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WHEN ARE BIRDS DIETARILY SPECIALIZED? DISTINGUISHING ECOLOGICAL FROM EVOLUTIONARY APPROACHES

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Abstract. Definitions of degree of dietary specialization are motivated by theories of the niche, optimal foraging, predator-prey theory, ecomorphology, comparative morphology, and phylogeny. These methods fall into two fundamentally different, but complementary approaches. The first is ecological (or tactical), emphasizing short-term responses of individual organisms to resource availability and abundance, given phylogenetic constraints. The second approach is evolutionary (or strategic), emphasizing longer-term, genetically based constraints and adjustments of consumers (via adaptive radiation) to patterns in the predictability of resources in both space and time.

Studies of diet specialization have emphasized individuals' tactical approaches to the exclusion of population strategic ones, and have often failed to distinguish between the two approaches. I discuss this distinction in terms of the kinds of information needed to characterize specialists and generalists. I argue that strategic specialists have stereotyped rather than narrow breadth diets, and I discuss the relationships between the two dietary dichotomies of monophagy-polyphagy and stereotypy-opportunism. Three examples illustrate the distinction between strategic and tactical approaches, and problems of failing to separate the two: (1) Cocos Flycatchers (*Nesotriccus ridgwayi,* Tyrannidae) are ecological generalists, but evolutionary specialists; (2) Neotropical flycatchers are specialized dietarily compared with temperate species using a strategic approach (appropriate for this comparison), but the two groups do not differ using the more traditional tactical approach; and (3) particular species of Neotropical frugivores are specialists by strategic definitions, but generalists by tactical ones, a distinction that resolves unnecessary controversy in the literature.

Key Words: Diet breadth, foraging behavior, generalist, niche breadth, opportunism, resource, specialist, stereotypy, Tyrannidae.

Questions concerning ecological specialization continue to fascinate and challenge biologists. Ecologists, for example, ask whether species-rich (especially tropical) communities have relatively specialized species, whether ecological specialists are better competitors than generalists, or whether specialization favors exploitation efficiency. Evolutionary biologists ask questions such as whether evolutionarily derived species are specialized compared with ancestral ones, whether adaptive radiation involves ecological specialization, whether specialization tends to increase over time in fossil lineages, or whether specialists are more extinction-prone than generalists. But what is a specialist? The literature contains a morass of definitions, conceptual approaches, and methods, with no concensus on their applicability.

One prevalent notion is that specialists select a relatively narrow range of foods. By this intuitive notion, some animals are unambiguously specialists: Pandas (*Ailuropoda melanoleuca*) on bamboo, Everglade Kites (*Rostrhamus sociabilis*) on snails. Each has specialized morphology and behavior with which to eat a consistently narrow range of food types throughout the year. However, most species are not so clearly specialized, thus necessitating operational methods to quantify degree of specialization (i.e., position along a hypothetical continuum from specialization to generalization). This need becomes more apparent when we consider the successful evolutionary radiation and abundances of terrestrial birds, particularly Passeriformes, the overwhelming majority of which are relatively generalized insectivores, frugivores, nectarivores, or granivores (Karr 1971, Morton 1973, Rotenberry 1980a).

Categorizing species as specialist or generalist can be ambiguous. The Cocos Flycatcher (*Nesotriccus ridgwayi*), for example, is a specialist or generalist depending on the frame of reference and the methods used to quantify specialization (T. W. Sherry 1985), as elaborated below. Wiens and Rotenberry (1979) and Rotenberry (1980a) equated opportunism with the absence of specialization, and noted that degree of opportunism was ambiguous for some species: The Grasshopper Sparrow (*Ammodramus savannarum*), for example, was opportunistic by the criteria of broad individual diet niches and high overlap with other species, but was relatively specialized based on a relatively narrow population niche breadth and little annual variation. Thus, compared with sympatric species in the shrub-steppe environment, Grasshopper Sparrows were relatively specialized; yet, if one considers that all these shrub-steppe species were at least partially migratory and that their diets varied more seasonally and geographically within than among species (Wiens and Rotenberry 1979), all were opportunists adapted to variable environments. Fox and Morrow (1981) also noted that herbivorous insects feeding on *Eucalyptus* were specialists or generalists depending on scale.

Resolutions to the above ambiguities depend on how we conceptualize and quantify "specialization," and the temporal and spatial scales of concern. Terminology about specialization and related phenomena (stereotypy vs. opportunism, monophagy vs. polyphagy) are used differently by biologists, leading to confusion. In this review I examine how conceptualizations about nature motivate operational methods, and conversely how methods clarify the (often unstated) assumptions of particular investigators.

Ellis et al. (1976) distinguished between "tactical" (ecological) and "strategic" (evolutionary) approaches to diet selectivity. They acknowledged that tactical approaches had received more attention, and then explicitly used a tactical approach. If anything, the emphasis on tactical approaches is greater today than when they wrote. Whatever the actual imbalance, however, the two approaches generate fundamentally different, and sometimes contradictory results, and in failing to distinguish between them one can draw incorrect conclusions. Thus, my second purpose is to distinguish these approaches, and show with explicit examples the dangers of confusing the two.

Although I concentrate on dietary specialization in this review, I ask how dietary specialization is related to an organism's phenotype, especially foraging behavior and morphology, to make the distinction between tactical and strategic approaches. I will focus on methods to quantify specialization, considering examples outside of the bird literature either where they would be useful to avian biologists or where examples are particularly clear.

TACTICAL APPROACHES TO DIETARY SPECIALIZATION

Here I trace some history of theory motivating methods to quantify dietary specialization to understand the necessity of the methods; I then briefly describe and in some cases evaluate these methods with examples wherever possible.

NICHE THEORY

Niche theory has arguably provided the greatest motivation for measures of specialization. Although ecological concepts of the niche were first developed in the early 1900s, G. E. Hutchinson, R. H. MacArthur, and others in the late 1950s and early 1960s formulated an operationally powerful concept (the n-dimensional hypervolume), which had an enormous impact on theoretical and empirical ecological studies (Pianka 1981, Ehrlich and Roughgarden 1987). This variety of studies has coalesced into a school of population ecology, based largely on a concept of the niche centering on competition for resources within a one- (or n-) dimensional space within which each species occupies its own resource space, often represented by a bell-shaped resource-use probability distribution (e.g., McNaughton and Wolf 1970, Vandermeer 1972, MacArthur 1972, Pianka 1981).

Niche breadth in these models is an important parameter used to describe the size of the individual species' niche, or the range of resources or resource states used by that species, and has been related to the number of species within a community. MacArthur (1972), for example, developed a geometric model for species diversity within a community based on the average niche breadth, niche overlap, and total resource spectrum. Many empirical studies have been undertaken to quantify niche parameters, especially niche breadth, based largely on food sizes or types, or on surrogates for food, such as foraging behavior and morphology. All of these quantities are considered substitutes for fitness, the quantity defining the success of a species within Hutchinson's (1957) original niche model.

In this review I divide niche breadth measures into those that are applicable to any consumer population versus those for an entire community. "Single-species measures" may be subdivided depending on whether relative proportions of food categories in the diet or availabilities of different resource categories are used in the calculations. "Multi-species measures," including multivariate statistical procedures, necessitate study of many species simultaneously, and are particularly useful to test hypotheses about multiple communities of organisms.

Single-species measures

Niche theorists view degree of ecological specialization as the inverse of niche breadth (Colwell and Futuyma 1971, Morse 1971b, Hurlbert 1978, E. P. Smith 1982, Holm 1985) and have developed measures to quantify them. The simplest dietary diversity index is the number (or richness) of food taxa in the diet (Herrera 1976, Wheelwright and Orians 1982, Wheelwright 1983, Moermond and Denslow 1985). This measure has the disadvantages of equating frequently with infrequently used foods, and of equating different items, such as adult and larval insects, which may not be functionally equivalent from the perspective of the predator (see below).

A second group of diversity indices incorporates the relative proportion, p_i, of resources or resource categories, where $\Sigma p_i = 1$, and i is one of the r resource states. Among the most widely used are those attributed to Simpson, Levins, Shannon-Wiener, and Brillouin (see Pielou 1975 for a general discussion of their derivation and use). Simpson's index, lambda = Σp_i^2, measures the concentration or dominance of observations (food types, for example) in one or a few categories, and forms the basis of several measures (Pielou 1975). Levins (1968) was the first to use such a measure (B) in a form sometimes (but not always) standardized for comparative purposes by the number (S) of resource states (i.e., $B = 1/[S \cdot \Sigma p_i^2]$). This index has desirable characteristics including simplicity and ease of calculation (e.g., Rotenberry 1980a). Another index is that of Brillouin, given by $H = (1/N) \cdot \log[N!/(n_1! \cdot n_2! \cdot \ldots \cdot n_i!)]$, where there are $n_1, n_2, \ldots, n_i$ prey items in each of i categories, with N total prey items in the collection. It measures the diversity or breadth of a complete collection of items, and the Shannon-Wiener index, $H' = -\Sigma (p_i \cdot \log[p_i])$, measures the diversity of a sample of items, providing an estimate of the unknown actual diversity of an entire population (Pielou 1975). All of these measures equate narrow breadth (specialization) with the use of few resource states, the opposite of information (or entropy) as measured by the information-theory indices. The latter two have the advantage of generalizeability to hierarchical measures of diversity, that is, the diversity weighted by the taxonomic similarity of items within the collection (Pielou 1975).

All these indices based on relative proportions of entities in different categories, whether used to quantify dietary diversity or "species diversity" in a community, confound two quantities, the total number of kinds (richness) of entities and the equitability (= evenness) of their use. The maximum evenness of resource use occurs when all resource categories are used equally, that is, $p_i = 1/r$, and evenness is often measured by the ratio of the actual diversity index to the maximum possible value (see Peet 1974 and Pielou 1975 for further discussion). Herrera (1976) developed a trophic diversity index for use with presence-absence data that reflects the richness rather than evenness component of diet, but is significantly correlated with the Shannon-Wiener diversity index.

None of the above indices provides realistic estimates of diversity when one is sampling a large number of species or resource categories, for which the total richness of entities in the population is unknown (Pielou 1975). For this situation, Pielou developed an asymptotic method in which diversity (calculated with the Brillouin index) is plotted as a function of sample size: With an adequate sample size one obtains a curve increasing from zero but at a decreasing rate towards an asymptote when new samples add little new information about the population. Diversity of the entire collection with unknown S, or number of species, is then estimated from the asymptotic (plateau) part of that curve. Hurtubia (1973) recognized that stomach contents of animals are usually incomplete, and nonrandom, samples of the larger population of potential prey types, and applied Pielou's method to a study of lizard diets. I (T. W. Sherry 1984, 1985) applied it to stomach contents of tropical flycatchers to show that their dietary diversity varied from zero in one flycatcher species, in which every stomach contained essentially one and the same prey type, to a large (unknown) dietary diversity for which available stomachs had too diverse prey types to estimate a population asymptote. This method merits further use with stomach-content data.

Organisms may specialize because few resources are available in a particular environment, or because characteristics of the organism constrain diets. One definition of specialization is thus "a deviation from random feeding by the animal as imposed by its own attributes rather than by the environment" (Holm 1985, after Hengeveld 1980). To measure this one can compare the diet with available resources using simple statistical procedures such as chi-square tests. Such comparisons overwhelmingly show that organisms, including birds, are specialists (e.g., Holmes 1966, Hespenheide 1975b, Morse 1976a, Abbott et al. 1977, Toft 1980, Steenhof and Kochert 1988; see also discussion of electivity and selective predation studies, below). Toft (1980) and T. W. Sherry (1985) documented cases in which an organism consumed prey types in proportions indistinguishable from those deemed available. In the latter case, Cocos Flycatchers ate prey in proportions indistinguishable from those sampled with beating nets in the leafy vegetation where this species feeds. Sampling of available resources in this case did not include tree-trunk insects, fruit, or nectar, foods that Cocos Finches consume in the same habitats (Werner and Sherry 1987), so they are thus available in an evolutionary sense to the flycatcher. Clearly it is operationally difficult to characterize prey effectively "available" from the predator's perspective, leading many (e.g., Ellis et al. 1976, Wiens 1984b, Hutto, this volume) to distinguish between food availability and abundance.

Johnson (1980) used contrived examples to show how inclusion or exclusion of particular resource categories can greatly influence one's conclusions. He developed a method based on differences between ranks of resources used and available, and he developed statistical tests for his method. Craig (1987) presented data on rank differences of resources used versus available in two species of waterthrush (*Seiurus*), but did not test the null hypothesis statistically. Johnson's method is a useful, if not overly simple, method with broad potential applicability.

E. P. Smith (1982) reviewed four indices (developed by Feinsinger, Petraitis, Hurlbert, and by Smith himself) that calculate niche breadth based on resources used and available. He showed that Hurlbert's index is relatively sensitive to rare items, whereas Feinsinger's index favors more abundant items. Petraitis' and Smith's own indices are less sensitive to selectivity by the predator, but Smith's measure is superior when used in statistical models such as ANOVA. All these metrics assume that the "resource vector is multinomial, and the resource availabilities are fixed and known" (p. 1679), circumstances which may not always obtain, thus complicating statistical analyses (E. P. Smith 1982). Hurlbert (1978) also discusses indices for niche overlap, patchiness (frequency of intra- or interspecific encounter with respect to resource states), and breadth, as well as their mathematical interrelationships. He points out the importance of how resources are defined (see below), whether they are arbitrary or discrete natural entities, whether or not "empty" resource states are excluded from analyses, and whether or not all individuals in a population are identical.

Multi-species measures

When we consider simultaneously the food resources of more than one consumer, the simplest operational procedure is to compare and contrast diets using simple statistics, just as in the comparisons of food used versus that available. One may use statistics such as chi-square, or the related, but more versatile and powerful G-statistic (Sokal and Rohlf 1981:692), to test hypotheses when data are counts of resource categories used. Craig (1987) showed in this way that two sympatric waterthrush species fed on different prey taxa and sizes, and Smith (1987) tested hypotheses about intraspecific resource partitioning. Reynolds and Meslow (1984) used parametric statistics to compare food sizes of different bird species.

With data on how two or more populations use the same set of resource states, one can calculate a variety of niche statistics such as mean niche breadth for each population or species as well as standardized indices for comparisons among sets of species or sites (Pielou 1975). Specifically, one needs frequencies of occurrences (such as numbers of individuals of population x in a quadrat, in the case of a species-by-quadrat matrix) as observations. Pielou recommended use of this method with sessile or relatively sedentary organisms, but others have relaxed this requirement, by choosing resource states appropriate in scale to the question of interest. Colwell and Futuyma (1971) devised a related method that weights each resource state in proportion to its distinctness from the perspective of the organisms under consideration (based on how much new information each category adds to the total resource information). This procedure corrects for problems involved in considering the range of resources used by an assemblage of organisms, but it has been used infrequently (Heyer 1974, Jacsic and Braker 1983). Hanski (1978) suggests using predator abundance as a surrogate for resource productivity. Both Pielou's (1975) and Colwell and Futuyma's (1971) methods and refinements could be used to compare niche breadths (and overlaps) among avian species by using a matrix of species (rows) by prey categories (columns), in which the entries are absolute frequency of occurrences or estimated energetic equivalents.

Multivariate statistics provide another tool to quantify diet or habitat niches. Discriminant function analysis (DFA) has been used most frequently for niche studies, because it is applicable to a data set with *a priori* groups (e.g., species), and DFA determines what combination of resource states maximizes the differences among the groups, giving it a geometric interpretability consistent with the Hutchinsonian niche (Green 1971, 1974; Carnes and Slade 1982). Use of DFA also follows from Levins' (1968) reference to the dimensionality of the niche as the number of factors that separate species ecologically (Carnes and Slade 1982). Principal components analysis (PCA) is another multivariate technique, whose axes are not selected with reference to any *a priori* groups, thus avoiding the bias towards finding differences among groups (Rotenberry and Wiens 1980b). In PCA, axes are selected that account sequentially for the maximum remaining variation in the distribution of all observations, regardless of group affiliation. In either case (DFA or PCA) one ends up with a set of orthogonal, i.e., statistically independent, axes among which the positions of observations (by species, for example) can be located and compared or various niche metrics calculated (James and McCulloch 1985).

Niche breadth is the distance through the n-dimensional cloud of points characterizing a particular species in multivariate space. Green (1974: 77), for example, noted that "niche breadth along a particular dimension can be defined and measured by the length of the projection of the k-dimensional probability ellipse on a given axis." Dueser and Shugart (1978, 1979) rejected Green's method used with DFA for small mammal microhabitat and habitat niches; instead they determined niche width as the coefficient of variation of distances, measured from the location of observations for each species to the centroid for all species in the community. Carnes and Slade (1982) and Van Horne and Ford (1982) criticized Dueser and Shugart's (1979) method because centroid locations depend on species sample sizes. Van Horne and Ford (1982) also noted that confidence ellipses, such as Green (1974) used, are dependent on sample size, and thus are inappropriate to compare species. One solution is to equalize sample sizes of common and rare species, including the use of rarefaction techniques (C. J. Ralph and M. L. Morrison, pers. comm.). With unequal sample sizes Carnes and Slade (1982) suggested that standard deviations or variances of canonical scores are preferable to coefficients of variation to quantify niche breadth. They recommended including resource states not occupied by species in the overall analysis (so that the centroid is weighted by both the abundance of species' sample sizes and the actual availability of habitats), and measuring niche width using mean squared distances for each species ($\Sigma\, d^2_{ij}/n_{ij}$), where d_{ij} is the distance of each observation of a species in canonical space to the species centroid in that space. This measure also lends itself to statistical comparisons of species (Carnes and Slade 1982). Multivariate methods have been used extensively in studies of avian habitat (e.g., Rotenberry and Wiens 1980b, Capen et al. 1986), but not dietary niche breadth, perhaps because some authors (e.g., Deuser and Shugart 1979) assume that habitat dimensions of the niche adequately reflect other resources.

Resource definition

A crucial consideration to most if not all niche breadth methods is how one operationally categorizes food resources, especially from the consumer's perspective. A common trend has been to concentrate on prey size categories, to the exclusion of prey taxa (Hespenheide 1975a, Greene and Jaksic 1983). Ehrlich and Roughgarden (1987) concentrate so heavily on prey and predator size relationships in treating community structure that other prey characteristics are seemingly unimportant to competition and predation. Other authors have discussed prey types explicitly. Hespenheide (1975a, b) recognized that insectivorous birds often have different dietary relationships based on prey types rather than sizes, because size and catchability of prey vary in complex ways among different insect taxa. Greene and Jaksic (1983) argued that prey taxa are more important than prey sizes in understanding competitive potential. Grant (1986:120) noted that small Darwin's finches (Geospizinae) ate a greater diversity of food resources than larger finches, because smaller species ate a great taxonomic diversity of small, soft seeds; larger finch species, on the other hand, ate a greater diversity of seed categories (based on hardness and size). Colwell and Futuyma (1971) clearly recognized the problem of identifying meaningful resource categories in proposing their method (discussed above) to scale resource categories so as to reflect their distinctness from the perspective of the organisms under consideration. I (Sherry 1984) solved the same problem by using cluster analysis of prey categories in stomachs of tropical flycatchers to obtain a recipe for pooling categories that tended to be correlated in their occurrence among flycatcher species' guts. Flycatchers with Orthoptera in their guts, for example, also tended to eat Lepidoptera larvae (caterpillars), probably because both prey types are often slow-moving and diurnally cryptic, so that a predator searching for one tended to encounter the other.

How finely one subdivides prey taxa can influence diet breadth calculations. Pooling prey taxa into large categories risks underestimating niche breadth as compared with calculations based on lower taxonomic levels, such as species and genera (Greene and Jaksic 1983). Indeed, vertebrate prey species may each pose distinctive challenges to their predators in terms of distribution, size, catchability, and other characteristics, and thus species-level prey categories may be appropriate (Greene and Jaksic 1983, Steenhof and Kochert 1988). To a tropical insectivorous bird, however, the tens of thousands of potential insect prey species cannot all be functionally distinctive from the birds' perspective, even if one could practically identify each prey item to species. The dozens of fruit species eaten by many frugivores may also not all be functionally distinct. Thus finely subdivided taxonomic categories can potentially overestimate niche breadth. I conclude that the level of resource identification is important, but probably no one method will suit all groups.

MECHANISTIC APPROACHES

Simulation models

Systems ecologists developed one approach to diet specialization based on conceptualizing all the processes affecting diets, modeling their effects mathematically, and measuring the necessary quantities both to provide necessary model parameters and to validate the model (Wiens and Innis 1974, Ellis et al. 1976; see Swartzman and Kaluzny 1987 for a general account of simulation modeling). The resulting model is usually designed to be precise and specific in its predictions and applications. Few avian studies have taken this approach, perhaps because of the large effort required to estimate all necessary parameters. Heuristic models, by contrast, attempt to characterize one or a few key processes such as diet selectivity as a function of food abundance (e.g., MacArthur and Pianka 1966).

Experimental approaches

Biologists have used experimental approaches to determine how individual consumers make prey choices over short time periods relative to the animals' generation time. Although such methods may not have been intended to characterize degree of specialization, I mention them here because some have been used to study diet selectivity.

One of the most obvious ways to study selectivity is to present animals with different food types under laboratory or field conditions. This approach has been used to study prey-handling abilities and mimicry (e.g., Smith 1975; Sherry 1982; Chai 1986, 1987), fruit acquisition and handling (review in Moermond and Denslow 1985), and seed-size selection in finches (Hespenheide 1966, Willson 1971, Grant 1986, Benkman 1987a). Chai's (1986, 1987) work, for example, showed that the behavior of an evolutionarily specialized butterfly predator, the Rufous-tailed Jacamar (*Galbula ruficauda*), led to different conclusions about mimicry than studies with nonspecialists that rarely consume butterflies. This experimental approach can elucidate factors involved in the evolution (or coevolution) of both prey and predator characteristics (see also Holmes, this volume), as well as identify tactical responses and capabilities of the predators.

In laboratory experiments behavior must be studied under conditions equivalent to those encountered in the field. In a study of rictal bristle function in flycatchers, for example, Lederer (1972) commendably tested functional morphological hypotheses with an experimental procedure, but performed the experiments under lighting conditions (not adequately specified) bright enough to allow high-speed photography; neither lighting conditions nor prey type (flesh flies, *Sarcophaga*) may have been appropriate to the hypothesis, since those flycatchers with the best-developed rictal bristles are tropical species such as *Terenotriccus, Myiobius,* and *Onychorhynchus,* all of which acrobatically pursue evasive insects (few of which are Diptera) in often poorly and variably lighted tropical rainforest understory (Sherry 1982, 1983).

A widespread approach to diet selectivity and electivity looks at how predators preferentially use or ignore specific food types, usually as a function of food abundance or other characteristics. Tinbergen (1960) showed in a classic paper that titmice (*Parus* spp.) consumption rate varied sigmoidally with caterpillar abundance, and proposed the concept of "specific search images" to explain his results. Ivlev (1961) conducted experimental laboratory studies of fishes, and coined the term electivity for their selecting particular prey in proportions not equal to availability. Subsequent studies have distinguished alternative predatory responses to changing resource abundance, including "switching" (Murdoch 1969, Murdoch and Oaten 1975) and functional responses (Holling 1959b). A popular quantitative approach to questions of electivity is to use indices designed to determine prey preferences when all prey are equally available: Essentially these indices are vectors of *m* different prey preferences (or aversions) for *m* prey types under consideration in a particular situation (reviewed by Chesson 1978, 1983). Statistical tests of the null hypothesis that a particular predator's electivities are all zero have also been devised and discussed (Neu et al. 1974, Johnson 1980, Lechowicz 1982). Most electivity studies are done in the lab to control prey types and abundances (e.g., Freed 1980, Chesson 1983, Annett and Pierotti 1984). Steenhof and Kochert (1987) quantified electivity for particular prey types of raptors in the field, and showed that their diets responded most to changes in preferred prey, as predicted by prevailing optimal diet methods, discussed next.

Optimal foraging and optimal diet studies

The voluminous literature on optimal foraging has been extensively reviewed (Krebs et al. 1983, Krebs and McCleery 1984, Stephens and Krebs 1986, Stephens, this volume); here I mention only a few findings relevant to dietary specialization. The first optimal foraging models predicted explicitly that diet specialization should vary positively with food abundance (Emlen 1966, MacArthur and Pianka 1966), and a variety of empirical studies essentially verified this prediction, at least in a qualitative sense (Krebs et al. 1983). More recent models have been developed to address such complicating matters as patch selection, learning and prey-recognition problems, conflicting demands (such as feeding and avoiding predators), and stochastic variation in resources (Krebs and McCleery 1984, Stephens, this volume). These more recent models have also tended to make fewer explicit predictions about diet breadth *per se* than the original models. The main point, however, is that most optimal foraging and optimal diet theories and tests are concerned with short-term (less than generation time) adjustments of behavior of individuals to changing environments. Such approaches explicitly take the phenotype as given, and ask how behavior changes with ecological circumstances given the phenotypic constraints (Krebs et al. 1983, Krebs and McCleery 1984, Stephens and Krebs 1986), rather than asking how the phenotype may have been shaped by ecological circumstances over evolutionary time. Thus optimal foraging or diet approaches have tended to be tactical rather than strategic.

EVOLUTIONARY APPROACHES TO DIETARY SPECIALIZATION

Adaptation as Specialization

Evolutionary biologists have often equated specialization with adaptation, often viewed as a "perfecting" force (e.g., Leigh 1971, Holm 1985). At the levels of organization of communities, biomes, or biogeographic realms, adaptive radiation into present-day faunas results from all processes leading to species specialized on nonidentical subsets of the total resources in the environment. Among avian biologists, Leisler (1980), Grant (1986), and Craig (1987) illustrate the use of diverse behavioral, genetic, and ecological methods to examine the evolutionary diversification of related species. The disadvantage of defining specialization simply as adaptation or adaptive radiation is its comprehensiveness: All species are automatically specialized in relation to other species, with no explicit notion about degrees of specialization. Studies of coevolution have added a related concept of specialization, namely the evolutionary interdependence of two species (or more, in the case of diffuse coevolution; Janzen 1980b).

Functional Studies

Comparative method

One must study the function of adaptations before asking questions about degrees of evolutionary specialization dependent upon those adaptations. Various methods have been developed to study adaptations, based on comparing different species' phenotypic characteristics (e.g., morphology, anatomy, physiology, behavior) with their ecological ones, such as habitat, feeding behavior, and diet. The "comparative method," perhaps the most flexible and widely used approach to adaptation, compares different adaptations with different ecological circumstances of two or more species to deduce the function of relevant traits, and is most powerful when it deals with instances of convergent evolution (James 1982, Futuyma 1986). Phylogenetic information is required to assess the possibility of convergence, and both experiments and analyses of fitness are necessary to test hypotheses about function (Futuyma 1986). VanderWall and Balda (1981), for example, documented in four corvid species a graded series of behavioral, morphological, and life-history adaptations for exploiting conifer seeds in mountains of the southwestern United States. The four species, ranked in decreasing order of evolutionary specialization on pinyon pine seeds (Clark's Nutcracker [*Nucifraga columbiana*], Pinon Jay [*Gymnorhinus cyanocephalus*], Steller's Jay [*Cyanocitta stelleri*], and Scrub Jay [*Aphelocoma coerulescens*]), showed corresponding reductions in seed selectivity, seed transport volume and distance, flight speed, cache size, bill length, development of seed-carrying structures, and ecological dependence on pine seeds both as adults over winter and as nestlings. The often implicit assumption that all phenotypic characteristics result from natural selection acting directly on particular traits, an operational approach referred to as the "adaptationist programme," has flawed some comparative studies (Gould and Lewontin 1979, Futuyma 1986).

Ecomorphology studies

Associated with niche conceptualizations of communities, ecomorphological studies often use multivariate statistics to explore the meaning of morphological characteristics. A basic premise is that by averaging evolutionary forces over long time periods, morphology provides the best measures of the ecological interactions of species (Karr and James 1975, Ricklefs and Travis 1980). Canonical correlation analysis (e.g., Karr and James 1975, Leisler and Winkler 1985) and correspondence analysis (Miles and Ricklefs 1984) are just two methods used to examine correspondences of morphological and ecological data. Foci of ecomorphological studies have varied (James 1982), but include the correspondence of morphology with behavior and ecology (e.g., Sherry 1982, Leisler and Winkler 1983, Miles and Ricklefs 1984), and "species packing" (Findley 1976, Karr and James 1975, Gatz 1980, Ricklefs and Travis 1980). Species packing should increase with either increased niche overlap or narrower niches (MacArthur 1972), but too few studies have looked at both overlap and packing to get at niche breadth.

Too few studies have paid attention to the function or efficiency of phenotypic characters in comparative studies (for nice recent examples see Greene 1982; Liem and Kaufman 1984; Moermond and Denslow 1985; Benkman 1987a, b; Moermond, this volume). In an elegant experimental study, Laverty and Plowright (1988) showed that naive individuals of a specialized bumblebee species (*Bombus consobrinus*) feed more efficiently on the preferred flower type (Monkshood, *Aconitum* spp.) than do either of two generalist congeners.

Common-garden methods

Any laboratory or field study in which different individuals or populations are exposed, usually experimentally, to the same conditions in one or more environments is a common-garden method, and can potentially provide information on relative performance, ecological efficiency, and fitness. In transplant experiments, for example, James (1983) showed that the environment contributes significantly to size and shape variation of nestling Red-winged Blackbirds (*Agelaius phoeniceus*). Sherry and McDade (1982) showed that a small tyrannid "sit-and-wait" predator (*Attila*) had significantly longer handling times for acridid-tettigoniid Orthoptera than a larger puffbird (*Monasa*) feeding on the same sizes and types of prey. Garbutt and Zangerl (1983) described a general method to analyze results from a common-garden experiment that provides a measure of niche breadth and performance efficiency. Their method can use any measure of performance (such as reproduction, growth, feeding efficiency, or other components of fitness), and could be used with animals.

Comparative psychology

Because species diverge in learning or behavioral traits, comparative psychology provides another class of evolutionary studies with relevance to diet specialization. For example, Greenberg (this volume) has documented differing degrees of "neophobia" among closely related birds. These apparently genetically based differences in fear of approaching novel microhabitats, based on studies of hand-reared individuals, influence the range of microhabitats (and thus diet breadth) of these species in the wild. Neophilia, the complementary behavior, seems particularly well developed in the Cocos Finch (*Pinaroloxias inornata*), living in an almost predator-free environment. Its diet is extremely broad, and individuals appear capable, at least as juveniles, of observing and learning from a diverse array of conspecific and other animals about how and where to feed (Werner and Sherry 1987; see also McKean, this volume). Juvenile Cocos Finches in particular appear to exhibit exploratory behavior towards potential prey objects and substrates, and to observe closely a variety of potential tutors (T. K. Werner and T. W. Sherry, pers. obs.).

A variety of other behavioral attributes can influence diet breadth and stereotypy. The ability of a species to learn from (and to teach) other animals, i.e., culture, is ultimately genetically determined (Bonner 1980) and can influence feeding behavior, as in the case of tool-use (Morse 1980a) and aggregative feeding and nesting behavior (Rubenstein et al. 1977; C. R. Brown 1986, 1988), the efficiency of locating or handling prey types (Waltz 1987), array of foods used (Rubenstein et al. 1977, Giraldeau 1984), acquisition of food aversions (Daly et al. 1982, Mason et al. 1984, Shettleworth 1984), and cooperative hunting (Bednarz 1988). Ability to memorize characteristics of an environment, such as where Clark's Nutcrackers have cached seeds (Kamil and Balda 1985), should facilitate specialization on the seeds. All of these behaviors vary among species, and can influence the range of food types eaten. Biologists have barely begun to explore these influences, let alone genetic constraints involved.

DIETARY INDICES

Dietary homogeneity

A predictable environment is a *sine qua non* of specialized evolutionary relationships such as complex adaptations, obligate mutualism, and other forms of coevolution. In a classic study of ant-plant coevolution, for example, Janzen (1966) stated explicitly the importance of environmental predictability allowing mutualism to evolve and persist in certain environments. Morse (1971b) recognized the importance of stereotypy versus opportunism of resource use patterns in birds. Colwell (1973) specified how certain strategies of species coexistence are favored by the relative predictability of tropical compared with temperate environments. Southwood (1977) noted that individuals, populations, and species should feed more flexibly in disturbed than undisturbed environments. Wiens and Rotenberry (1979) characterized all their shrub-steppe bird species as opportunistic, stressing the unpredictability of these environments from the perspective of birds (see also Futuyma 1986, and literature cited, and Howe and Estabrook 1977). Both empirical and theoretical studies concur that environmental predictability favors the evolution of individual feeding specializations (Werner and Sherry 1987). Glasser (1982, 1984) developed from niche theory a model of trophic specialization based explicitly on resource predictability. It follows that environmental predictability allows some organisms to evolve relatively obligate dependence on resources or on other organisms, and thus to evolve more efficient, elaborate, or complex adaptations appropriate for those specific, predictable environmental circumstances. Resource predictability is probably a function of abundance.

One may test hypotheses about the evolution of dietary specializations by assuming that resource variability over short time periods today is proportional to what the organism has experienced evolutionarily, and then measuring this variability. Direct measures of resource variability have been made in several cases, such as arthropod abundances in rainforest understory versus other tropical habitats (Sherry 1984). Variability in resource types among individuals of a population provides a surrogate measure of resource predictability from the organism's perspective. I (Sherry 1984) thus sampled diets (using stomach contents) of tropical flycatchers across a broad geographic area in Caribbean Costa Rica during the period of year (October–December) inferred to be most food-limiting to these birds, over a 3-year period. I calculated "population dietary heterogeneity" (*PDH*) from a matrix of prey taxa by stomachs using the *G*-statistic (Sokal and Rohlf 1981) divided by degrees of freedom. The result was that several of these tropical insectivorous species had extraordinarily homogeneous stomach contents, expected in relatively constant tropical environments (see below). Steenhof and Kochert (1988) used this index to show that diets were most homogeneous within years in the raptor species with the most consistent diets over an 11-year period (encompassing dramatic changes in prey abundance). Werner (1988) also used it to quantify effects on foraging behavior of foraging location, individual bird, time of day, season, and error variation in a Cocos Finch population. Kincaid and Cameron (1982) used a multivariate coefficient of variation in diets, and Roughgarden (1974) partitioned niche width into two components, between-phenotypes (a high value indicating considerable variation among individuals) and within-phenotypes. Other authors have examined dietary correspondence with morphology in species with continuous (Grant 1986) or polymorphic (Smith 1987) morphological variation.

When diets vary among individual animals (e.g., Smith 1987, Werner and Sherry 1987), inferences about resource variation from dietary variation depend on how individual animals feed over long time periods. This is because dietary variability can arise either because environments vary (e.g., Wiens and Rotenberry 1979, Sherry 1984) or because individuals vary independently of each other within constant environments. Foraging behavior of Cocos Finches varied dramatically among individuals within a constant oceanic island environment (Werner and Sherry 1987, Werner 1988), for example, but the foraging consistency of marked individuals year-round indicated that they perceived the environment to be predictable. Conversely, a short-term study might document a misleading degree of dietary homogeneity for the actual variability of the environment, if observations spanned a short time period (e.g., a season) within which all individuals opportunistically fed on the same relatively profitable food (e.g., Fenton and Thomas 1980). Thus studies of dietary homogeneity must span multiple seasons and multiple years to indicate different degrees of variability in long-lived vertebrates such as birds.

Unique food types

Comparatively extreme species along a particular phylogenetic pathway may be identified by relatively unique phenotypic, foraging behavioral, or dietary characteristics. Fitzpatrick (1985) referred to particular tyrannid species that are both highly stereotyped in terms of foraging behavior and represent extreme morphological development in a particular lineage (such as the genus *Todirostrum*). Leisler (1980) spoke of the Lesser Whitethroat (*Sylvia curruca*) as a specialist in this sense (see also Toft 1985). I (Sherry 1982, 1984) showed that a few flycatcher species ate peculiar foods eaten by few other species (e.g., some *Todirostrum* spp. ate relatively alert and agile muscoid Diptera that few other birds appear capable of capturing). Meylan (1988) identified hawksbill turtles (*Eretmochelys imbricata*) as sponge specialists, in part based on how few other vertebrates eat sponges regularly, and in part on the consistency of their diets over much of their geographic range. Multivariate statistical procedures should be appropriate to quantify extreme dietary characteristics (e.g., using the deviation in morphological space from a particular species to the centroid for all species; but see "Multi-species measures" above for dangers inherent in this approach), or distance (in some evolutionary units) from a hypothetical ancestor for the group as a whole. To my knowledge, no one has yet developed quantitative indices for degree of "extremeness," as reflected in dietary or morphological characters.

A special case of specialization on unique prey items, suggested by H. A. Hespenheide (pers. comm.), is specialization on prey types that are distasteful or repugnant to most predators. Some predators have evolved special abilities to overcome this, such as woodpeckers that prey on ants (that contain formic acid), Nunbirds (*Monasa morphoeus*) that prey on aromatic and aposematic stinkbugs (Pentatomidae; Sherry and McDade 1982), orioles (*Icterus* spp.) and the Black-headed Grosbeak (*Pheucticus melanocephalus*) that select palatable parts of unpalatable monarch butterflies (*Danaus plexippus*) (Calvert et al. 1979), and bee-eaters (Meropidae) that devenom bees prior to ingestion (Fry 1969).

Inclusive-niche Model

A common pattern within guilds of species (Root 1967) is for one species to have its fundamental niche nested within that of another species, and for the socially dominant—usually larger—species to have the smaller niche (Miller 1967, Case and Gilpin 1974, Morse 1974b, Sherry and Holmes 1988, Sherry 1979, Colwell and Fuentes 1974, Rosenzweig 1985). Thus, the dominant species is specialized relative to the other in the range of environmental circumstances tolerated. In the case of diets, we expect dominant species to tolerate a narrower range of food types or show less feeding flexibility and opportunism than subordinates (Morse 1974b, Sherry 1979). Insofar as this nested pattern of niches involves the fundamental, rather than realized, niche, this pattern involves evolutionary responses of one of the organisms to the other (or reciprocal evolutionary responses), but the causes and consequences of such patterns remain unclear.

Summary of Methods to Quantify Dietary Specialization

The foregoing review indicates diverse conceptual approaches to quantifying dietary specialization. Some of this diversity results from the use of different time scales: some indices involve short-term (behavioral, cognitive) responses of organisms; others involve ecological time-periods; yet others involve evolutionary time-scales. These different time scales also involve different levels of organization (e.g., tactical individual vs. strategic population or species approaches) and Sherman (1988) argued that behavioral questions often have different answers at different levels of organization. Approaches to dietary specialization are thus not mutually exclusive, which probably explains why none has emerged as the best under all circumstances.

ECOLOGICAL VERSUS EVOLUTIONARY DIETARY SPECIALIZATION

The preceeding review considered intentions as well as limitations of particular paradigms and studies. In this section I evaluate how these methods quantify either tactical or strategic aspects of dietary specialization, but rarely both.

Tactical Approaches

Studies of dietary specialization motivated by niche theory have generally characterized foraging behavior or diet by either the range of resources used by a species, or by the degree to which resource use matches availability. Operationally, the procedure is to gather data on some individuals within a population, and pool the data into a population-, or species-specific characterization. These characterizations are then used to study the entire niche space of many species, the packing of species into this space, the overlap of individuals or populations with respect to resource use, and related niche parameters. None of these measures or procedures contains information about the variability of resources experienced by populations at present, let alone over past time periods. Moreover, much of niche theory was developed from the Lotka-Volterra population growth equations (e.g., MacArthur 1972), which describe ecological-scale processes in response to either resource abundance or the competitive influences of other species.

Ignoring differences among individuals provides no perspective about stereotypy and opportunism, information needed in evolutionary approaches to specialization, and pooling data can lead to statistical problems as well (Hurlbert 1984). I emphasize that these sources of individual variation in dietary and other parameters are not only useful statistically, but are critical to strategic questions about populations and communities.

Optimal diet and optimal foraging studies have also tended to examine tactical questions, often by taking the phenotype as a given, thus defining away the question of how the phenotype came to be the way it is. Optimality studies also tend to examine short-term responses, rather than long-term evolutionary responses of organisms to variability and other patterns of resource abundance. Several authors have explicitly recognized this distinction between tactical and strategic approaches to diets (e.g., Ellis et al. 1976, Glasser 1984, Krebs et al. 1983, Holm 1985, Stephens and Krebs 1986), but have usually taken a tactical approach.

Evolutionary questions need not fall outside the domain of optimality studies. The theory of evolutionarily stable strategies models the conditions for evolutionary persistence of alternative strategies (e.g., of resource use or mating tactics). Glasser's (1982, 1984) studies of trophic strategies incorporate resource predictability as well as abundance, thus incorporating an evolutionarily critical parameter. A variety of design and engineering approaches to the analysis of adaptations (e.g., Leigh 1971) are essentially optimality models as well.

Strategic Approaches

Strategic approaches to dietary specialization begin with the recognition that some taxa are more specialized than others. Howe and Estabrook (1977), for example, noted that some frugivores are highly specialized in depending on one or a few species of fruiting plants, whereas other frugivores are more opportunistic. Fitzpatrick (1980, 1985) recognized degrees of evolutionary specialization within the adaptive radiation of the Tyrannidae (see also Green 1981). Specialized species often show extreme structures along some evolutionary pathway, for example, and show the greatest degree of foraging stereotypy. In addition, the existence of guilds of organisms with nested ranges of resources, habitats, or other fundamental niche axes—the so-called "inclusive niche" pattern (see above)—means that, even within guilds different species are differentially specialized.

Some of the most important components of evolutionary specialization are illustrated by two hypothetical species, one of which is more specialized than the other (Fig. 1). One intuitive notion is that some combination of phenotypic characteristics confers greater efficiency on specialists than generalists, as illustrated by either (a) the higher maximum benefit: cost ratio of feeding on preferred food items, or (b) the higher benefit: cost ratios on nonpreferred items (Fig. 1b). The Darwin's finches (Geospizinae) illustrate case (a), in which deeper-billed, large-seed specialists are more efficient than shallower-beaked species at handling the most profitable, larger seeds (Grant 1986). Liem (1984) illustrates case (b) with cichlid fishes, in which specialist morphs have greater efficiency than generalists on least preferred foods. Phenotypic characteristics relevant to specialization include anatomical, morphological, behavioral (and psychological; see above), or physiological (for example, Toft 1985) traits. Comparative studies are an important way to compare performance of different phenotypes, populations, or species, and assess the extent of phenotypic diet constraints (Moermond, this volume). The extent of coevolution of the predator and prey also affects specialization, in that a more obligate relationship between the consumer and consumed depends on the predictability of resources and often involves increased efficiency of trophic exploitation by the consumer.

Ultimately, evolutionary notions of specialization must involve genetic and phylogenetic studies, if only to establish the evolutionary units, heritability of feeding behaviors (see Arnold [1981] and Gray [1981]) and the geographic scales on which selection is acting.

Behavioral stereotypy (vs. opportunism) is also relevant. Stereotypy is permitted when critical resources for growth, survival, or reproduction have been predictable in the history of a population. Foraging and dietary stereotypy are thus better measures of evolutionary specialization than tactical measures, most of which are based on resource abundance. The dietary heterogeneity index (*PDH*), discussed previously, is useful for calculating directly ecological opportunism.

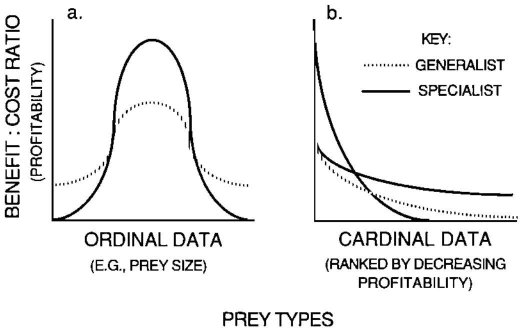

FIGURE 1. Benefit: cost ratios, or prey type profitability, for two hypothetical predators, a generalist and a specialist, when prey are arranged (a) ordinally (e.g., by prey size); or (b) cardinally, by some category of decreasing ranks of benefit: cost ratio. In part (b) the hypothetical specialist could be more efficient than the generalist on higher-ranked food (specialist with highest maximum prey profitability) or on lower-ranked food (specialist with lowest maximum profitability). See text for explanation and examples.

Wiens and Rotenberry (1979) defined opportunism as the behaviorally flexible use of abundant and variable resources, and argued that birds breeding in scrub-steppe environments are all relatively opportunistic. Klopfer (1967) conducted laboratory tests of the idea (Klopfer and MacArthur 1960) that tropical birds are more stereotyped in foliage preferences and movement patterns than temperate birds, although his results were inconclusive. As predicted by ecological theory, species living in depauperate island environments have tended to forage in less stereotyped ways than mainland species (e.g., Morse 1980a, Feinsinger and Swarm 1982, Whitaker and Tomich 1983), but exceptions are known. Feinsinger et al. (1988) found mixed support for the relationship between feeding opportunism in hummingbirds and disturbance in Costa Rican forests.

How is feeding opportunism related, if at all, to dietary niche breadth? Morse (1971b, 1980a) proposed that the stereotypy vs. opportunism (= plasticity in his usage) dichotomy is independent of the specialization vs. generalization dichotomy, so that birds can be stereotyped and specialized, stereotyped and generalized, opportunistic and specialized, or opportunistic and generalized (Fig. 2a). Martin and Karr (this volume) found empirical support in migratory warblers for Morse's view. They found that foraging opportunism, determined by seasonal variation

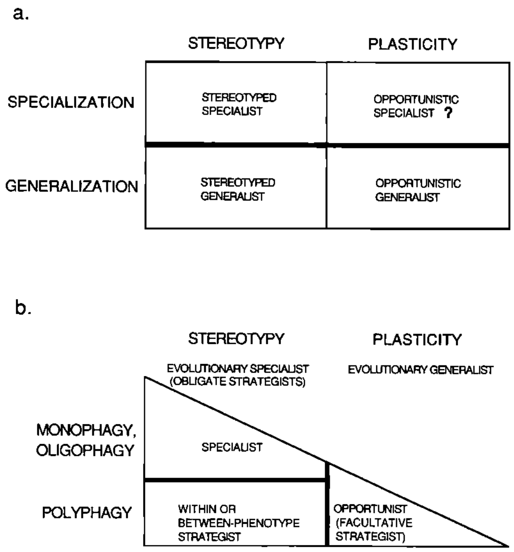

FIGURE 2. Two alternative schemes for the relationships between diet breadth (ecological specialization versus generalization) and diet predictability (stereotypy versus plasticity): (a) Morse's (1971b) scheme, viewing these two dichotomies as independent, and (b) the scheme developed in the present paper, distinguishing ecological from evolutionary specialization. In scheme (b) evolutionary specialization is synonymous with dietary stereotypy (regardless of diet breadth), evolutionary generalization is synonymous with opportunism or dietary plasticity, and ecological specialization versus generalization corresponds with diet breadth (monophagy or oligophagy versus polyphagy). Heavy lines distinguish specialists from generalists, and illustrate the lack of a simple dichotomy in the scheme advocated in the present paper.

in foraging tactics, was not related to foraging generalization, as determined by the range of foraging behaviors. However, the distinction between evolutionary and ecological aspects of specialization made in the present review suggests a different relationship between these two dichotomies (Fig. 2b). Specifically, I argue that an evolutionary generalist is an ecological opportunist (Wiens and Rotenberry 1979, Feinsinger et al. 1988), making it of necessity dietarily broad-niched or polyphagous. However, the converse is not true, because an organism can eat a broad array of foods in a stereotyped way, as illustrated by the Neotropical flycatchers discussed below. Moreover, an organism can have simultaneously broad and stereotyped diets in two fundamentally different ways, namely, by individuals all feeding identically ("within-phenotype strategists" of Roughgarden 1974), or by individuals feeding consistently as specialists relative to one another ("between-phenotype strategists"; e.g., Werner and Sherry 1987). Morse's scheme (Fig. 2a) is also problematic because of his category of "opportunistic specialists," which is an oxymoron by my scheme since evolutionary specialization and opportunism are mutually exclusive. Thus Figure 2b suggests that degree of opportunism and diet breadth may often be correlated, particularly if relatively few species fall into the lower left box (Fig. 2b) of species categorized by both broad and stereotyped diets. Finally, studies of cichlid fish functional anatomy suggest that evolutionary specialists may be more behaviorally versatile and potentially generalized in diet than evolutionary generalists (Liem and Kaufman 1984), contrary to my hypothesized scheme in Figure 2b.

Opportunism must be a widespread phenomenon, judging from its many synonyms. Fenton (1982; Fenton and Fullard 1981) described "short-term specializations" and "mosaic specialization" as widespread, if not predominant, feeding patterns in insectivorous bats. Analogous dietary specializations are termed "local feeding specializations" (Fox and Morrow 1981) or "facultative specializations" (Glasser 1982, 1984). Murdoch (1969) defined "switching generalists" experimentally in a similar way. Greene (1982) used the term "apparent specialists" for species whose specializations are not obviously related to phenotypic characteristics, and he discussed the evolution of behavioral versus phenotypic manifestations of specialization in lizards. Ralph and Noon (1988) used the term "opportunistic specialist" for Hawaiian birds using a narrow range of foraging behaviors, but using different behaviors in different seasons.

Testing ideas on evolutionary versus ecological approaches to diets and the hypothetical scheme on diet breadth in relation to plasticity (Fig. 2) are challenging tasks, and include understanding of patterns in resource variation (Wiens 1984b). Colwell's (1974) suggestions on how to conceptualize and quantify periodic phenomena and time-series analysis are two possible quantitative approaches. A second consideration is how individual animals use resources. A third aspect concerns functional studies, and how different organisms are constrained behaviorally, morphologically, or otherwise to have different capabilities or efficiencies, depending on the particular resources available. A fourth point is that degree of dietary specialization often depends critically on resource abundance, as does niche overlap (e.g., Schoener 1982, Ford, this volume), which has implications for the timing of studies. Finally, the categories specified in Figure 2 are not discrete, but represent endpoints of continuously distributed behavioral patterns. Thus comparative studies (following section) will remain useful to test these ideas.

ECOLOGICAL VERSUS EVOLUTIONARY APPROACHES: THREE EXAMPLES

Three examples below illustrate both different methods to analyze diets and the difference between tactical vs. strategic approaches to diets, by which contradictory conclusions are sometimes reached. The main problem is the use of tactical methods to study strategic questions.

COCOS FLYCATCHER

The Cocos Flycatcher is one of four year-round resident landbirds, three of which are endemic on the humid (and almost aseasonal), heavily rainforested Cocos Island, isolated approximately 480 km southwest of Costa Rica (5°32′57″N, 86°59′17″W). During a breeding and nonbreeding season visit, I (T. W. Sherry 1982, 1985) quantified diets using stomach samples, available prey with beating nets, foraging behavior, and standard morphological dimensions.

Two widely used tactical approaches to dietary specialization are the diversity of prey types in the diet and the relationship between food consumed and that available. When the diet diversity of Cocos Flycatchers was compared with that of mainland Costa Rican flycatchers occupying species-rich, lowland rainforest, the Cocos Flycatcher had a relatively broad diet based on both prey taxa and especially foraging behaviors (Fig. 3). It also consumed a variety of arthropod taxa in proportions indistinguishable from those available in at least one of the habitats (T. W. Sherry 1984, 1985). The broad array of foraging behaviors and arthropod types in the diet and the close match of diet to available arthropods suggested that the Cocos Flycatcher is a classical ecological generalist, expected on an isolated oceanic island with few competitors.

Strategic approaches provide a different conclusion. The Cocos Flycatcher is closely related to the Yellow Tyrannulet (*Capsiempis flaveola*) and the Mouse-colored Tyrannulet (*Phaeomyias murina*) (Lanyon 1984, Sherry 1986); the latter is an actively foraging perch-gleaner (Traylor and Fitzpatrick 1982), feeding on both insects and fruit in semi-arid scrubland habitats (Fitzpatrick 1980, 1985; pers. comm.). Because of its mostly insectivorous diet, the Cocos Flycatcher is a specialist compared with the tyrannulet. Second, both foraging behavior and prey appear to be constrained by morphology in a variety of Costa Rican flycatchers including the Cocos Flycatcher (Sherry 1982, 1984; Leisler and Winkler 1985; see also Fitzpatrick 1980, 1985). For example, bee and flying ant specialists are relatively large-bodied, narrow-winged, hawking species; Homoptera specialists (including the Cocos Flycatcher) are broad-winged pursuers with long rictal bristles; and generalist flycatchers and specialists on Coleoptera, Hemiptera, and worker ants have intermediate morphological characteristics (Fig. 4). The fact that the Cocos Fly-

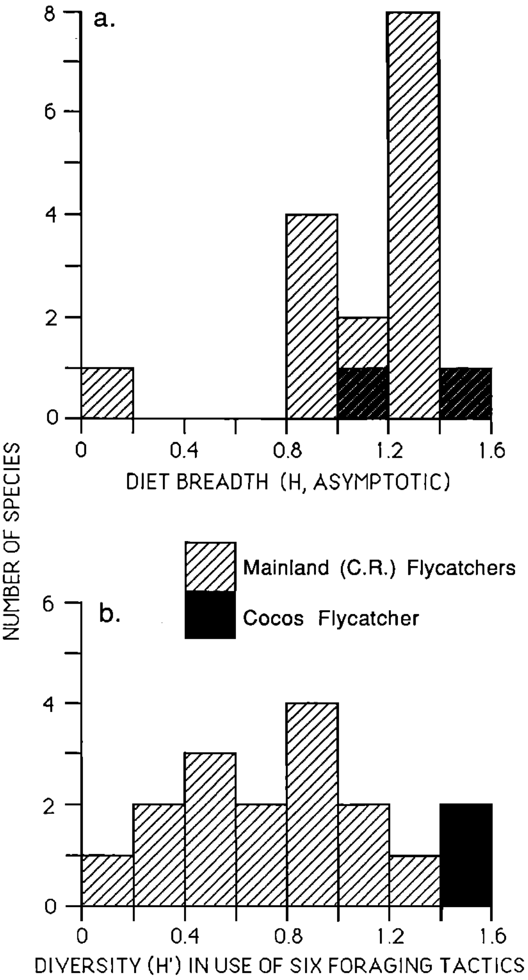

FIGURE 3. Frequency histograms of (a) diet breadth, and (b) diversity or breadth of foraging tactics of the Cocos Flycatcher, based on two different samples—one from a breeding and another from a nonbreeding season—contrasted with mainland (Costa Rican) flycatchers in the Caribbean lowlands of Costa Rica (based on T. W. Sherry 1984, 1985). Mainland flycatcher sample sizes are 16 and 15 for diet breadth and foraging diversity, respectively, because stomach samples were available for a species (*Tolmomyias sulphurescens*) for which foraging behaviors were not observed in this region.

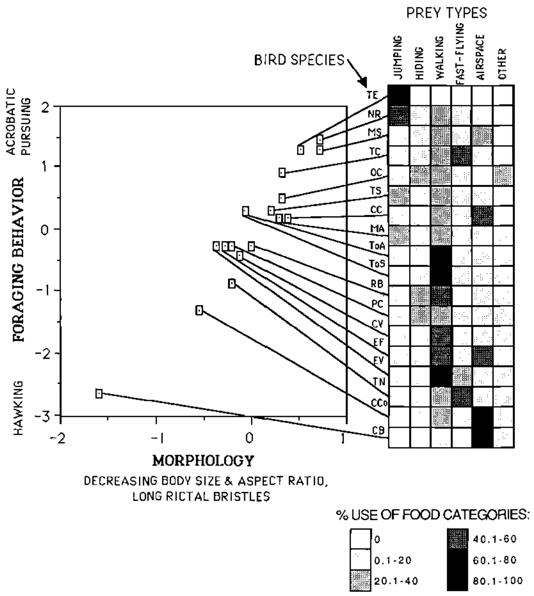

FIGURE 4. Correlations between foraging behavior, morphology, and diet of 18 species of Central American tyrannid flycatchers (based on data and analyses in T. W. Sherry 1982, 1984, 1985; Leisler and Winkler 1985). Both axes are species scores for canonical variate I, based on canonical correlation analysis and principal components analysis of original variables (Leisler and Winkler 1985). Species codes and corresponding names are CB (*Contopus borealis*), CC (*Contopus cinereus*), CCo (*Colonia colonis*), CV (*Contopus virens*), EF (*Empidonax flaviventris*), EV (*Empidonax virescens*), MA (*Myiornis atricapillus*), MS (*Myiobius sulphureipygius*), NR (*Nesotriccus ridgwayi*), OC (*Oncostoma cinereigulare*), PC (*Platyrinchus coronatus*), RB (*Rhynchocyclus brevirostris*), TC (*Todirostrum cinereum*), TE (*Terenotriccus erythrurus*), TN (*Todirostrum nigriceps*), ToA (*Tolmomyias assimilis*), ToS (*Tolmomyias sulphurescens*), and TS (*Todirostrum sylvia*). Prey types and corresponding arthropod taxa are "jumping" = Homoptera; "hiding" = Orthoptera and Lepidoptera larvae; "walking" = Coleoptera, Hemiptera, and non-flying Formicidae; "fast-flying" = Diptera and parasitoid Hymenoptera; "airspace" = Odonata, Apoidea, and flying Formicidae; and "other" = Arachnida, Lepidoptera adults, Dermaptera, and Chilopoda.

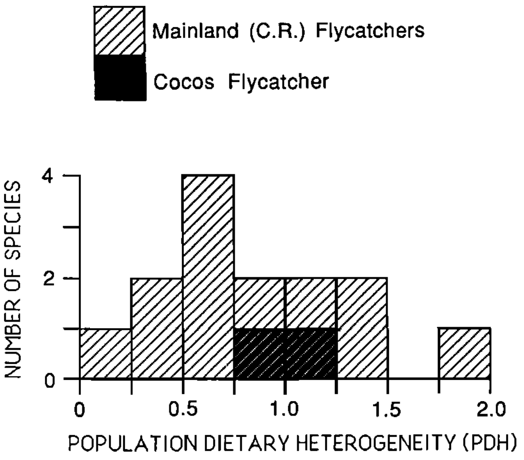

FIGURE 5. Comparison of population dietary heterogeneity, *PDH* (a measure of dietary opportunism, based on stomach contents; see text), in 14 species of mainland (Costa Rican) flycatcher and the Cocos Flycatcher. Mainland stomach samples for these calculations come from the breeding season, whereas Cocos Flycatcher samples were taken from both breeding and nonbreeding seasons (data from T. W. Sherry 1984, 1985).

catcher has similar foraging behavior and morphology to dietarily similar mainland flycatchers reinforces the conclusion that its specialization on Homoptera is both facilitated and constrained by phenotype. Finally, the population dietary homogeneity of the Cocos Flycatcher is indistinguishable from values for typical mainland flycatchers (Fig. 5), indicating that the Cocos Flycatcher is as stereotyped in diet as flycatchers inhabiting lowland rainforest of Caribbean Costa Rica, perhaps because of comparable levels of prey predictability in both environments. These data show that tactical and strategic approaches can lead to contradictory conclusions, and that the Cocos Flycatcher is not the dietary generalist that the tactical approach indicates.

SPECIALIZATION IN TROPICAL VERSUS TEMPERATE INSECTIVOROUS BIRDS

The question of latitudinal gradients is evolutionary, because the comparisons involve species in different biogeographic realms (Nearctic versus Neotropical, in the present case), and because diets are often constrained by phenotypic traits. Most empirical comparisons of tropical and temperate communities have indicated that the majority of avian species added to tropical communities can be accounted for by uniquely tropical resources, and thus by an expanded community niche volume rather than by increased specialization (e.g., Orians 1969b, Terborgh and Weske 1969, Schoener 1971a, Karr 1975, Ricklefs and O'Rourke 1975, Stiles 1978, Askins 1983). Terborgh (1980a) argued instead that increased diversity in a lowland Amazonian bird community in Peru, compared with a south-temperate site in the United States, results from both an expanded tropical resource dimension and greater species packing (implying greater niche specialization). Remsen (1985) reached a similar conclusion.

Stomach-content data for tropical flycatchers (Sherry 1984; unpubl.) show that resident tropical flycatcher species are indeed more specialized than migratory ones, but only if the data are analyzed using a strategic approach (see also Murphy 1987). Niche breadths, calculated using Pielou's asymptotic method, a tactical approach, were not narrower in the thirteen resident than the three migratory species (Mann-Whitney *U*-test, $P > 0.05$; Fig. 6). Heterogeneity values of stomach contents, by contrast, were lower in the 14 resident species than in four migratory ones (Mann-Whitney *U*-test, $P < 0.05$, Fig. 6; based on Sherry 1984). The dominance of stomach contents by one or a few arthropod taxa in two flycatcher species—by fulgoroid Homoptera in the Ruddy-tailed Flycatcher (*Terenotriccus erythrurus*) and by *Trigona* bees in the Long-tailed Flycatcher (*Colonia colonis*)—is extraordinary compared with other insectivores (Sherry 1984). Correspondence between morphology, foraging behavior, and diet (Fig. 4) also reinforces the strength of evolutionary contraints to diets in these birds.

Different conclusions resulting from tactical vs. strategic approaches result primarily because some tropical birds have taxonomically broad, but homogeneous diets (Sherry 1984). Cocos Flycatchers, as well as Common Tody Flycatchers (*Todirostrum cinereum*), ate similar prey types in both breeding and nonbreeding periods, based on cluster analysis (T. W. Sherry 1985). Rosenberg (this volume; unpubl.) documented the phenomenon in several antwren species (*Myrmotherula*) inhabiting Peruvian and Bolivian rainforest. Individual antwrens were highly stereotyped in their use of dead leaf foraging microhabitat, from which they took diverse arthropod types. Every individual antwren's stomach contained the same broad array of prey types, indicating a degree of dietary stereotypy only possible in tropical forests where dead-leaf arthropods are relatively predictable (Remsen and Parker 1984).

The homogeneity among tropical insectivorous birds' diets and foraging behavior, both within and between seasons, contrasts sharply with diet data from temperate birds and arctic birds, whose diets are notoriously variable (e.g., Holmes 1966). This is illustrated in community studies in which food abundance or types fluctuate from year to year (Ballinger 1977, Dunham 1980, Kephart and Arnold 1982, Linden and Wikman 1983), and for different species to converge on abundant, preferred food types at a particular time or location (Wiens and Rotenberry 1979, Rotenberry 1980a, Rosenberg et al. 1982, Steenhof and Kochert 1988). Woodpeckers studied by Askins (1983) provide an exception that helps prove the rule about the relationship between specialization and resource predictability. Askins found little difference between tropical and temperate sites in the number of species or degree of dietary specialization, largely because woodpeckers experience similar degrees of seasonal resource stability at different latitudes.

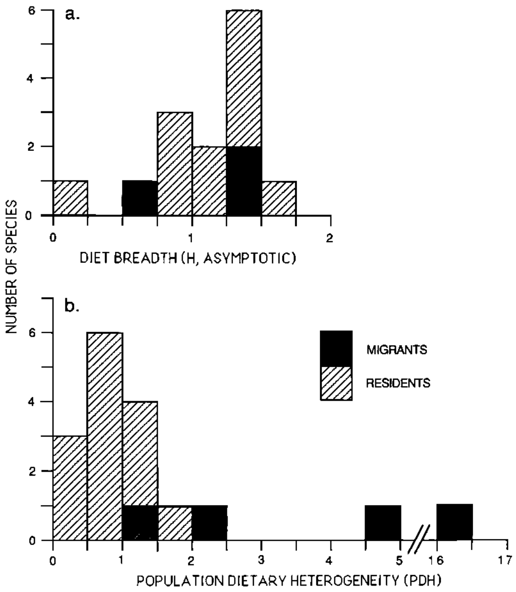

FIGURE 6. Comparison of migrant and resident flycatcher species' diets with respect to (a) diet breadth (using asymptotic Pielou-Hurtubia method, see text; and based on 13 resident and 3 migrant species), and (b) population dietary heterogeneity (based on 14 resident and 4 migrant species—the additional resident and migrant species in part b compared with part a are *Aphanotriccus capitalis* and *Empidonax flaviventris*, respectively). Cocos Flycatcher data are not included in these comparisons. Data from T. W. Sherry (1984, 1985).

Dietary data thus suggest that opportunistic foraging behavior and diets predominate in temperate communities, whereas behavioral stereotypy is more important in the tropics; thus tropical birds appear to be more specialized. However, the question of latitudinal gradients remains unresolved, because of the shortage of evolutionarily meaningful analyses, not to mention the shortage of dietary data from a sufficiently broad spectrum of tropical species.

FRUGIVOROUS BIRDS

McKey (1975) and Howe and Estabrook (1977) proposed that some frugivores are more specialized than others, and that both frugivores and fruits in particular taxa have co-evolved relatively obligate interdependence. Wheelwright and Orians (1982), Wheelwright (1983, 1985), and Moermond and Denslow (1985) questioned whether such frugivores are indeed specialists, based on the richness of fruit taxa eaten. This definition is inappropriate for discussions of evolutionary specialization; instead, information is needed about dietary and foraging behavioral consistency (stereotypy), reliability of fruit production, ecological interdependence of fruit and frugivores, and phenotypic adaptations for frugivory. In the same paper in which Wheelwright (1983) noted that the Quetzal (*Pharomacra mocinno*) is a generalist species by consuming at least 41 taxa of fruit in its diet, he also stated (p. 286) that, "Mutual dependence and, possibly, general coevolution between quetzals and the lauraceous trees whose seeds they disperse are suggested by the birds' morphology, distribution, behavior, and life history." Quetzals are thus specialized evolutionarily (*sensu* McKey 1975 and Howe and Estabrook 1977). The broad spectrum of fruit eaten by Quetzals thus comprises essentially one or a few resource types, not 41 different resources. Thus, part of the problem of quantifying evolutionary specialization is a failure to appreciate how a predator characterizes resources.

RELATION BETWEEN TACTICAL AND STRATEGIC APPROACHES TO DIETARY SPECIALIZATION

An evolutionary perspective helps one understand both strategic and tactical approaches to dietary specialization. Strategically speaking, all organisms are dietarily specialized in the sense that their unique evolutionary histories have led to a variety of differences that constrain their foraging capacities. In addition, different organisms may be differentially opportunistic because of the differences in food predictability in the environments where they have evolved.

Tactically speaking, all species must be ecologically flexible, because food abundances and distributions change. Tactical approaches to specialization thus examine what factors influence dietary selectivity within an animal's lifetime in response to variable resource distributions. Many authors have looked, for example, at how the range of food taken changes seasonally (e.g., Smith et al. 1978, Schoener 1982, Ford et al., this volume). The extensive literature on optimal foraging and optimal diets deals explicitly with how organisms respond to variable environments. Tactical studies will probably be most illuminating in organisms that have evolved the greatest ability to respond plastically to changing conditions, and it is probably no coincidence that well studied species from a tactical point of view (e.g., the Great Tit, *Parus major*) are species that have evolved in relatively variable temperate environments. It follows that neither a tactical nor strategic approach is best, and that no definition of specialization is suitable for all occasions.

Feeding behavior, like all other kinds of behavior, results from both genetic and environmental factors interacting during ontogeny and afterwards (Gray 1981, McKean, this volume) and strategic and tactical approaches provide complementary information about the myriad forces shaping feeding behavior. Tactical approaches indicate the kinds of developmental and post-developmental flexibility (including learning behavior) of which organisms are capable, and strategic approaches include the constraints on tactical capabilities. It will often be difficult to distinguish the relative influence of environmental and genetic causal factors acting on feeding behavior and specialization because: (1) phenotypic characters may have an environmental component, which is difficult to determine without experimentation (Gray 1981, James 1983); and (2) environmental stability depends in part on how the organism interacts with its environment (for example, seed-caching behavior serves to dampen seasonal fluctuations of resource availability). Even determining what a resource is, let alone the critical environmental influences on resources and on how organisms use them, is difficult. Thus a variety of approaches—experimental, comparative, observational, genetic, and behavioral—will be needed to distinguish environmental from genetic influences on dietary specialization.

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