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FOOD RESOURCES OF UNDERSTORY BIRDS IN CENTRAL PANAMA: QUANTIFICATION AND EFFECTS ON AVIAN POPULATIONS

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Abstract. Habitat associations of birds inhabiting the understory of tropical moist forests vary in time and space. We investigated whether this variation was related to changes in resource abundance. Foliage and litter arthropod abundances were estimated at about 60 sampling sites in central Panama from 1983 through 1985. Bird activity was also determined with mist nets at these sites. Activity (i.e., capture rates) of about 20 species and five foraging guilds revealed widely varying consumer-resource associations. Certain species were positively correlated with variation in arthropod abundances, whereas others were less common when and where their presumed resources were comparatively abundant. Microclimate (i.e., humidity) influenced the nature of bird-food interactions; dry sites appeared to be unsuitable habitat for certain species despite sometimes abundant arthropods. We conclude that habitat associations of birds in central Panama are not solely food-resource mediated.

Key Words: Understory birds; food resources; Panama; arthropods; tropical forest.

Understanding the nature of consumer-food interactions is critical to the study of tropical avian ecology. For example, the notably high species richness in many neotropical habitats may stem from the variety of available food resources, associated feeding locations, and the tendency for many species to be omnivorous. At least 20–35% of tropical forest species consume some combination of fruits, insects, and nectar (Karr 1975, Karr et al. in press). Two factors make observation of foraging behavior especially difficult for a large proportion of Neotropical forest species. First, many species are rare, secretive, or both (Karr 1971, Terborgh 1985). Second, even if a species is common, its mobility can impede observations of behavior in tropical forest habitats (Remsen 1985). Large frugivores, such as parrots and toucans, and many insectivores travel over large areas, often in mixed-species flocks. Thus, complete description of "community foraging space" of birds is clearly difficult in tropical moist forests.

These logistical problems have, understandably, led to a research emphasis on long-term studies of selected species or guilds with relatively sessile and quantifiable resources or easily observed foraging behavior. Studies of nectarivores (Wolf et al. 1976, Feinsinger 1978, Stiles 1978), frugivores (Snow 1981, Moermond and Denslow 1983), army ant followers (Willis and Oniki 1978), and flycatchers (Fitzpatrick 1980, Sherry 1984) are examples.

Problems in estimating consumer and resource abundances in tropical moist forests exacerbate the difficulty of studying avian foraging ecology. Estimating avian abundances is laborious and time consuming (e.g., mist-netting), or demands bird identification skills that can take considerable time to develop in tropical forests (e.g., spot-mapping, Terborgh 1985). Standardized protocols for estimating variation in food resources of, say, insectivorous birds have not been established (Wolda, this volume). Estimating arthropod abundance is tractable for certain groups of consumers (e.g., arthropods in hanging litter; Gradwohl and Greenberg [1982b]), but not for others (e.g., canopy-dwelling birds). Arthropod abundances on understory foliage and in litter can be estimated, but the method used can strongly affect results (Wolda and Wong 1988). Further, the often high diversity of plant species with specialized leaf-eating arthropods present formidable sampling difficulties. Finally, the natural histories of many neotropical birds are so poorly documented that even the elementary step of choosing which resources to study may be problematic (Remsen 1985). For example, hummingbirds routinely feed on arthropods in many neotropical habitats (Remsen et al. 1986), but few efforts to apply foraging theory to nectarivores have considered the importance of arthropods in their diet (Karr 1989).

Much theory in ecology proceeds from assumptions about the relationships among organisms and their foods. We believe that the aforementioned uncertainties justify caution in acceptance of general, often paradigmatic, statements about the habitat, population, and community ecology of tropical birds (e.g., narrow niches, the stability-diversity dogma).

The diversity of tropical birds and their resources precludes detailed study of all groups, so we adopted a compromise between the number of species studied and the level of detail of the study. We sought to estimate variation in resource availability and its influence on habitat use by selected undergrowth birds in moist lowland forests of central Panama. We consider two topics that are integral to the understanding of relationships among birds and their food resources: (1) methods used to estimate variation in leaf litter and foliage arthropods; and (2) relationships between arthropod abundances and avian activity, including examination of the effects of variation in understory microclimate.

METHODS

SAMPLING

Birds

Bird activity was sampled with mist nests (Northeastern Bird Banding Association ATX, 12.0 × 2.6 m, 36 mm mesh) at over 60 net sites in the undergrowth of forest in Parque Nacional Soberania in central Panama (Karr and Freemark 1983). Nets were operated at each site for 3–6 days in March (dry season) and July (wet season) from 1979 through 1986. Additional samples were collected in January and May 1983. Sampling effort included 45,008 net hours and yielded 6896 captures. We analyzed activity of the 20 most commonly netted species and of five foraging guilds each composed of 3–4 species (Table 1). Several guilds represented by only one species were not included in the latter analysis. A total of 1754 captures ($\bar{X}$ = 88/species, range = 36–382) are used here from data collected during 1983–1985. Assignments of species to guilds was based on similarities in food type and foraging location (Karr 1971, pers. obs.; Stiles 1983a).

Activities of species and guilds were estimated as number of captures/100 net hours. Capture rates for each guild were based on total number of captures for all species in the guild, not the average of individual species capture rates. We assumed that capture rates estimated intensity of activity at our sample sites (Karr and Freemark 1983). Nets were open all day, except during heavy rains, so variation in activity as a function of time of day was not a concern. Nets used in this way assessed changes in avian activity in a mosaic of habitats and thus reflected a dynamic habitat selection process (see Karr and Freemark 1983:1489).

The objective of evaluating associations between measures of bird activity and resource availability presents a problem of selecting the appropriate sampling method to detect ecological relationships. General indexes of food availability can indicate broad connections between birds and resources (Martin and Karr 1986b), but stronger inferences are likely with direct measures of food resources (Blake and Hoppes 1986). Moreover, direct estimates of resource abundance are most useful when derived from samples that coincide in space and time with the collection of bird data.

Accordingly, we sampled bird activity and resources thought or known to be consumed by birds at the same sites and in the same months. All resource sampling was done within a 10- × 25-m quadrat adjacent to each net site. The choice of quadrat size was somewhat arbitrary but reflected our goal of sampling a reasonably sized area associated with each mist net. The center line of each quadrat's long axis ran perpendicularly from the center of each net. Quadrats were successively alternated from the right to the left sides of nets along a line of net sites. Three general categories of resources were sampled: leaf-litter arthropods, undergrowth-foliage arthropods, and undergrowth fruit. Other types of food resources were too ephemeral (e.g., fruit fallen to the ground) or difficult to sample efficiently (e.g., bark arthropods) to justify estimation of availability. Only the arthropod data will be presented in this paper. Foliage arthropods and birds were sampled four times in 1983 and twice in 1984; litter arthropods were sampled in these periods and during one additional period in 1985.

TABLE 1. WEIGHTS, FORAGING-GUILD ASSIGNMENTS, AND NUMBER OF CAPTURES FOR EACH OF THE 20 MOST FREQUENTLY CAPTURED SPECIES, PARQUE NACIONAL SOBERANIA, PANAMA, JANUARY 1983 TO MARCH 1985

Species	Number of captures	Weight (g)	Foraging guild[a]
Geotrygon montana (dove)	47	128	GRFR
Phaethornis longuemareus (hermit)	105	6	NI
Dendrocincla fuliginosa (woodcreeper)	70	41	ANTF
Automolous ochrolaemus (foliage-gleaner)	40	40	FGIN
Sclerurus quatemalensis (leaftosser)	86	34	GRIN
Thamnophilus punctatus (antshrike)	49	22	FGIN
Myrmotherula axillaris (antwren)	45	8	FGIN
M. fulviventris (antwren)	41	10	FGIN
Gymnopithys leucaspis (antbird)	151	30	ANTF
Hylophylax naevioides (antbird)	95	17	ANTF
Phaenostictus mcleannani (antbird)	58	51	ANTF
Formicarius analis (antthrush)	40	57	GRIN
Pipra coronata (manakin)	75	10	UNFR
P. mentalis (manakin)	382	15	UNFR
Terenotriccus erythrurus (flycatcher)	54	7	FLIN
Myiobius sulphureipygius (flycatcher)	44	12	FLIN
Platyrinchus coronatus (spadebill)	91	9	FLIN
Mionectes oleaginea (flycatcher)	159	10	UNFR
Cyphorhinus phaeocephalus (wren)	86	20	GRIN
Cyanocompsa cyanoides (grosbeak)	36	32	UNOM

[a] Foraging guilds: GRFR = ground frugivore (1 species); NI = nectarivore insectivore (1); FGIN = foliage-gleaning insectivore (4); GRIN = ground insectivore (3); ANTF = ant follower (4); UNFR = undergrowth frugivore (3); FLIN = flycatching insectivore (3); UNOM = undergrowth omnivore (1).

Foliage arthropods

Our goal in sampling foliage arthropods was to mimic the search methods of foliage-gleaning birds. Therefore, we used an approach mentioned briefly by Janzen

(1980a). We conducted timed visual surveys within each sampling quadrat by counting arthropods on leaves from 0.5 to 2.0 m high during unpatterned walks through each quadrat. All samples were done between 07:30 and 14:00 during periods with little or no cloud cover. A flashlight was occasionally used to aid in detection of arthropods on the undersides of leaves. Each arthropod observed was categorized according to taxonomic group (Order, sometimes Family), size (<5 mm, 5–15 mm, and >15 mm), and leaf surface (upper or lower). Taxonomic groups used for adults were: Arachnida, Coleoptera, Hemiptera, Homoptera, Lepidoptera, Diptera, Formicidae, and Orthoptera. Uncommon taxa were lumped as "other." Small numbers of cryptic insects may have been missed despite our best efforts. We do not include detailed analyses of arthropod taxa here. As more specific data on diets of tropical birds (e.g., Sherry 1984) become available, analysis of patterns between individual bird species and insect groups might be useful. We excluded ants from our analyses because adult ants are rarely consumed by the species commonly captured in our net samples (J. R. Karr, pers. obs.).

During January 1983, variation among four observers in simultaneous counts varied by less than 10% for abundances and taxonomic assignments. Consequently, we made no additional effort to evaluate variation among observers. All observers conducting these counts had training in insect identification.

Leaf-Litter arthropods

We followed procedures established by Willis (1976) for sampling litter arthropods. One sample was collected at each net site at randomly determined coordinates within each sampling quadrat. Samples were collected by placing a 29- × 34-cm (0.10 m^2) plastic container on the forest floor and sliding a plexiglass sheet beneath to gather the litter. Samples were than placed in plastic bags, arthropods immobilized with Kahle's Solution (Borror et al. 1976), weighed, and sorted. Although we were unable to obtain dry weights of our samples, other studies (S. Levings, unpubl. data) provided estimates of moisture content of litter in wet and dry periods. Moisture content of leaf litter in central Panama averaged 25% in late March and 53% in July (S. Levings, unpubl. data). All weight-based analyses of litter arthropods were standardized to estimate dry weights of litter and were expressed as number of arthropods/100 gm of litter. Each litter arthropod was classified according to size (2–5 mm, 5–10 mm, 10–15 mm, >15 mm) and taxonomic group (Phalangidae, Acarina, Arachnida, Isopoda, Diplopoda, Blattaria, Orthoptera, Isoptera, Hemiptera, Homoptera, Neuroptera, Coleoptera, Lepidoptera, Diptera, Formicidae, and other Hymenoptera, "other," and unknown). Cast skins and arthropods <2 mm were not counted.

ASSOCIATIONS OF BIRDS WITH ARTHROPODS ALONG A MOISTURE GRADIENT

Microclimate in the undergrowth varied little among net sites during the wet season, but appreciable variation among sites existed in temperature and humidity during the dry season (Karr and Freemark 1983). Microclimate at our sample sites was influenced by local topography, presence of nearby streams, and vegetation structure (e.g., canopy openness). Each sample location was assigned to one of four moisture classes (1 = driest, 4 = wettest) based on these factors, and temperature and humidity data were collected with sling psychrometers during several dry seasons (Karr and Freemark 1983). All net sites were sampled hourly (07:00–17:00) on the same day during both wet and dry season sample periods.

STATISTICAL ANALYSES

Our approach in analyzing relationships between avian activity and variation in arthropod abundances was primarily correlative and exploratory. For temporal variation, we combined (i.e., averaged) data from all sampling sites (net locations) or those within a moisture class and calculated Spearman's rank-order correlations between mean arthropod abundance (foliage or litter) and capture rates of species or guilds. We combined sampling sites because of uncertainties in independence of observations among nets; thus, our results are conservative.

RESULTS

RELATIONSHIPS AMONG ABUNDANCES OF BIRDS AND ARTHROPODS

Variability in abundances of understory foliage and litter arthropods

Abundances of arthropods varied considerably among sampling periods (Table 2). Foliage arthropod abundances were relatively low from January thru July 1983, but increased sharply in 1984. Abundances of foliage arthropods in March 1984 were, on average, about 125% greater than those observed during the previous year's March sample. About 45% of the 1983 to 1984 increase was due to increased numbers of small adult Diptera.

Litter arthropods displayed the same general pattern of temporal variation in abundance as the foliage arthropods; numbers were higher in 1984, a result consistent with another study of litter arthropods in central Panama (Wheeler and Levings, in press). The patterns were not always concordant, however. For example, the peak period in abundances of litter arthropods (July 1984) lagged behind that of foliage arthropods (March 1984).

Arthropod abundances and capture rates of five foraging guilds

No correlations between capture rates by guild and either foliage or litter arthropod abundances were significant ($P > 0.05$; critical values = 0.83 for foliage and 0.75 for litter arthropods), but differences among the guilds were striking (Fig. 1). Spearman rank correlations ranged from 0.61 for the ground foraging insectivores with litter arthropods to −0.54 for flycatchers with foliage arthropods. Ground-foraging insectivores and flycatchers had the most positive and negative

TABLE 2. ABUNDANCES OF UNDERSTORY FOLIAGE AND LITTER ARTHROPODS IN CENTRAL PANAMA

Sampling period	Foliage (No. observed/hour) X̄ (SE)	Litter (No. individuals/ 100 g litter) X̄ (SE)
January 1983	37.8 (2.3)	5.4 (4.3)
March 1983	53.5 (4.8)	4.6 (1.0)
May 1983	54.4 (3.1)	5.4 (1.0)
July 1983	63.9 (2.8)	3.7 (0.3)
March 1984	120.4 (16.1)	11.2 (3.5)
July 1984	108.0 (4.9)	14.1 (2.6)
March 1985	No data	6.7 (1.2)

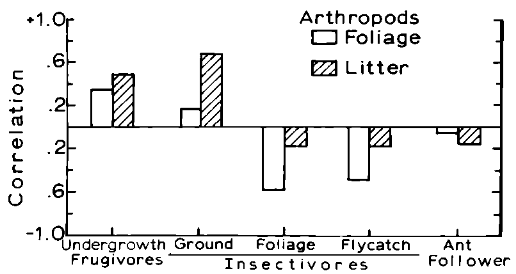

FIGURE 1. Correlations (Spearman's Rho) of capture rates for five avian foraging guilds with abundances of foliage and litter arthropods for 1983 to 1985 in central Panama.

associations with arthropod abundances, respectively.

Arthropod abundances and capture rates of the 20 most common species

The associations of individual species with arthropod abundances also varied (Fig. 2). Spearman correlations between capture rates and foliage arthropod abundances (Fig. 2A) averaged 0.02 and ranged from 0.61 for the Black-faced Antthrush (*Formicarius analis*) to −0.71 for the Sulphur-rumped Flycatcher (*Myiobius sulphureipygius*).

Correlations of individual species capture rates with abundances of litter arthropods (Fig. 2B) averaged 0.18 and ranged from −0.32 for Ochre-bellied Flycatcher (*Mionectes olivaceus*) to 0.77 for *Formicarius analis* ($P < 0.05$). Associations of bird activity with litter arthropods were therefore generally weak, but more positive than those with abundances of foliage arthropods. Moreover, species within guilds were more consistent regarding litter arthropods; all correlations for the ground insectivores were positive and all those of the flycatchers were negative.

Associations of species capture rates and foliage arthropod abundances were especially heterogeneous within certain foraging guilds (Fig. 3). For example, two antfollowers, Ocellated Antbirds (*Phaenostictus mcleannani*) and Spotted Antbirds (*Hylophylax naevioides*), had Spearman correlations of 0.60 and −0.54, respectively. The three-member ground-foraging guild was the most consistent. Wald-Wolfowitz runs test on the Spearman's rank correlations suggested a systematic difference betwen flycatchers and ground gleaners in their associations with litter and foliage arthropods ($P < 0.05$).

Arthropod abundances and capture rates of birds along a moisture gradient

In the wet season foliage arthropod abundances were similar at dry and wet sampling sites, but during dry periods moist sampling sites had lower abundances than more xeric sampling sites. Litter-arthropod abundances were less variable along the moisture gradient, but tended to be higher at comparatively wet and dry sites.

We found no consistent pattern of covariance (Table 3) between capture rates of undergrowth bird species and arthropod abundances along the moisture gradient. Capture rates did not increase or decrease systematically within any guild along the moisture gradient. Bird-arthropod associations were somewhat more positive at relatively mesic sampling sites (e.g., Moisture class 2 for litter arthropods). Moreover, at the most xeric sites, capture rates of all guilds were negatively associated with abundances of foliage arthropods (Table 3). Correlations of capture rates with abundances of litter arthropods were more positive, especially for ground insectivores. Activities of flycatchers and foliage gleaners were negatively associated with foliage-arthropod abundances at all moisture conditions. The association of foliage gleaners with foliage arthropods at the driest sites was distinctly negative.

DISCUSSION

The clear differences in arthropod abundances between 1983 and 1984 coincided with an extremely dry dry season, possibly caused by the severe El Niño in 1983 (Brawn and Karr, unpubl. data). The dry season in 1983 was the longest and driest recorded in central Panama since 1929. Only 26 mm of rain were recorded at nearby Barro Colorado Island from January to March (40-year mean ± 1 SD = 122 ± 96 mm [Karr and Freemark 1983]). During early 1983 many trees and shrubs exhibited signs of moisture stress (e.g., wilting, excessive leaf abscission [J. Karr, pers. obs.]). Moreover, rarity of intermittent dry-season rains in 1983 delayed development of new leaves, flowers, and fruits of many tree species in central Panama (D. Windsor, pers. commun.); thus, phenological differences in availability of

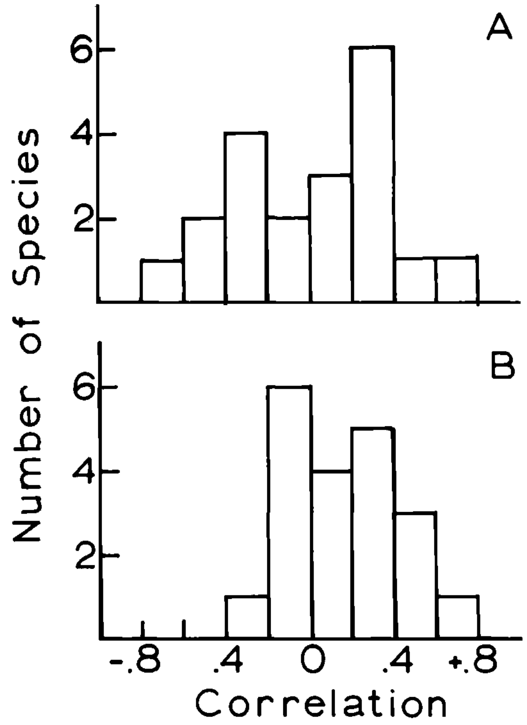

FIGURE 2. Frequency histograms of Spearman's Rho correlations between capture rates and abundances of (A) foliage arthropods and (B) litter arthropods based on the numbers of species that exhibited given levels of correlations for the 20 most common species for 1983 to 1985 in central Panama.

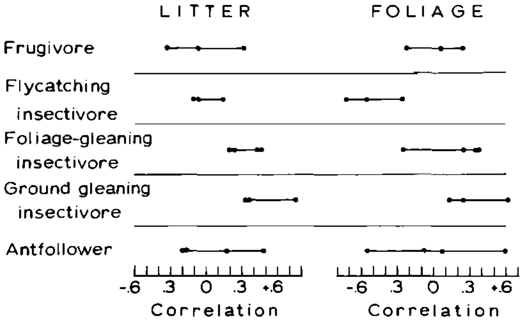

FIGURE 3. Distributions within five foraging guilds of Spearman's Rho correlations for capture rates and arthropod abundances for 1983 to 1985 in central Panama.

resources for insects or direct moisture effects on insects may have indirectly influenced resource availability for birds. The influence of the 1983 drought may have been more direct on litter arthropods; observational and experimental evidence indicates that numbers of litter arthropods in central Panama are enhanced by soil moisure (Levings and Windsor 1984).

Overall, the direction of associations between birds and arthropods was not consistent with the notion that birds were "tracking" food resources. For example, the strong positive correlation of ground-foraging birds with litter arthropods suggests a bird-food association, but contrasts with the negative associations between capture rates of foliage-gleaning birds and foliage arthropods. Positive correlations between undergrowth frugivores and both foliage and litter arthropods are puzzling.

Karr and Freemark (1983) observed that patterns of habitat selection by undergrowth birds in central Panama are partly explained by inter- and intraspecific variation in activities of birds along microclimatic gradients. Each species exhibited some preference among the range of moisture conditions and many species altered their primary habitat association over time as they appeared to track changing microclimate conditions. Karr and Freemark suggested two underlying mechanisms for nonrandom distribution of activity along a moisture gradient: birds seek micro-climatic optima for physiological reasons, or they track food resources whose abundances are directly related to moisture conditions, or both. Our results do not show a clear association between bird abundances and their food resources. Therefore, as hypothesized by Karr and Freemark (1983), physiological factors may impede these species from exploiting sometimes abundant food resources at dry sites.

Results of correlative analyses can be discussed for their biological significance or judged critically owing to perceived problems in analytical issues such as validity of sampling method. Certain biases are inherent in sampling with mist nests as with any survey or census method (Karr 1979, 1981). However, mist nets minimize problems associated with detecting species that are difficult to observe or that vocalize rarely, problems that introduce unknown biases into more conventional census procedures.

Variations in foraging activity and mobility among species and even among sex and age classes of the same species (Karr 1971, 1979, 1981) yield capture rate variation among species. High capture rates of very mobile species such as Red-capped Manakin (*Pipra mentalis*) do not necessarily reflect higher densities than those of seldom-captured species such as Spotted Antbirds. High recapture rates in our study (consistently 50–70% of captures), however, suggest that birds do not learn to avoid nets. In addition, we find no variation in recapture rates of sedentary

TABLE 3. CORRELATIONS OF FORAGING GUILD CAPTURE RATES WITH ARTHROPOD ABUNDANCES AT DIFFERENT MOISTURE CLASSES FROM DRY (1) TO WET (4) FOR 1983 TO 1985 IN CENTRAL PANAMA

Arthropod group	Moisture class	Undergrowth frugivores	Ground insectivores	Foliage-gleaning insectivores	Flycatching insectivores	Antfollowers
Litter	1	0.27	0.57	−0.57	−0.11	0.18
	2	0.27	0.57	0.33	0.32	0.79
	3	−0.46	0.36	−0.18	0.21	−0.14
	4	0.57	−0.17	−0.01	−0.39	−0.05
Foliage	1	−0.46	−0.14	−0.83	−0.29	−0.43
	2	0.64	0.17	−0.49	−0.37	−0.09
	3	−0.03	−0.77	−0.02	−0.43	0.09
	4	0.71	−0.49	−0.02	−0.31	0.02

species in several guilds, suggesting that different guilds do not vary systematically in their ability to detect and avoid nets.

We also note that imprecision should not be confused with systematic error, a distinction that is critical when evaluating results of field studies. Our estimates of bird activity and resource abundance were derived from sampling a full range of microclimates and vegetation structure within a 90 ha area. In addition, counts of birds and their presumed food were done in the same plots over short time periods, a goal that has rarely been attained over so many sample plots (about 60 net sites).

Our data on arthropod abundances and avian activity are, admittedly, "blunt instruments" for determining the effects of food availability on habitat selection by insectivorous birds. All the arthropods detected in our abundance estimates were not potential prey items for birds; some may be unpalatable or require excessive time or energy for capture (Martin 1986; Wolda, this volume). Sherry (1984) demonstrated that, for flycatchers in Costa Rica's moist lowland forests, what is or is not a food item for an insectivore is a function of a predator's foraging technique as well as prey distribution and body size.

Associations between capture rates of birds and arthropod abundances vary among species and guilds, suggesting that foraging mode may determine how "opportunistic" a given species can be. Ground insectivores (by species and as a guild) appear to track temporal variation in resource availability more precisely than species in other guilds regardless of environmental conditions. In contrast, flycatchers seem to be *less* common when and where arthropod abundances are high. Unfortunately, we have no information about the relationship between foliage and flying-insect abundances. Other studies of Neotropical flycatchers suggest that a species' diet can be influenced by time and energetic-physiological constraints (Fitzpatrick 1981, Sherry 1984). Our results support these suggestions and add that such constraints may be more rigid in dry areas. A study incorporating physiological and energetic measurements evaluated along environmental gradients would be useful in clarifying habitat use and resource ecology of birds of tropical forest undergrowth.

As empirical evidence accumulates, it seems that the factors responsible for ecological pattern vary among populations and communities. Accordingly, the value of pluralistic theory, though not a new idea, is gaining acceptance (Schoener 1986a). The expectation of finding valid univariate explanations is thus naive. Our results clearly indicate that species and guilds do not respond in concert to variation in environmental factors. Even within a species, the influence of food availability, physiological conditions, and predation may vary in importance with vegetation structure, macroclimate, and microclimate. The concept of a "normal" or typical bird species, population, or community is simply inappropriate (Wiens and Rotenberry 1987).

We believe that pluralism is also appropriate in the field. The complexity of tropical forest avifaunas and their food resources invites an especially high diversity of valid approaches to understanding ecological patterns. Further, the system being examined can influence the types of questions that can be effectively addressed. For example, experimental manipulations of avian abundances or supplemental feeding experiments, formidable in any habitat (Wiens et al. 1986a), would be difficult for most insectivores in tropical forests. Similarly, supplemental feeding might be possible in the case of frugivores, but the scale of habitat use by many tropical frugivores may make tractable manipulations inappropriate for evaluating bird-food associations in the real world.

Two final points are important—one specific to our study and one a general observation. First, the methods and results described here considered general patterns, but also served to identify specific aspects of the foraging ecologies of certain species and guilds that merit more detailed examination (e.g., more detailed analysis of the insect taxa consumed by specific bird species, the comparative stability of fruit vs. insects as food resources, or the mechanisms of omnivory that allow survival through crunch periods). Second, tropical species have long been considered to be ecological specialists (Klopfer and MacArthur 1961). Many species are habitat or food specialists, but many also repeatedly exhibit an ability to alter their behavior (foraging and habitat selection) in response to changing environmental conditions. An exploration of the temporal reliability of resources and the evolution of plasticity to exploit a broader range of resources, although a difficult task, could help clarify the role of food resource availability in governing the ecology of species and the development of assemblages of species.

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