Studies in Avian Biology No. 13:104–109, 1990.

DIETARY SIMILARITY AMONG INSECTIVOROUS BIRDS: INFLUENCE OF TAXONOMIC VERSUS ECOLOGICAL CATEGORIZATION OF PREY

ROBERT J. COOPER, PETER J. MARTINAT, AND ROBERT C. WHITMORE

Abstract. In a study of dietary relationships among nine species of insectivorous birds from an eastern deciduous forest, we examined two approaches to prey categorization: (1) taxonomic, using arthropod orders, and (2) subdivisions of orders into ecologically relevant categories. Dietary similarities (correlations) were generally higher within bird species than within period of collection using both categorizations. Similarities using taxonomic categorization generally were higher but were significantly ($P < 0.01$) less than those using ecological categorization. Using similarity measures and cluster analysis, similarities within bird species and time period that were evident using ecological categorization were not evident using taxonomic categorization. While we cannot specify strict rules concerning appropriate method and level of taxonomic categorization in studies of this sort, we suggest that: (1) prey categories should have sufficient observations to make analysis meaningful and to avoid large numbers of zero counts; (2) prey categories should not be so numerous that procedures such as cluster analysis cannot be readily interpreted; (3) large taxonomic levels (i.e., order) should be subdivided ecologically if subgroups exhibit very different characteristics (e.g., size, location, abundance, behavior); and (4) we encourage input from entomologists in problems of prey categorization.

Key Words: Arthropod prey; diet analysis; dietary similarity; diets; insectivorous birds.

A frequent objective of avian dietary studies is to compare diets among species that feed in similar ways. While some attention has been paid to biases involved in diet analysis, little is known about how the method of prey categorization affects similarity measures. Greene and Jaksic (1983) examined effects of prey identification level in analyses of raptor diets. We know of no similar studies for insectivorous birds, which eat a wide variety of arthropods encompassing many orders and families. Researchers may or may not be able to identify arthropods to the species level, especially if diets are analyzed using highly fragmented stomach contents.

Due to the difficulty of identification of insect parts to species and sometimes family levels, many researchers have compared diets of insectivorous species by categorizing prey at higher taxonomic levels. Arthropod orders are used most often (e.g., Root 1967, Orians and Horn 1969, Robinson and Holmes 1982). Others have used arthropod families or have combined families in some manner (Rotenberry 1980a, Rosenberg et al. 1982, Sherry 1984). Because some studies have involved a limited number of prey types, a few researchers have been able to identify all prey (e.g., caterpillars) to the species level (Tinbergen 1960, Royama 1970). Yet the method by which insect prey are categorized is likely to affect both similarity measures and conclusions drawn from them. Here we address that problem, using dietary data from stomachs of nine foliage-gleaning bird species in an eastern deciduous forest in West Virginia.

METHODS

Cooper (1988) described details of the study area and methods. The study area included 400 ha in Sleepy Creek Public Hunting and Fishing Area, an oak-hickory forest located in Berkeley and Morgan counties, West Virginia. A major feature of this study area is the spring emergence of many larval Lepidoptera, which feed on new foliage of deciduous trees. These caterpillars are a preferred food source eaten by many resident and migrant birds. We collected birds with shotguns from 6 May to 31 July 1985, and from 13 May to 22 July 1986 between 06:00 and 13:00, immediately removing the proventriculus and gizzard and injecting them with formalin to stop digestion. Stomach contents were analyzed in the laboratory under a dissecting microscope. Most prey items could be identified to family.

Several points merit emphasis here. First, intensive sampling of location, abundance, and behavior of canopy arthropods was done by Cooper (1989) simultaneous to collecting. Second, an extensive collection of arthropod voucher specimens was prepared. Third, at least one entomologist was available at all times in the field and laboratory to provide expertise in arthropod identification.

Our unit of measurement was a species-month, pooling all diet samples for a given species in a month (Table 1). Using the Brillouin diversity index (Pielou 1975; also see Sherry 1984), we determined that collection of 3 or 4 individuals/month was adequate to represent the monthly diet of a species. Collections with fewer than four individuals were eliminated from the analysis.

Relative abundances of prey were expressed as percent of total number of dietary items identified. We measured dietary similarity among monthly collections using Spearman's rank-order correlation, which is commonly used as a similarity measure (Clifford and Stephenson 1975). Overall trends of similarity were examined using cluster analysis. Ward's method, which is similar to centroid linkage, was employed using CLUSTER in the Statistical Analysis System (SAS Institute 1985). These analyses used two categorization methods. First, taxonomic categorization used orders as categories with the exception that Lepidoptera were divided into larvae, pupae, and adults (10 total categories). Second, ecological categorization used 15 prey categories based on taxonomy, size, abundance, typical location, and escape behavior of each group (Table 2).

For example, larval Lepidoptera were divided into three categories based on size, substrates occupied, and predator avoidance mechanisms. Smooth-bodied caterpillars typically avoid predation through crypsis, nocturnal feeding, and remaining inactive during the day on the undersurfaces of leaves (see Heinrich 1979c, Heinrich and Collins 1983). They were divided into two groups based on size. A third group, "hairy caterpillars," have long, stiff setae that deter many predators; they commonly forage diurnally in exposed locations. Coleoptera were similarly divided into two categories. One group (primarily Cerambycidae and Elateridae) included individuals that were large (8–16 mm), diurnally active, and found on leaf topsides or bark. The other group (primarily Alleculidae, Chrysomelidae, and Curculionidae) included individuals that were small (5–8 mm), diurnally inactive, and found on leaf undersurfaces.

In this example, we used cluster analysis to examine dietary patterns within and between species and time. If foliage-gleaning species were highly opportunistic, eating the most abundant prey available at any given time, then meaningful clusters should include many species collected at the same time. Conversely, if each species consistently ate unique prey items, meaningful clusters should contain one or a few species regardless of when they were collected.

RESULTS

On average, similarities among collections using taxonomic categorization were greater but were less often significant ($P < 0.01$, Table 3) than those using ecological categorization (Table 4). Both similarities and significance levels were affected by number of prey categories. Within-species comparisons were correlated more often than within-time-period comparisons using both categorization methods. Several discrepancies between our intuition and results observed using taxonomic categorization were noted. For example, 43% of the May 1986 collections were correlated when prey were categorized ecologically, because many species ate small (<20 mm), smooth-bodied, recently-emerged larval Lepidoptera. However, only 14% of those collections were correlated when prey were categorized taxonomically. Also, no within-species comparisons were significant for Worm-eating Warbler (scientific names appear in Table 1) or Yellow-billed Cuckoo when prey were categorized taxonomically. Cuckoos actually had unique diets, because only they consumed large numbers of gypsy moth (*Lymantria dispar*) larvae. Because gypsy moth larvae were combined with other caterpillars, this trend was hidden.

Cluster analysis using insect orders as prey categories resulted in a dendrogram showing few clear patterns within species or time (Fig. 1). Four major clusters were identified (scree test, Dillon and Goldstein 1984:48–49), each of which contained at least one collection from May, June, and July. Cluster I reflected large percentages of Homoptera in the diet and included collections

TABLE 1. SUMMARIES OF MONTHLY COLLECTIONS MADE OF NINE INSECTIVOROUS BIRD SPECIES DURING 1985–1986

Species	Collection	No. stomachs	No. items identified
Yellow-billed Cuckoo	June 1985	5	93
(*Coccyzus americanus*)	July 1985	7	137
	May 1986	5	217
	June 1986	4	94
Black-capped Chickadee	June 1985	13	282
(*Parus atricapillus*)	July 1985	25	301
	June 1986	4	29
	July 1986	6	89
Tufted Titmouse	June 1985	8	78
(*Parus bicolor*)	July 1985	37	382
	May 1986	5	65
	June 1986	7	47
	July 1986	5	46
Blue-gray Gnatcatcher	June 1985	10	105
(*Polioptila caerulea*)	July 1985	21	257
	May 1986	6	85
	June 1986	8	117
	July 1986	6	59
Red-eyed Vireo	May 1985	9	85
(*Vireo olivaceus*)	June 1985	12	106
	July 1985	17	143
	May 1986	6	81
	June 1986	8	93
	July 1986	5	85
Pine Warbler	June 1985	8	101
(*Dendroica pinus*)	July 1985	18	282
	May 1986	5	44
	June 1986	7	72
Cerulean Warbler (*Dendroica cerulea*)	May 1986	4	40
Worm-eating Warbler	June 1985	8	94
(*Helmitheros vermivora*)	May 1986	4	38
	June 1986	5	48
Scarlet Tanager	May 1985	4	29
(*Piranga olivacea*)	June 1985	17	173
	July 1985	22	182
	May 1986	7	91
	June 1986	9	97
	July 1986	6	70

TABLE 2. SIZE, SUBSTRATES USED, AND PREDATOR AVOIDANCE MECHANISMS OF ARTHROPOD CATEGORIES USED IN ECOLOGICAL CATEGORIZATION IN THIS STUDY

Prey category	Taxon	Length (mm)	Substrate	Predator avoidance mechanism
Spiders	Arachnida	2–10	Various	Dropping on thread, crawling
Large, active beetles	Coleoptera			
	Cerambycidae	8–16	Leaf tops, bark	Flying, falling
	Elateridae	8–12	Leaf tops, bark	Falling
Small, inactive beetles	Alleculidae	5–8	Leaf undersides	Falling
	Chrysomelidae	5–8	Leaf undersides	Falling
	Curculionidae	5–8	Leaf undersides	Falling
Large, predatory Hemiptera	Hemiptera			
	Pentatomidae	8–18	Leaf tops	Flying
	Reduviidae	8–18	Leaf tops	Falling
Small, phytophagous Hemiptera	Miridae	5–8	Leaf undersides	Falling
Homoptera	Homoptera			
	Membracidae	5–10	Twigs, branches	Crypsis
	Other	3–10	Foliage	Jumping, flying
Adult Hymenoptera	Hymenoptera			
	Formicidae	3–10	Various	Crawling, flying
	"Wasps"	3–12	Air, foliage	Flying
Orthoptera	Orthoptera			
	Tettigoniidae	>10	Foliage	Crypsis
	Gryllidae	6–18	Foliage	Crypsis
Large "flies"	Mecoptera	10–20	Air, leaf tops	Flying
	Diptera			
	Asilidae	10–20	Air, leaf tops	Flying
	Tipulidae	10–30	Air, foliage	Flying
Small flies	Other	<10	Air, foliage	Flying
Small, smooth-bodied eruciform larvae	Lepidoptera Hymenoptera	8–20	Leaf undersides, rolls or ties	Crypsis
Large, smooth-bodied eruciform larvae	Lepidoptera Hymenoptera	>20	Leaf undersides, rolls or ties, bark	Crypsis
"Hairy" caterpillars	Lepidoptera	>8	Foliage, bark	Unpalatability
Pupae	Lepidoptera	5–20	Foliage, bark	Crypsis
Moths	Lepidoptera adults	3–20	Air, leaf undersides	Flying, crypsis

from four species and all three months of study. All five Blue-gray Gnatcatcher, four of six Red-eyed Vireo, and two of four Pine Warbler collections were included in this cluster. Cluster II reflected diets with a large percentage of Coleoptera. One Worm-eating Warbler and five of six Scarlet Tanager collections were in this cluster. Cluster III reflected a large percentage of larval Lepidoptera in diets. Seven species were represented in this cluster. Cluster IV reflected a moderate percentage (10–20%) of "unusual" prey such as spiders or Orthoptera, and included one representative each of five species.

The dendrogram suggested some dietary similarities within species, especially Blue-gray Gnatcatcher and Scarlet Tanager, but few time patterns, although we strongly suspected their occurrence. For example, the large Cluster III in Figure 1 contained collections with large percentages of Lepidoptera larvae. These included (1) Yellow-billed Cuckoos, which ate many gypsy moth larvae, (2) Tufted Titmice and Black-capped Chickadees, both of which ate numerous longer (>20 mm), smooth-bodied caterpillars in June and July of both years, and (3) a variety of other species that ate smaller, smooth-bodied caterpillars when they were abundant in May and June. These and other patterns might emerge if a more meaningful method of categorization was used.

The cluster analysis that used ecological categorization (Table 2) resulted in a more informative dendrogram (Fig. 2). Five major clusters were identified. Cluster I again reflected a large percentage of Homoptera in diets, including four of five Blue-gray Gnatcatcher collections and both 1985 Pine Warbler collections from June and July. Cluster II contained seven of nine parid

TABLE 3. NUMBER OF COMPARISONS, NUMBER OF SIGNIFICANT ($P < 0.01$) COMPARISONS, AND AVERAGE SIMILARITY IN DIET BETWEEN MONTHLY COLLECTIONS USING TAXONOMIC PREY CATEGORIZATION (ARTHROPOD ORDERS)

Collections compared	Similarity[a]	Number comparisons	Number significant	Percent significant
Within species				
Tufted Titmouse	0.77 ± 0.03	10	4	40
Black-capped Chickadee	0.74 ± 0.04	6	3	50
Worm-eating Warbler	0.67 ± 0.07	3	0	0
Blue-gray Gnatcatcher	0.65 ± 0.05	10	3	30
Pine Warbler	0.64 ± 0.08	6	1	17
Red-eyed Vireo	0.62 ± 0.04	15	3	20
Scarlet Tanager	0.60 ± 0.06	15	4	27
Yellow-billed Cuckoo	0.52 ± 0.07	6	0	0
Total	0.65 ± 0.02	71	18	25
Within collection periods				
May 1985	0.76 ± 0.00	1	0	0
June 1985	0.45 ± 0.04	28	1	4
July 1985	0.39 ± 0.06	21	2	10
May 1986	0.51 ± 0.05	28	4	14
June 1986	0.41 ± 0.05	28	1	4
July 1986	0.50 ± 0.07	10	0	0
Total	0.45 ± 0.02	116	8	7
All other comparisons	0.44 ± 0.01	516	46	9

[a] Values are mean Spearman's rank correlation coefficients among the collections of interest and reported as the mean ± SE.

collections, all from June and July. Those two species had similar diets, including medium-sized caterpillars (20–30 mm), pupae, and spiders. Cluster III reflected large numbers of smaller, smooth-bodied caterpillars taken during the early part of the breeding season. Seven species were represented in this cluster and all collections except one (YBC 7/85) were from May and June. The Yellow-billed Cuckoo collection was, incidentally, the last single collection to join a cluster and probably reflected a different diet from that in any other collection. Clusters IV and V were both monospecific and reflected the high dependency of Scarlet Tanagers on large beetles at all

TABLE 4. NUMBER OF COMPARISONS, NUMBER OF SIGNIFICANT ($P < 0.01$) COMPARISONS, AND AVERAGE SIMILARITY IN DIET BETWEEN MONTHLY COLLECTIONS USING ECOLOGICAL PREY CATEGORIZATION

Collections compared	Similarity[a]	Number comparisons	Number significant	Percent significant
Within species				
Pine Warbler	0.81 ± 0.05	6	4	67
Black-capped Chickadee	0.74 ± 0.04	6	5	83
Tufted Titmouse	0.70 ± 0.04	10	7	70
Blue-gray Gnatcatcher	0.68 ± 0.03	10	7	70
Worm-eating Warbler	0.62 ± 0.13	3	2	67
Scarlet Tanager	0.58 ± 0.05	15	9	60
Red-eyed Vireo	0.54 ± 0.05	15	5	33
Yellow-billed Cuckoo	0.52 ± 0.09	6	3	50
Total	0.63 ± 0.02	71	42	59
Within collection periods				
May 1985	0.57 ± 0.00	1	0	0
June 1985	0.31 ± 0.06	28	3	11
July 1985	0.36 ± 0.07	21	3	14
May 1986	0.44 ± 0.06	28	12	43
June 1986	0.32 ± 0.06	28	5	18
July 1986	0.55 ± 0.06	10	3	30
Total	0.37 ± 0.03	116	26	22
All other comparisons	0.36 ± 0.01	516	82	16

[a] Values are mean Spearman's rank correlation coefficients among the collections of interest and reported as the mean ± SE.

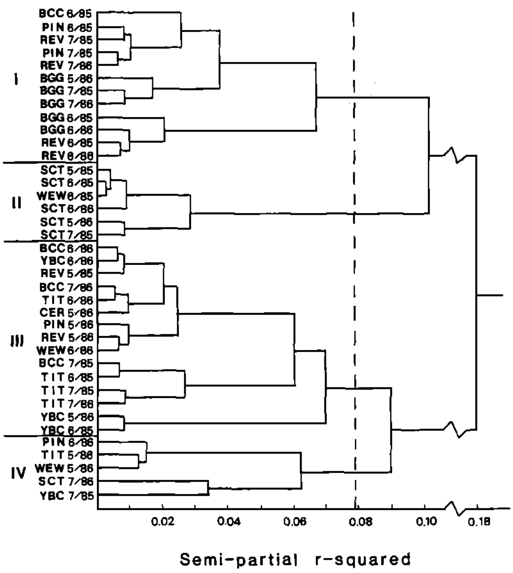

FIGURE 1. Dietary relationships from taxonomic prey categorization (orders) among nine species of insectivorous birds determined by cluster analysis. Dissimilarity measures are semipartial r^2 values. BCC = Black-capped Chickadee, BGG = Blue-gray Gnatcatcher, CER = Cerulean Warbler, PIN = Pine Warbler, REV = Red-eyed Vireo, SCT = Scarlet Tanager, TIT = Tufted Titmouse, WEW = Worm-eating Warbler, YBC = Yellow-billed Cuckoo.

times and of Yellow-billed Cuckoos on gypsy moth larvae in May and June.

DISCUSSION

If the method of prey categorization in studies of dietary similarity affects similarity measures, conclusions based on techniques such as cluster analysis that use similarity measures may also be affected. One alternative, strictly taxonomic categorization, represents a convenient and superficially logical level to categorize prey. Yet, results were not intuitive or consistent with patterns of prey abundance, location, and behavior, or the manner in which different bird species captured prey on the study area. Use of 15 ecologically relevant categories (Table 2) produced results consistent with observations and ecological knowledge of arthropods. The sometimes subtle distinctions between prey categories were determined as a result of familiarity with prey characteristics through direct observation and input from team entomologists.

Other researchers have used analyses similar to those in this study and similarly derived prey categories. Rotenberry (1980a) used 19 arthropod prey categories, some of which were orders but most of which were families or combinations of families. Justification for level of identification was that the prey taxon had to occur in at least 5% of all stomachs examined. That criterion is arbitrary and may cause potentially important or distinguishing prey categories to be omitted or lumped with other categories. For example, Lepidoptera pupae seldom were eaten by most species in this study, but the few that were eaten by parids seem to have contributed to those species' clustering separately from other species (Fig. 2). However, Rotenberry's prey categories probably reflected real patterns of prey abundance and opportunistic predation by birds over time in shrubsteppe habitats, as evidenced by dependence of those species on such prey as Curculionidae, Orthoptera, and larval Lepidoptera at different times of the study.

Sherry (1984) used 15 prey taxa in his study of neotropical flycatcher diets. The taxa were often orders but also contained superfamilies. No justification for that categorization was given, but subsequent descriptions of flycatcher foraging behaviors and methods of capturing different prey taxa indicated a knowledge of locations, escape behaviors, and patterns of emergence and abundance of arthropods under study.

Both orders and lower taxonomic categories were used by both of the above authors and in this study. When should one identify prey at the ordinal level and when at a lower level of identification? While hard and fast rules do not exist, some suggestions may be helpful. Prey levels should be constructed to contain enough observations for a meaningful analysis, although exceptions occur (see above). Practical considerations include: (1) Variables (prey categories) with many zero counts will not be normally distributed and usually cannot be transformed to normality. Consequently, multivariate statistical procedures such as principal components and discriminant function analysis lose validity. (2) Large numbers of prey categories in a procedure such as cluster analysis produce results that are often difficult to interpret. Thus, division of arthropod orders into smaller categories may be impractical for some relatively uncommon orders.

In analyses such as those used here, where knowledge of dietary similarity both among species and over time is of interest, prey can actually be identified at too low a taxonomic level. As a simplified hypothetical example, consider two predators that feed on four different prey items that vary in abundance temporally (Fig. 3). Suppose those prey can be divided into two higher taxonomic levels, A and B, which can be further divided into two finer taxonomic levels, 1 and 2. Let A and B be very different in ecology and behavior, but let A1 and A2, and B1 and B2, be very similar. Both A1 and B1 are present in period 1 but not in period 2, and A2 and B2

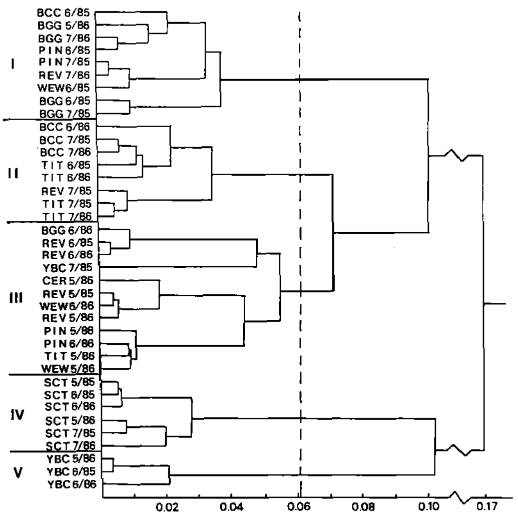

FIGURE 2. Dietary relationships from ecological prey categorization among nine species of insectivorous birds determined by cluster analysis. Dissimilarity measures are semipartial r^2 values. Species codes as in Figure 1.

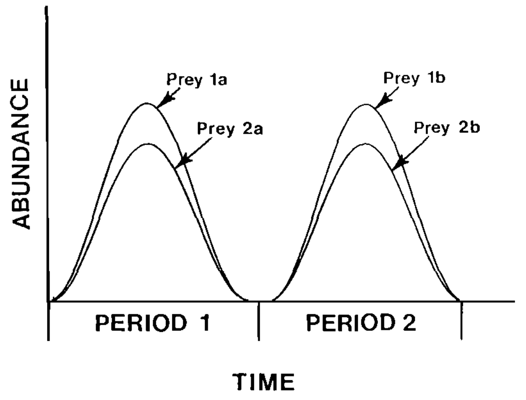

FIGURE 3. Hypothetical patterns of abundance of four prey taxa over time. See text for explanation.

are present in period 2 but not in period 1. Assume that predator diets reflect prey differences so that the diet of predator one contains 90% of taxon A and 10% of taxon B at all times, and the diet of predator two contains 10% of taxon A and 90% of taxon B at all times. If prey are categorized as A and B, then diets would be most similar within species across time periods, which is meaningful in terms of functional ecology of predator and prey. If prey are categorized as A1, A2, B1, and B2, then diets would be most similar within time periods across species, which is meaningful taxonomically but not ecologically, because prey are not present during both periods.

We experimented with cluster analysis using prey categories defined by the lowest taxonomic level (family, genus, or species) to which prey could be identified with confidence. Eighty-five categories were developed. Results (not shown) were difficult to interpret, partly because of the large number of categories, but also because of the hypothetical situation presented above. Bird species with very different diets, such as Scarlet Tanagers and Blue-gray Gnatcatchers, sometimes clustered together because a few individuals occasionally ate the same prey that were not available at other times.

Thus, an important consideration is whether anything is really achieved by dividing a particular order into lower levels. That is, if two families or groups of families within an order are not very different ecologically, then subdivision of the order will probably not provide much additional information. Conversely, if several subgroups within an order exhibit very different characteristics, such as size, location, or behavior, then additional information is likely to be obtained by subdivision. Input from entomologists is extremely helpful in this regard.

This study demonstrates that the method of categorization selected for diet analysis can substantially influence interpretation of results. The problem is similar to analysis of bird-habitat relationships, which can be greatly influenced by the variables selected for inclusion in models (e.g., Noon 1981b, Whitmore 1981). Ideally, the prey classification scheme should be developed independently or prior to analysis of stomach contents. Also, when publishing study results, researchers should explain how prey categories were chosen. Entomological information is therefore necessary to construct meaningful prey categories. Ornithologists undertaking studies of bird-insect relationships should incorporate knowledge of insect ecology into their study design to assure ecologically sound conclusions.

ACKNOWLEDGMENTS

Funding for this research was provided through the McIntire-Stennis program, by USDA Forest Service Cooperative Agreements 23-043 and 23-144, and by a Sigma Xi grant-in-aid of research. The authors are grateful to P. W. Brown, K. M. Dodge, D. E. Fosbroke, E. J. Harner, M. L. Morrison, C. J. Ralph, K. G. Smith, and J. Verner for reviewing the manuscript and to the summer field crews of the Forest Arthropod Research Team for assistance in data collection. L. Butler provided entomological expertise. S. Smith typed the manuscript. Published with the approval of the Director, West Virginia University Agriculture and Forestry Experiment Station as Scientific Paper No. 2121. This is contribution No. 8 of the Forest Arthropod Research Team.