MA | Cryptic, relatively immobile and homogeneously distributed arthropods and some Homoptera (primarily Membracidae) |
| TS | Cryptic, relatively immobile and homogeneously distributed arthropods |
| TC | Many insects including relatively evasive Diptera and parasitoid wasps, perhaps at extrafloral nectaries |
| TN | Many insects including evasive Diptera and some parasitoid Hymenoptera, perhaps around flowering trees |
| OC | Cryptic, relatively immobile arthropods |
| RB | Almost any arthropods within vegetation, except relatively small and/or more evasive Diptera and parasitoid Hymenoptera |
| PC | Cryptic, relatively immobile, and homogeneously distributed arthropods, and some jumping Homoptera |
| TOA, TOS | Relatively active, conspicuous, or easily catchable prey, perhaps in productive vegetation zones |
| EV | A variety of active, probably ephemeral prey |

of the diet to both foraging behavior and morphology (Sherry 1982; see also references in Introduction). Specialization on different prey taxa is not unusual for vertebrate carnivores (e.g., Hespenheide 1975b, Herrera and Hiraldo 1976, Toft 1980, Jaksic et al. 1981, Robinson and Holmes 1982, Findley and Black 1983), although some authors have emphasized the taxonomic overlap of prey eaten by such predators (Wiens and Rotenberry 1979, Rotenberry 1980, Fenton 1982, Humphrey et al. 1983).

Factor analysis in the present study helped identify the nature of flycatcher specializations. Identification of four significant independent "factors" (Table 2) indicates that certain prey taxa were intercorrelated because they tended to be found together in the diet of particular flycatcher species. The distribution, behavior, and other characteristics of prey taxa similarly loaded on each factor in combination with flycatcher behavior suggest how different flycatchers find, capture, or handle different prey.

Factor 1 distinguishes prey that hide within vegetation from those that are conspicuous flying outside of vegetation. Four flycatchers with the highest scores on this factor (MA, TS, OC, and PC, Table 3) are all small-bodied (5.3–8.8 g) upward-strikers (Table 1) that typically forage within vegetation (Fitzpatrick 1978; T. W. Sherry, *personal observation*). Their diets include many Arachnida, Lepidoptera larvae, cercopoid Homoptera, and Orthoptera. Most of these taxa co-occur in stomachs of “foliage-gleaners,” birds that search for and glean prey without sallying in vegetation (H. A. Hespenheide 1975a, and *personal communication*). Many more arthropods dwell on lower than on upper leaf surfaces in tropical forests (Greenberg and Gradwohl 1980), and Orians (1969) suggested that large understory leaves in lowland tropical forests help account for the many species of upward-strikers (“hover-gleaners” in Orians’ terminology), a distinctively tropical component of the avifauna. Arthropods on the centers of large leaves or on leaves without nearby twigs or petioles for support would be more accessible to small upward-striking flycatchers, which could leap against the foliage, than to birds confined to prey reachable only on foot (Croxall 1977). Robinson and Holmes (1982) have suggested that this is why the understory Black-throated Blue warbler (*Dendroica caerulea*, Parulidae) hovers more than congeners in north-temperate deciduous forests in New Hampshire. It thus appears that a group of small-bodied, upward-striking tropical flycatchers searches in vegetation for arthropods that are relatively inaccessible to nonsallying foliage-gleaners.

A second group of species (CB, CC, CV, CCO) with negative scores on factor 1 comprises larger bodied hawking species in open spaces (generally pastures, marshes, or above the canopy; see Tables 1 and 3). These latter species have relatively long attack distances and long intervals between successive attacks compared with other insectivorous flycatchers (Sherry 1982). Giving-up time for a perch is relatively long for hawking flycatchers, and the probability of returning to the same perch is consequently relatively high, because of the large areas scanned for prey (indicated by long attack distances), because of high renewal rates of flying prey (Davies 1977, Fitzpatrick 1981, and Sherry 1982), or because of a restricted number of good perches (Verbeek 1975). The prey types eaten by hawks (flying Formicidae, Apoidea, and Odonata; see Tables 2, 3, and Appendix) are large and conspicuous when flying outside of vegetation. Social Hymenoptera (Formicidae and Apoidea) when foraging or dispersing in flight are likely to be particularly renewable, if not concentrated, prey from the birds’ perspective. Other birds that hawk aerial prey often consume social Hymenoptera (Fry 1970, Herrera and Ramirez 1974, Burton 1976). Therefore, I suggest that social Hymenoptera provide a resource without which many hawking birds could not persist. Some hawking birds persist without

social Hymenoptera (e.g., Pauraques [*Nyctidromus albicollis*, Caprimulgidae] feeding largely on Coleoptera; H. A. Hespenheide, *personal communication*); and other birds than hawks feed on social Hymenoptera (e.g., swifts and swallows which can fly long distances in search of ephemeral reproductive swarms or other aggregations of Hymenoptera; Hespenheide 1975b).

The second factor distinguishes two behaviorally different groups of flycatchers. Two upward-striking congeners that forage in canopy vegetation (TOA and TOS) have positive scores on factor 2, whereas two pursuers in rainforest understory (TE and MS) have negative factor scores (Table 3). Hemiptera, Coleoptera, and worker Formicidae, all positively loaded on factor 2 (Table 2) are often hard-bodied and conspicuous. More importantly, they are not as quick to jump or fly from the vegetation as Diptera or Homoptera. Even sluggish upward-strikers should have little trouble capturing such prey as Coleoptera, especially the Curculionidae prominent in *Tolmomyias* spp. diets (Appendix). The typical beetle response of dropping from the site of disturbance (T. W. Sherry, *personal observation*) puts the prey in an upward-striker’s mouth. The abundance of both Coleoptera and Hemiptera in productive zones of vegetation (Janzen 1973), e.g., the canopy where TOA and TOS forage, could also explain the association of these two prey taxa in flycatcher stomachs. Another flat-billed flycatcher (*Aphanotriccus capitalis*, 10.8 g mass) occurs locally in the foothills and lowlands of the Caribbean side of northeastern Costa Rica (Slud 1964); it occupies very productive, seasonally flooded, riparian habitat in the Sarapiqui lowlands, where it eats Hemiptera, Coleoptera, and Formicidae (8.5, 78.7, and 6%, respectively, of 47 prey items identified from two stomachs; T. W. Sherry, *personal observation*).

Fulgoroid and cercopoid Homoptera, which are negatively loaded on factor 2 (Table 2), readily leap up to 1 m from the substrate before flying erratically away from a disturbance (T. W. Sherry, *personal observation*). Such Homoptera behavior, which likely evolved to protect them from vertebrate predators, could explain why most flycatchers (especially TOA and TOS) do not eat these insects. By contrast, flycatchers such as TE exploit the predictable “defensive” behavior of Homoptera by pursuing them acrobatically through vegetation, often after flushing them into flight (Robinson and Holmes 1982, Sherry 1982). Greater insect mass could increase the effectiveness with which Homoptera evade many predators because the potentially greater momentum during a jump would propel the insect a greater distance before air resistance (drag) slowed the insect to a velocity at which the insect became vulnerable. Large prey size relative to predator size and/or vulnerability when prey velocity decreases after the jump are possible reasons why a predator such as TE might recognize Homoptera as a food resource.

Diptera and parasitoid Hymenoptera distinguish TC and TN diets from those of other species (compare

Tables 2 and 3). I interpret the diet of these species in the context of a variety of peculiar morphological and behavioral traits (Sherry 1982). These flycatchers surprise-attack prey whose agility and wariness elude flycatchers with a slower rate of acceleration from takeoff. An alternative explanation for the association of particular prey types in *Todirostrum* diets is that particular ecological factors concentrate these prey taxa. Specifically, Diptera, parasitoid wasps, and nonflying (worker) ants around extrafloral nectaries of such plants as *Bytneria*, *Sterculiaceae* (Hespenheide 1983a, and T. W. Sherry, *personal observation*), could be associated in diets of individual TC that foraged near these nectaries. More than other Sarapiqui flycatchers, TN forages for prolonged periods in flowering trees (e.g., *Inga*; T. W. Sherry, *personal observation*). Many of the arthropods which TN does catch (Diptera such as muscoid flies and Syrphidae, Lepidoptera adults, and Apoidea) are often abundant in flowering trees (Fogden 1972). These two hypotheses for the association of particular arthropod taxa in the gut—how vs. where the birds forage—are not mutually exclusive. TN and TC could forage in flowering trees or near extrafloral nectaries because such birds effectively capture arthropods attracted to these sites. Hespenheide (1975b) suggests that swifts may also be attracted to the insects around flowering trees. If flowering trees or plants with extrafloral nectaries are important feeding sites to any Sarapiqui flycatchers, then plant species could be an important habitat parameter (Holmes and Robinson 1981).

Factor 4 was the most ambiguous of all four significant ones, and there may be no one ecological basis for this factor. Several of the taxa with significant loadings on this factor (Dermaptera, Lepidoptera adults, and Orthoptera; Table 2) often hide diurnally on bark and tree trunks (T. W. Sherry, *personal observation*), suggesting that substrate may be important to these flycatchers. Alternatively, several of the flycatchers with highest scores on factor 4 (particularly EV, CV, and MS) often feed in or near tree-fall gaps (T. W. Sherry, *personal observation*). These gaps could attract some birds (see also Schemske and Brokaw 1981) because rapid vegetation regrowth attracts arthropods (Janzen 1973), because the fallen tree itself concentrates insects (Hespenheide 1983b), or because solitary ants (or other agents) cause bark-inhabiting insects to become conspicuous.

Number of items per stomach.—Differences in prey size and aggregation, amount of digestible tissue per prey body mass, digestion rates and thus persistence times of different taxa in the gut, and energetic (or nutrient) demand by the birds could all help explain variability in number of prey items per stomach in the flycatchers studied. Without quantifying all these variables simultaneously it is difficult to make definitive statements, yet several cases merit discussion. (1) Among the small-bodied upward strikers, TC relative

to TN, and TS relative to OC had more items per stomach, on average (Fig. 7). Since prey types were similar within these two species-pairs (Fig. 1) and since the species all have similar molt and reproductive seasons (thus energy demands), I hypothesize that either prey size or energetic value per prey items is greater in TN relative to TC and in OC relative to TS. Such a difference parallels differences in these species in foraging behavior and morphology (Sherry 1982). (2) CV and CC eat many of the same prey types (Fig. 1), yet the former has significantly more items per stomach than the latter (Fig. 7). This difference could arise from the need for CV individuals to re-fuel, by feeding more actively, just after a migratory flight from the breeding grounds. Alternatively, CV and CC could eat different-sized prey. (3) The consistently low number of items per stomach in TE (Fig. 7) could result from short persistence times of Homoptera in the gut. This explanation is unlikely since Homoptera parts persist in the stomachs of other species such as MA and TS (Appendix). TE, furthermore, consumes large insects for its size (e.g., Nogodinidae and Dictyopharidae), and its acrobatic pursuit flights could be costly enough energetically to require rewarding prey. The hypothesis that TE eats relatively few, energetically rewarding, prey per unit time suggests that its frequent “attack” flights (Sherry 1982) are instead attempts to flush prospective prey into the airspace where TE could more readily catch them (Sherry 1983b; see also Robinson and Holmes 1982).

The range of body sizes (5.3–31.6 g; Table 1) and the different numbers of items per stomach, even in congeners (Fig. 7), tempt one to conclude that food size differences are important for ecological segregation, but such a conclusion is premature. For example, prey size differences could result from selection of different prey taxa whose mean size differs (Hespenheide 1975a, b). The flycatchers studied here select different prey taxa, as discussed above.

Schoener (1968) predicted that heavier predators will take fewer food items per unit time than lighter predators. If the items eaten by flycatchers are a prey sample captured over comparable time periods, then stomach content data are appropriate to test his hypothesis. The surprising absence of a negative relationship between body mass and number of items per stomach (Fig. 7, Results) has several possible explanations, of which I mention one that is testable with available data. This positive correlation is an artifact of the positive correlation between body mass and a confounding variable, namely dietary patchiness (Spearman rank correlation = 0.41, $P < .05$). A spatially patchy prey distribution (e.g., with swarming social Hymenoptera) could maintain feeding profitability even if each prey item were small and/or energetically poor, because wait intervals and attack distances would be relatively short (Davies 1977). The significant correlation between dietary patchiness and number of items per stomach in

these species (Spearman rank correlation = 0.56, Results) suggests that "patch-feeders" ate more, smaller prey per unit time than "item-feeders," just as Schlüter (1982) has observed in Darwin's Finches feeding on seeds. Similarly, swifts (Hespenheide 1975b) and occasionally Eleonora's Falcons (Walter 1979:146–149) eat large numbers of small but aggregated arthropods. The dietary diversity of tropical flycatchers, particularly with respect to dietary patchiness, causes difficulty in tests of Schoener's (1968) hypothesis.

Diet breadth.—A variety of models based on short-term diet optimization have predicted that organisms should broaden their diets during periods of food scarcity and narrow them, using the most rewarding food, when food is abundant (review in Pyke et al. 1977). This prediction of optimal diet theory could explain generalized diets of several rainforest upward-strikers (PC, EV, and RB) which search vegetation. Chronically low arthropod abundance within the rainforest interior (Elton 1973, Janzen 1973) may require broad diets for some birds to persist there. An aspect of flycatcher diets that seems inexplicable from diet optimization models is the range of diet breadths of flycatchers that forage similarly in the same habitat. I discuss two examples.

1) The specialization on Homoptera by TE (94% of its diet, 71% fulgoroid Homoptera; Fig. 3; Appendix) is remarkable because insectivorous birds tend to have generalized diets (e.g., Fogden 1972, Janzen 1973, Beaver and Baldwin 1975). Optimal diet theory as currently developed is most suited to explain diet changes in ecological time. The fact that dietary specialization by TE is correlated with morphological and behavioral characteristics (Sherry 1982, 1983b) suggests that evolutionary factors constrain its diet more than ecological ones.

What combination of factors have favored the specialization by TE, over evolutionary time, on a diet of Homoptera? Dependability of a food source should be a necessary but not sufficient condition for dietary specialization. I hypothesize that understory Homoptera have been predictable both seasonally and over many TE generations for TE to have evolved a reliance on them. A corollary of this hypothesis is testable; namely, that TE is currently limited in distribution to where Homoptera (Fulgoroidea in particular) occur predictably. The few available data suggest that this corollary does not hold: TE occurs on Barro Colorado Island (BCI), Panama, where Homoptera undergo marked population changes seasonally (Wolda 1977, 1978). It is possible, however, that Homoptera on BCI exceed a critical threshold abundance from the perspective of TE throughout the annual cycle.

Both TE and MS upward-strike and hawk within undergrowth of rainforest and second-growth vegetation (Table 1) in the humid lowlands of Costa Rica (Slud 1964). Fitzpatrick (1978) characterizes MS as a "behaviorally aberrant" tyrannid which forages much like *Setopaga* and *Myioborus* (both Parulidae; see

"flush-and-chase" category of Robinson and Holmes [1982]), and TE forages much like MS (Sherry 1982, 1983b). Despite their behavioral and morphological similarity (Sherry 1982), TE and MS had the extreme narrow and broad diets, respectively, of all species studied (Fig. 3). Both species consumed several individuals of a cercopid homopteran species; yet in addition to Homoptera, MS consumed Odonata, Orthoptera, Dermaptera, Coleoptera, adult Lepidoptera, Diptera, Hymenoptera, and Arachnida (Appendix).

Nearly obligatory occurrence of MS with mixed-species antwren and other bird flocks in Sarapiquí rainforests (T. W. Sherry, *personal observation*; see also Skutch 1960, Slud 1964, Willis 1972) suggests a simple hypothesis for its catholic and heterogeneous (see below) diet. Such flocks might constitute a "feeding opportunity" because MS can pursue and capture within understory vegetation the arthropods fleeing other flock members. (For other examples and a discussion of the phenomenon see Charnov et al. 1976, Morse 1977a.) Flock species searching with different techniques on different substrates (Wiley 1971, Jones 1978) would flush diverse insect taxa to account for the range of arthropods eaten by MS. The high loading of MS on factor 4 (Table 3), tentatively identified as a branch and trunk substrate factor, appears to result from those flock members that forage on such substrates (e.g., Jones 1978). Other *Myioibius* species than MS systematically follow mixed-species bird flocks (Fitzpatrick, *personal communication*, and T. W. Sherry, *personal observation*). To the extent that *Myioibius* depends on such flocks to provide a foraging opportunity, the genus is specialized in feeding behavior, even though the range of insect taxa eaten can be broad as illustrated by MS.

2) Two *Contopus* hawks (CV and CC) substantially overlap CCO with respect to foraging behavior, habitat, and stratum (Table 1). The *Contopus* species have a greater diet breadth than CCO (Fig. 3), and this diet-breadth difference probably contributes to the diet difference (Fig. 1), even though all three species eat many social Hymenoptera (Formicidae and Apoidea, Appendix).

The narrow, patchy (yet homogeneous) diet of CCO (Appendix; Figs. 3, 5, and 6; Table 5) suggests that CCO responds to a very different aspect of insect prey than do the other hawking flycatchers. All bees eaten by CCO (67% of its diet) were stingless bees in the genus *Trigona* (including *T. amalthea* Olivier, *T. fulviventris* Guerin, and *T. fuscipennis* Friese), and each CCO stomach contained on average 2.9 *Trigona* species (range 2–4 species) (R. Snelling, *personal communication*). One hypothesis for the narrow, homogeneous (yet patchy) diet of CCO compared with *Contopus* species is that CCO somehow recognizes stingless bees and bee-like insects randomly flying past a perch, and ignores other insects. I prefer a simpler hypothesis; namely, CCO may preferentially forage near *Trigona* nests. In support of this hypothesis, I observed CCO

forage frequently from atop dead trees (where *Trigona* often nests) and rarely near flowering trees. At least two of the *Trigona* species eaten (*amalthea* and *fuscipectoralis*) often nest well above ground (Schwarz 1948). Furthermore, *Trigona* colonies are abundant enough, especially in parts of the humid tropics (Schwarz 1948), that an individual CCO could encounter several colonies in a small area, to account for the fact that each CCO stomach contained several *Trigona* species. If CCO individuals forage preferentially near concentrations of *Trigona* nests (and it should not be difficult for a year-round resident to learn the locations of such nests within its home range), then CCO forages on patchy prey whose patch density is high enough to provide a reliable food resource. The *Contopus* species studied (CB, CC, and CV) appear to feed like CCO on patchy prey (Table 5), but on prey whose patches are much less predictable from the perspective of a bird.

Dietary specialization by tropical flycatchers such as TE and CCO delineates interesting, unresolved issues. To what extent if any have these specialists lost the flexibility to use other prey taxa? Is diffuse coevolution (see Janzen 1980) operating in these predator-prey systems? Do relatively constant climatic conditions such as occur in some tropical habitats allow more extreme or more frequent dietary specializations? Do such environments necessitate such specializations?

Diet patchiness.—Relatively high patchiness indices need not indicate feeding on truly aggregated prey. This issue is best investigated by examination of types and behavior of prey eaten by flycatcher species with greatest dietary patchiness. The task is relatively simple for hawking flycatchers. One stomach of CB, the species with greatest mean patch size (Table 5), contained 31 identical *Odontomachus* (Formicidae) queens. This reproductive swarm was almost certainly a "patch" in both space and time. Another CB stomach contained 19 and 6 individuals of two bee species out of 28 prey items. A stomach of CV contained 5 bees of one species, 5 ant queens (4 of one species, 1 of another), and 8 eucharitid wasps (parasitoids of ants which often aggregate near reproductive swarms of their hosts; T. W. Sherry, personal observation). Almost all stomachs of CC contained numerous bees or winged ants. Since reproductive (winged) ants and bees are often localized around a nest or flowering tree, respectively, I conclude that these *Contopus* species often fed on truly patchy prey. The discussion of CCO above suggests that it locates real aggregations of *Trigona* bees.

The two open-country upward-strikers with greatest dietary patchiness (TC and TOS; Fig. 5) consumed a variety of prey that were probably patchy in space and time. The larger patches in stomachs of TC (\geq three individuals per morphospecies in a stomach) were Formicidae, parasitoid Hymenoptera (Chalcididae, Eucharitidae, and Braconidae), Diptera, and Homoptera (Membracidae). Clumps of worker ants in TOS stomachs may have resulted from feeding near ant nests.

Other relatively large clumps of TOS were Hemiptera (Largidae, coreid nymphs) and Coleoptera (halcine Chrysomelidae).

Dead wood attracts wood-boring insects which may have increased patchiness and PDH in some flycatcher species. Stomachs of CV often contained wood-boring beetles: 8 platypodids and 5 scolytids (of 36 items) in one stomach; 5 platypodids, 3 cerambycids, 2 ostomatisids, and 1 scolytid (of 36 items) in another stomach; and 15 platypodids and 1 scolytid (of 35 items) in a third stomach. Stomachs of TOA contained cerambycid, erotylid, anthribid, and buprestid beetles, and weevils (Curculionidae: Zygopinae, Rhynchophorinae, Cryptorrhynchinae, Baridinae, and Ceutorhynchinae). All of these taxa except Ceutorhynchinae are attracted to dead wood (H. A. Hespenheide, personal communication). Thus, while TOA travels with mixed-species flocks of birds in forest canopy (T. W. Sherry, personal observation), it may seek patches of standing dead wood, but unlike MS, TOA does not appear to feed on insects flushed by flock members. A stomach of TC, collected in June (thus not included in analyses above) in an area where trees had been felled preparatory to planting, contained 34 platypodid beetles (four species) out of 52 total prey individuals (T. W. Sherry, personal observation).

Thus patchiness in stomachs of most hawks and of open-country upward-strikers (especially TC and TOS) probably resulted from feeding on arthropods that were actually aggregated in space and time. I conclude that the flycatchers under study vary greatly on a continuum from item feeders to patch feeders. Although most patch feeders appear to exploit unpredictable prey patches opportunistically (as suggested by high PDH), the extreme patch feeder (CCO) specializes on what appear to be predictable patches of stingless bees. The degree to which prey are patchy profoundly affects foraging behavior and prey selection. Among other things, patchily distributed prey can cause birds to (1) return to the same perch after a foraging sally (Davies 1977, Fitzpatrick 1981) (2) search intensively for food in a restricted area (Baker and Baker 1973, Smith 1974, Pyke et al. 1977, Zach and Falls 1979), (3) make successive prey-capture attempts during a foraging flight (Burton 1976, Fitzpatrick 1981), and (4) feed on apparently smaller, less rewarding prey (see above).

Diet heterogeneity.—Heterogeneous diets within a local population may result from at least three alternative circumstances.

- 1) According to the "niche-variation" hypothesis (Van Valen 1965) phenotypic variation that leads to ecological (e.g., dietary) variation could be selectively advantageous within populations exploiting diverse resources (e.g., on an island relatively free of competitors). My data were not collected in such a way as to evaluate this hypothesis quantitatively. Individual stomachs usually contained some fraction of prey types

that a population used (Fig. 3). In no case could I be sure an individual could not, given more time, consume the entire range of prey types consumed by the local population. Recent discussion of the niche-variation hypothesis based on the ratio of the average number of prey taxa per individual stomach to the total number of prey taxa in all stomachs of the species (Wiens and Rotenberry 1979) is inappropriate, since the former is potentially a function of digestion and feeding rates, neither of which has any obvious relationship to phenotypic variation, and the latter is a function of sample size (Fig. 3).

2) By means of early experience or other learning processes, individuals may become canalized into some subset of the feeding behaviors exhibited by the entire population (e.g., Rabinowitch 1969). This process might occur in plastic species whose total range of available behaviors exceeds what an average individual could master effectively. Majoring in bumblebees (Heinrich 1976, 1979), individual feeding specializations in trout (Bryan and Larkin 1972), and individual feeding specializations in Cocos Island Finches (*Pinaroloxias inornata*; T. K. Werner and T. W. Sherry, *personal observations*) are possible examples of the phenomenon. I have not observed such persistent individual behavioral specializations in any flycatchers studied here, but neither have I ruled out the possibility that they occur. These flycatchers tended (with the exception of TC and MS; T. W. Sherry, *personal observations*) to be stereotyped in feeding behavior.

3) The best documented cause of heterogeneous diets is opportunistic foraging on ephemeral prey. Heterogeneity in stomach contents accordingly reflects the heterogeneity in arthropod distributions from hour to hour, day to day, habitat to habitat, and year to year. American Redstarts (*Setophaga ruticilla*, Parulidae), for example, track diurnal changes in insect abundance and activity, and at any one time of day, individual foraging differences, and thus diets, by inference, reflect habitat and food-resource patchiness (Holmes et al. 1978). The temporary diet similarity between species, and seasonal changes within species of a community are interpreted as opportunistic responses to patchy and unpredictable food resources in bats (Fenton and Morris 1976, Fenton et al. 1977, Bell 1980, Fenton and Thomas 1980), and in grassland and shrubsteppe birds (Wiens and Rotenberry 1979, Rotenberry 1980). That birds in seasonal and unpredictable habitats should have less dietary specialization than those in more climatically stable habitats (Stiles 1978, Wiens and Rotenberry 1979) is not surprising.

I propose that heterogeneity in insect availability where tropical insectivorous flycatchers forage (hypothesis 3) accounts for much of the observed variation in PDH. In the humid lowland tropics, understory and forest interior habitats should be relatively protected from the desiccating effects of sunlight and wind, thus

relatively buffered microclimatically. Seasonally, insects in tropical understory appear to undergo smaller fluctuations in abundance than those in other habitats (Fogden 1972, Smythe 1974). Understory bird communities compared with those in the canopy, moreover, tend to be more dominated by insectivores than by omnivores (Greenberg 1981), and to have correspondingly smaller fluctuations in population abundances (Karr 1976, Greenberg 1981). Similar changes occur with vegetation succession in temperate bird communities (May 1982). I infer from the relative seasonal constancy of understory insects that their distributions are also more spatially homogeneous within a season in interior vegetation compared with less physically buffered vegetation (see Schoener and Janzen 1968, Fogden 1972). This pattern in arthropod distributions, if confirmed, could explain the tendency for understory flycatchers to have low PDH compared with canopy and open-country species (Fig. 5).

Fogden (1972) anticipated this hypothesis in reference to open spaces (in and above vegetation) where hawks feed on flying insects whose numbers often fluctuate greatly. Fogden even anticipated the observation in the present study that forest understory insectivores (e.g., the upward-strikers TS, OC, and especially PC) would have relatively broad, homogeneous diets of cryptic, nonpatchy and immobile groups of prey (Fig. 6, Tables 5 and 6). An extreme diversity and low density of such arthropods typifies lowland tropical forest understory (Elton 1973). Fogden (1972:316) noted that "The low density of insects is partly a direct consequence of the great species diversity, but the dispersion must largely result from the need to make cryptic adaptations as effective as possible . . . crypsis itself will be favoured by scarcity and a widely dispersed distribution."

The range of ecological conditions an organism can tolerate is frequently commensurate with the range experienced in the organism's customary habitat (Janzen 1967). The relatively low PDH values of tropical understory flycatchers (Fig. 4) suggest these species should be more sensitive to changing environmental conditions, especially those which affect food abundance, than species in other tropical habitats. If so, then diets of these insectivores (1) support Karr's (1982) suggestion that ecological inflexibility has contributed to the disproportionate number of extinctions among ground-foraging and understory birds on BCI, Panama, and (2) help explain Mac Arthur's (1972) observation that second-growth and open-country species tend to make good island colonists.

What is the food resource?

To an insectivorous bird, the food resource is that subset of all arthropods that is effectively available because of where, when, and how the organism hunts, captures, and handles prey. In the present study a food

resource comprised from one or a few superfamilies to many orders or even classes of arthropod. Since the food resource did not always correspond with one arthropod taxon (e.g., different ant castes were eaten by different flycatcher species), I asked what prey characteristics or environmental circumstances cause a flycatcher species to recognize some combination of arthropod taxa as a resource. I inferred the nature of these resources for each species primarily from the nature of prey taxa statistically associated in the species' stomachs. Species differences in other dietary parameters (breadth of prey taxa, dietary patchiness, PDH) suggested additional prey characteristics (e.g., an ephemeral distribution) which could be important to the birds.

The food resource of each species (Table 6) resulted from diverse factors: (1) predictable antipredator behavior of Homoptera (TE); (2) predictable, probably patchy, distribution of stingless bees (CCO); (3) disturbance of concealed arthropods by foraging antwren flock members (MS); and (4) sparse but homogeneous distribution of relatively cryptic, immobile arthropods in thick or shaded vegetation (PC, TS, and OC). Other flycatchers (e.g., CB, CV, CC, and EV) appeared to feed opportunistically (see below) on patchy, unpredictable prey such that no single prey characteristic (except aggregated, probably ephemeral distribution) stood out. Thus these flycatchers responded to a variety of arthropod characteristics: spatial distribution, predictability, conspicuousness, antipredator adaptations, substrate (airspace, vegetation, bark surfaces), and source of concentration (e.g., antwren flocks, extrafloral nectaries, flowering trees, or productive vegetative zones).

Identification of the food resource of each species serves several purposes. An hypothesis implicit in Table 6, i.e., that the food resource is a species-specific characteristic in these tropical flycatchers, generates testable predictions. For example, their intraspecific dietary variation across seasons, habitats, and geographic ranges should be less than interspecific variation within the assemblage. Moreover, testable predictions about the distribution, behavior, and other characteristics of the prey are implicit in the description of the food resource (see Table 6). When predators have evolved dependence on a particular prey taxon (such as may be the case with CCO on *Trigona* bees, or TE on fulgoroid Homoptera), then knowledge of prey distribution and seasonality will help predict predator distribution. The nature of the food resource is allied to how a species exploits that resource, and each should help interpret the other. For example, the observation that *Todirostrum* species eat more Diptera than sympatric tyrannids focuses attention on how a flycatcher can be morphologically adapted to capture such prey (Sherry 1982). The nature of the food resource suggests potential ecological and evolutionary

processes structuring communities (see below). Finally, the nature of the food resource could predict other aspects of demography and of life history. Species whose food resource suggests an opportunistic exploitation pattern, for example, should have relatively high recruitment rates and relative tolerance to unpredictable ecological circumstances. The relationship between demography and ecology could be studied fruitfully in a genus such as *Todirostrum*, whose many species vary with respect to geographic distribution and nesting behavior (Fitzpatrick 1976, Sherry 1982, 1983a), not to mention diet (Tables 3 and 6, Figs. 5 and 7).

Dietary characteristics of the tropical flycatchers discussed here appear in many cases to be phylogenetically constrained, whether because of behavioral or morphological limitations. I hypothesize that such constraints cause the major part of the dietary variation observed in these birds. Within the range of prey types and habitats a species can use, however, ecological models concerning optimal diet and patch selection have considerable potential to explain dietary variation. Many authors have already applied such models to the study of how animals feed on patchy prey (see references cited under Diet patchiness, above), and PDH is another dietary parameter for which optimal foraging models may be particularly applicable.

Opportunism

Are all species opportunists?—Some contemporary ecologists maintain that because resources are patchy in space and unpredictable in time, consumers rarely outcompete each other, but rather exploit resources opportunistically, each species doing so independently of every other one (see Introduction). If one defines an opportunistic diet as a broad one (Rotenberry 1980), then clearly tropical flycatchers are not equally opportunistic (Fig. 3). The occurrence of broad yet homogeneous diets (PC and TS; Fig. 6) in physically buffered, humid tropical habitats suggests that diet breadth is not a sufficient condition for opportunism. More realistically, opportunistic insectivores may be characterized by their rapid discovery and exploitation of ephemeral prey (Fenton and Morris 1976, Fenton et al. 1977, Bell 1980). Many tropical insectivorous flycatchers studied here were clearly not opportunistic by this definition since many species had homogeneous diets (Fig. 3). Hawking species, especially *Contopus* spp., had heterogeneous diets (though not necessarily broad ones; Fig. 6), and fed on clumped arthropods such as Hymenoptera (see above) whose distribution must be ephemeral at least on some spatial scales. Opportunistic feeding may account for the high PDH of MS, an anomaly (Fig. 5, and above), and Fitzpatrick (1981) describes opportunistic feeding in other tropical flycatchers.

Physical conditions that influence arthropod abundance may vary spatially and seasonally, often unpre-

dictably, in highly seasonal habitats (e.g., many temperate, arctic, and xeric regions). The opportunism of insectivores in these climates likely reflects the ephemeral nature of the prey (Wiens and Robenberry 1979, Bell 1980, Fenton and Thomas 1980, Rotenberry 1980). Even in these habitats, however, species are differentially opportunistic: The Grasshopper Sparrow (*Ammodramus savanarum*, Emberizidae), for example, has more dietary homogeneity and less diet breadth than sympatric breeding grassland species (Wiens and Rotenberry 1979). In the present study several hawks (CB, CV, CC) compared with CCO, TC compared with its congeners, and MS compared with TE, had less homogeneous, in some cases broader, diets suggesting a more opportunistic feeding style, despite superficial similarities in foraging behavior and habitats exploited. Differences in diet breadth, habitat range, and foraging plasticity appear to be critical components of ecological interactions between two migratory "flycatchers" (Sherry 1979). Detailed dietary and behavioral study has shown that differentially opportunistic species exploit many of the same resources at the same time among shorebirds (Holmes and Pitelka 1968), spruce-woods warblers (Mac Arthur 1958, Morse 1971a, 1977b, Rabenold 1978), blackbirds (Orians and Horn 1969), army-ant-following bird flocks (Willis 1966b, 1967, 1972, Willis and Oniki 1972), tropical hummingbirds (Colwell 1973, Feinsinger 1976, Wolf et al. 1976), migratory sylviid warblers (Laursen 1978), and temperate wintering flocks (Morse 1970).

Although sympatric species, both tropical and temperate, appear to rely differentially on particular foods, the tropical insectivores studied here appear to differ as a group from species that live in more seasonally variable climates. Temperate grassland birds, for example, have diets that overlap highly in any one season and change dramatically from season to season (e.g., Rotenberry 1980). Prey taxa of some tropical flycatchers, by contrast, change insufficiently seasonally to obscure a predator-specific identity (Sherry, *in press*).

Opportunism and migration.—The three migratory flycatcher species studied here help to establish the link between heterogeneous diets and an opportunistic food-exploitation pattern. Migrant flycatchers (CB, CV, and EV) tended to have significantly more heterogeneous diets than residents (see Results). I have already discussed the opportunism of CV and CB. The third migrant, EV, occupies forest interior habitats, but hawks more often than it snatches prey (Willis 1966a). It is most similar to the opportunistic hawks CV and CC on the basis of prey types, diet heterogeneity, and morphology (Figs. 1 and 4; Sherry 1982). Willis (1966a) noted that EV regularly, but opportunistically, attends army ants because of the ephemeral patches of arthropods resulting from ant activity. Opportunism has been linked with the migratory habit, during both the breeding and wintering seasons, in flycatchers (Fitzpatrick 1980b) and in birds generally (Willis 1966a, Morse

1971b, Karr 1976, Herrera 1978, Keast 1980, and references cited therein).

Community structure

From the foregoing analyses and discussion, one may identify several ways in which diets influence or reflect processes that structure flycatcher communities over ecological or evolutionary time scales. This list is not exhaustive with respect to either species interactions or processes structuring communities.

1) Direct competition is an obvious process that can limit the number of species in a community, and is tentatively identified by an abrupt replacement of one species by another, often closely related species, along some environmental gradient (e.g., elevation, habitat type, foraging height above ground). Direct competition is symmetric if each species limits the range of ecological conditions exploited by the other, and is most likely when diets include similar taxa. The Sarapiqui flycatchers contain several potential examples of direct competition (T. W. Sherry, *personal observation*) although experimental evidence is lacking in all these cases. (a) Three widely distributed rainforest spadebill/flatbills forage in the understory, midstory, and canopy (PC, RB, and TOA, respectively). (b) The flatbill TOA replaces its congener TOS in a progression from scattered trees in open country to continuous rainforest canopy. (c) In parallel with example (b), MA (in rainforest) replaces the edge and second-growth TN in canopy vegetation. (d) The dietarily similar TS, OC, MA, and PC (Table 6) rarely co-occur in the same habitats (Table 1). Hespenheide (1971a) and Fitzpatrick (1976, 1980b) have noted that many groups of small Tyrannidae exhibit segregation of habitat or geographic range. Slud's (1964) observation that TS is most abundant in Costa Rica where OC is rare or absent suggests a direct competitive interaction, and their dietary similarity (Fig. 1) strongly supports this possibility. Direct or diffuse competition (e.g., Mac Arthur 1972) of tyrannids with other vertebrates, or even invertebrates, is of course possible, but beyond the scope of this study.

2) When one species exceeds the ability of a second one to interfere for, or exploit resources, then competition is asymmetric. The poorer exploiter (or the subordinate) will then perceive the resources to be less abundant and perhaps less predictable than does the superior competitor (Morse 1974). Subordinate species often have broader fundamental niches than dominants (Miller 1967, Morse 1974, Colwell and Fuentes 1975, Sherry 1979). In the present study, specialization on stingless bees by CCO may have necessitated over evolutionary time broader diets and more opportunism (suggested by more heterogeneous diets) of *Contopus* species (CB, CV, and CC), all of which eat some stingless bees. Army-ant following bird flocks probably exclude the migratory EV from some of the most reliable ant swarms (i.e., food sources), and thereby rein-

force the opportunistic habit of such birds (Willis 1966a). Many avian examples of variable reliance, within guilds, upon a particular food source (see above) are evidence of hierarchical guild organization that could have resulted from social interactions between species.

3) Indirect (coevolutionary?) mutualism results when one predator exploits the predator-avoidance behavior evolved against another predator. Thus TE has a syndrome of behavioral and morphological traits, which are most simply explained as adaptations to exploit the predictable antipredatory (jumping) behavior of Homoptera (Sherry 1982, 1983b, and above). As a result TE benefits from clumsy Homoptera predators that have selected for the predictable, evasive behavior of Homoptera. Because PC snatches some Homoptera sitting on leaf surfaces of understory vegetation (Table 1, Appendix), PC could benefit if TE has selected evolutionarily against Homoptera which jump readily from an approaching predator. In other faunas, one predator has exploited behavior with which its prey avoids other predators (e.g., Hamilton 1971, Hoogland 1982). Charnov et al. (1976) describe an ecological analog of this evolutionary mutualism: coexistence of predators via behavioral enhancement.

4) Several additional processes that can affect the composition and structure of a biota operate on relatively broad spatial and temporal scales. How are diets related to such processes? Seasonal migration between habitats, both in elevation and latitude, is one process that adjusts populations to seasonally inconstant food supplies, and migrants are an important component of many avian communities (e.g., Mac Arthur 1959, Feinsinger 1976, 1980, many references in Keast and Morton 1980, Stiles 1983). The present study suggests that diet heterogeneity accompanies a migratory life history, and one might predict that the range of conditions that migrants encounter preadapts them to withstand environmental perturbations better than similar species that do not migrate. For similar reasons, I predict from flycatcher diets that subordinate compared with dominant guild members and open-country compared with understory species will be more widely distributed geographically and also more tolerant of unpredictable environmental conditions. Species characteristics such as dietary flexibility and geographic range are probably related to speciation, extinction, and colonization processes, although in ways not yet understood. Fowler and MacMahon (1982) have discussed such historical processes, particularly speciation and extinction, in the context of community ecology.

CONCLUSIONS

1) The flycatchers under study differed strikingly with respect to all dietary parameters quantified. Dietary variation was conspicuous within and between genera, within guilds, and across habitats. Study of the variations and why they occur is as compelling as cate-

gorizing all members of a group as opportunists or generalists. The present study documents (1) wide variation in foraging opportunism, the evidence for which comes from the dispersion of prey types, and variable dietary patchiness and dietary heterogeneity; (2) a wide range of diet breadths, whose explanation must take into account prey behavior and the nature of resource concentrations; and (3) consistent differences in prey type, i.e., specializations.

2) The dietary variations observed appear to be predator-specific traits in many cases, and as such reflect the adaptive radiation that Tyrannidae underwent during the Tertiary Period. Aerially foraging insectivores comprise a small part of that radiation, yet diets have diverged not just with respect to prey type (a process frequently attributed to interspecific competition), but also with respect to prey diversity, heterogeneity, patchiness, and other dietary parameters. Characteristics of the habitat(s) where a bird feeds and of the prey trophic level (e.g., arthropod abundance, distribution and predictability, and behavior) are as important to understanding of this radiation of flycatcher diets as are species interactions within a trophic level.

3) These dietary variations are the result of processes operating on different temporal and spatial scales. Prey type, if not other parameters, has been shaped over evolutionary time to the extent that it is constrained by morphology and other heritable traits. Other dietary characteristics are apparently the result of ecological circumstances such as within-guild position in interspecific dominance hierarchies, patchy vs. even dispersion of prey spatially and temporally, decreasingly predictable prey distributions going from forest interior to less physically buffered habitats, and the range of conditions experienced in organism-lifetimes (e.g., contrast migrants with year-round residents). Flycatcher diets are also constrained by time and energy limitations over short time intervals (e.g., Davies 1977, Fitzpatrick 1981), although such constraints were not investigated in the present study.

4) The above conclusions, taken together, indicate the need for a pluralistic approach to studies of community structure (see also Sabo and Holmes 1983, Strong 1983). Diverse kinds of species interactions, only one of which is competition, are implicated by the dietary characteristics observed, and the present study considered only food-related species interactions. Species could also interact via the higher trophic level, i.e., predators on nests and on adult birds. Besides species interactions, historical processes including speciation and extinction determine community structure (Fowler and MacMahon 1982), but it is not yet clear how diets are related to such processes.

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APPENDIX

Number of the indicated prey items observed for each of 16 flycatcher species inhabiting the Caribbean lowlands, Costa Rica (the number of stomachs in which these items were observed is given in parentheses), and total sample sizes (no. of prey, no. of stomachs) for each species.

| | CC | CV | CB | CCO | TE | MS | MA | TS | TC | TN | OC | RB | PC | TOA | TOS | EV | |
|------------------------|-------|--------|-------|-------|--------|-------|--------|--------|--------|--------|-------|--------|--------|---------|--------|--------|-------|
| Fruit | | | | | | | | 1 (1) | 12 (1) | 24 (2) | | 4 (1) | 39 (1) | | 20 (3) | 12 (1) | |
| Odonata | | | | | | | | | | | | | | | | | |
| Anisoptera | | | | 3 (1) | | | | | | | | | | | | | |
| Zygoptera | 2 (2) | 2 (1) | 4 (1) | | | 3 (2) | | | | | 5 (4) | 1 (1) | | | | | |
| Orthoptera | | | | | | | | | | | | | | | | | |
| Tettigidae | | | | | | | | | | | | | | | | | |
| Undetermined | 1 (1) | 5 (3) | | | 3 (2) | | 4 (3) | 13 (8) | 14 (5) | 1 (1) | | 12 (5) | 5 (3) | 34 (10) | 6 (4) | 1 (1) | 5 (4) |
| Dermaptera | | | | | | | | | | | | | | | | | |
| Undetermined | 1 (1) | 4 (4) | | | | | | 2 (2) | | | | | | 1 (1) | | 1 (1) | |
| Heteroptera | | | | | | | | | | | | | | | | | |
| Miridae | | | | | | | | | | | 1 (1) | | | | | | |
| Reduviidae | 1 (1) | 1 (1) | | | | | | | | | | | | | | | |
| Phymatidae | | | | | | | | | | | | | | | 4 (4) | 2 (1) | |
| Tingidae | | | | | | | | | | | | | | | 1 (1) | 1 (1) | |
| Lygaeidae | | | | | 2 (2) | | | | | | 1 (1) | 1 (1) | | | | | |
| Pyrrhocoridae/Largidae | | | | | | | | | | | | | | | | 10 (4) | |
| Coreoidea | | | | | | | | | | | | | | | 1 (1) | 5 (1) | |
| Aradidae | | | 4 (3) | | | | | | | | | | | | | | |
| Cydnidae | 7 (2) | 6 (3) | | | | | | | | | | | | | | | |
| Pentatomidae | | 4 (3) | | | | | | | | | | | | | | | |
| Undetermined | | | | 3 (1) | 6 (4) | | | 2 (2) | 6 (4) | | 1 (1) | 3 (3) | 2 (2) | 1 (1) | 4 (2) | 4 (3) | 2 (2) |
| Homoptera | | | | | | | | | | | | | | | | | |
| Membracidae | 2 (2) | 2 (2) | | 4 (4) | 1 (1) | 1 (1) | 18 (8) | 1 (1) | 18 (7) | 5 (4) | 3 (3) | 3 (2) | 6 (3) | 8 (5) | 4 (3) | 2 (2) | |
| Cicadellidae | | 3 (2) | | 3 (3) | 6 (4) | 6 (3) | 11 (6) | 14 (4) | 9 (5) | 2 (2) | 5 (3) | | | | | | |
| Cercopidae | | 3 (2) | | 4 (3) | 7 (6) | 4 (3) | 9 (5) | 1 (1) | 2 (2) | 2 (2) | | | | | 2 (2) | 2 (1) | |
| Undet. Cercopoidea | 1 (1) | 2 (2) | | | | | 1 (1) | | 2 (2) | 1 (1) | | | | 1 (1) | 2 (1) | 1 (1) | |
| Fulgoroidea | 1 (1) | 10 (2) | | 1 (1) | 46 (9) | 8 (5) | 13 (8) | 19 (5) | 11 (5) | 5 (4) | 7 (5) | 1 (1) | 4 (4) | | | 1 (1) | |

APPENDIX
Continued.

| | CC | CV | CB | CCO | TE | MS | MA | TS | TC | TN | OC | RB | PC | TOA | TOS | EV | |
|-----------------------------------|--------|--------|--------|----------|--------|--------|--------|---------|--------|--------|--------|--------|---------|--------|--------|--------|--------|
| Coleoptera | | | | | | | | | | | | | | | | | |
| Carabidae | | | | | 1 (1) | 2 (1) | 1 (1) | | | | | | | | 1 (1) | | |
| Histeridae | | | | | 2 (1) | | 3 (1) | | | | | | | | 1 (1) | | |
| Staphylinidae | | | | | 1 (1) | | 2 (2) | | | | | | | | 2 (2) | | |
| Cantharidae | | | | | | | | | | | | | | | | 2 (1) | |
| Lampyridae | | | | | | | | | | | | | | | | | |
| Cleridae | | 1 (1) | 2 (1) | | | | | 5 (5) | | | | | | | | | |
| Cebriionidae | | | | | | 1 (1) | | | | | | | | | | | |
| Elateridae | | | | | 1 (1) | | | | | | | | | | | | |
| Buprestidae | | 2 (1) | | | | | | 1 (1) | | 1 (1) | | | | | 2 (2) | | |
| Ptilodactylidae | | | | | | | | | | | | | | | 2 (2) | 1 (1) | |
| Erotiidae | | | | | | | | | | | | | | | 1 (1) | | |
| Languriidae | | | | | | | | 1 (1) | | | | | | | 3 (1) | | |
| Nitidulidae | 10 (4) | 3 (2) | | | 3 (1) | | 6 (4) | 1 (1) | 1 (1) | 2 (2) | 1 (1) | | | | 2 (2) | 3 (1) | |
| Coccinellidae | | 1 (1) | | | | | | | | 2 (2) | 1 (1) | | | | | | |
| Anthicidae | | | | | | | | | | | | | | | | | |
| Meloidae | | | | | | 1 (1) | | | | | | | | | | | |
| Mordellidae | | | | | | 1 (1) | | | | | | | | | | | |
| Tenebrionidae | | | | | | | 1 (1) | | | | | | | | | | |
| Bostriichidae | | | | | | | | 2 (1) | | | | | | | | | |
| Scarabacidae | | 3 (2) | | | | | | 1 (1) | 1 (1) | | | | | | | 1 (1) | |
| Cerambycidae | | 3 (1) | 3 (2) | | | | | | | | | | | | 1 (1) | 1 (1) | |
| Chrysomelidae | 8 (4) | 14 (7) | | | 21 (9) | | 3 (3) | 11 (7) | 11 (4) | 10 (7) | 13 (4) | 17 (5) | 3 (2) | 24 (8) | 27 (9) | 21 (6) | 14 (5) |
| Ostomidae | | 2 (1) | | | | | | | | | | | | | | | |
| Hispidae | | | | | | | | | | | | | | | 2 (1) | | |
| Bruchidae | | | | | | | | 1 (1) | | | | | | | | 1 (1) | |
| Anthribidae | | | | | | | | 2 (2) | 1 (1) | 2 (2) | | | | | | | |
| Curculionidae | 27 (7) | 2 (2) | 6 (3) | | 10 (3) | 9 (6) | 1 (1) | 12 (6) | 5 (3) | 5 (3) | 10 (3) | 21 (6) | 52 (10) | 25 (6) | 15 (4) | | |
| Platypodidae | 10 (3) | 41 (7) | 1 (1) | 8 (4) | 6 (2) | 2 (2) | | 2 (2) | | 1 (1) | 1 (1) | | | | | | |
| Scolytidae | | 8 (4) | | 2 (2) | | 2 (2) | | 1 (1) | | | | | | | | | |
| Undetermined | 5 (3) | 21 (7) | 1 (1) | 18 (7) | 7 (5) | 18 (8) | 13 (5) | 12 (7) | 12 (6) | 7 (5) | 3 (2) | 23 (9) | 33 (9) | 14 (5) | 26 (5) | | |
| Lepidoptera | | | | | | | | | | | | | | | | | |
| Larvae | 2 (2) | | | | | | | 21 (10) | 6 (4) | 1 (1) | 1 (1) | 8 (3) | 4 (3) | 18 (9) | 4 (2) | 2 (1) | 1 (1) |
| Adult | 8 (7) | 3 (3) | 2 (1) | 2 (2) | | 4 (3) | 5 (3) | 1 (1) | 1 (1) | 10 (4) | 1 (1) | | 1 (1) | 1 (1) | 3 (2) | 5 (2) | |
| Diptera | | | | | | | | | | | | | | | | | |
| Nematocera | | | | | 1 (1) | | | 2 (1) | | | 51 (9) | 5 (2) | 2 (2) | 5 (3) | 1 (1) | | 1 (1) |
| Brachycera | | | | | | | | 3 (2) | 2 (2) | | 10 (3) | 5 (3) | | | | | |
| Acalyptrate Muscoid | | 4 (4) | | | | | | | | | 6 (3) | | | | 4 (1) | | |
| Calypterate Muscoid | | | | | | | | 1 (1) | | | 6 (2) | 32 (8) | | | | | |
| Syrphidae | | 2 (2) | | | | | | | | | 4 (3) | | | | | | |
| Undetermined | 3 (2) | 8 (3) | | 1 (1) | | 11 (5) | | 8 (5) | 21 (8) | 9 (5) | 2 (2) | | 9 (7) | 1 (1) | | 1 (1) | |
| Hymenoptera | | | | | | | | | | | | | | | | | |
| Braconidae | 2 (2) | 2 (1) | | | | | 1 (1) | | 2 (1) | 10 (4) | | | 3 (2) | 1 (1) | | 1 (1) | |
| Ichneumonidae | | | | | | | 2 (1) | | | | | | 1 (1) | | | | |
| Eucharitidae | 4 (4) | 15 (4) | | | 1 (1) | | 7 (3) | | 1 (1) | 36 (8) | 3 (2) | | | | | 1 (1) | |
| Chalcidae | 3 (3) | 1 (1) | | | | | | | | 7 (3) | | | | | | | |
| Chalcidoidea | | 1 (1) | | | | | | | 1 (1) | | 4 (4) | 1 (1) | | 4 (2) | | 1 (1) | |
| Formicidae | 32 (5) | 30 (8) | 34 (1) | 22 (10) | | | 3 (2) | 6 (5) | 3 (2) | 18 (5) | 12 (5) | 2 (1) | 2 (2) | 49 (9) | 45 (6) | 9 (4) | |
| Apoidea | 69 (9) | 26 (6) | 44 (4) | 244 (11) | | | 31 (4) | 15 (1) | 1 (1) | 9 (2) | 2 (1) | | 2 (1) | 2 (2) | 2 (2) | 4 (3) | 9 (3) |
| Undetermined | 9 (4) | 23 (7) | 2 (1) | 4 (4) | 1 (1) | 18 (6) | 4 (3) | 5 (3) | 11 (6) | 4 (4) | 1 (1) | 1 (1) | 5 (4) | 5 (3) | 6 (4) | 1 (1) | |
| Arachnidae | | 2 (2) | | | | 3 (3) | 3 (2) | 31 (12) | 14 (5) | 10 (5) | 7 (5) | 22 (6) | | 31 (8) | 14 (7) | 1 (1) | 6 (3) |
| Other | | | | | | 1 (1) | | | | | 1 (1) | | | 1 (1)* | | 1 (1) | 2 (2)† |
| No. of prey (not including fruit) | 184 | 294 | 102 | 364 | 65 | 153 | 205 | 128 | 289 | 157 | 98 | 43 | 212 | 263 | 163 | 114 | |
| No. of stomachs | 9 | 9 | 4 | 11 | 9 | 7 | 12 | 5 | 10 | 10 | 6 | 3 | 10 | 10 | 6 | 5 | |

* = 1 larval leaf-miner.

† = 1 scorpion, 1 centipede.