

INFLUENCE OF PERIODICAL CICADAS ON FORAGING BEHAVIOR OF INSECTIVOROUS BIRDS IN AN OZARK FOREST

CHRISTOPHER J. KELLNER, KIMBERLY G. SMITH, NOMA C. WILKINSON,
AND DOUGLAS A. JAMES

Abstract. Six aspects of foraging behavior of Tufted Titmouse, Red-eyed Vireo, Acadian Flycatcher, and Blue-gray Gnatcatcher were quantified before, during, and after an emergence of 13-year periodical cicadas in 1985 and during the same three periods in 1986 when no cicadas were present. Comparisons were made among the three periods within years and within periods between the two years to determine the effect of a superabundant food supply on foraging behavior of birds. No obvious effects of cicadas on avian foraging behavior were detected among periods in 1985 and variability in foraging behaviors among periods in 1986 was similar to 1985. In both years, the greatest changes in foraging behavior occurred between the first two periods, suggesting a seasonal component to foraging behavior in the Ozarks. Comparing the period when cicadas were present in 1985 with the same period in 1986 also failed to show an obvious effect of cicadas on foraging behavior. Substantial variability existed between years in all three periods, suggesting annual behavioral flexibility within species for the six variables that we measured. Substantial seasonal and annual variations limited our ability to detect an effect of cicadas on foraging behavior. That suggests that combining data from different seasons and years may bias results and that the traditional approach of defining microhabitat and foraging variables a priori may be inadequate.

Key Words: Arkansas; foraging behavior; predator swamping; periodical cicadas; seasonal variation.

Outbreaks of arthropods provide opportunities for examining the importance of food on many aspects of avian ecology. For instance, irruptions of spruce budworms (*Choristoneura fumiferana*), bark beetles, gypsy moths (*Lymantria dispar*), termites and periodical cicadas (*Magicicada* spp.) provide numerous species of insectivorous birds with a superabundance of food (e.g., Forbush 1924, Morse 1978b, Otvos 1979, Dial and Vaughan 1987, Steward et al. 1988a). It is well known that birds will concentrate in such patches of abundant food.

One of many aspects of avian ecology that could be affected by a superabundance of food is foraging behavior. It is often assumed that insectivorous birds are behaviorally flexible, allowing them to respond opportunistically to changes in arthropod abundance (e.g., Rotenberry 1980a), and that they are able to partition resources by selecting different microhabitats or using different foraging modes (e.g., Hespenheide 1975a). Thus, a common approach to studying foraging behavior of insectivorous birds is to examine foraging mode and microhabitat use (e.g., MacArthur 1958, Morse 1968), often comparing foraging behaviors of sympatric species (e.g., Root 1967, Rice 1978, James 1979).

Two potential problems common to such studies are (1) selection of appropriate variables and (2) combining data collected over more than one season. Avian ecologists often focus on parameters that describe microhabitat, i.e., that subset of available habitat that a species actually uses in searching for and obtaining prey. However, a

researcher's definition may not coincide with a bird's perception of a given microhabitat, especially when discrete categories are arbitrarily formed for variables that are actually continuously distributed (e.g., relative height, relative position). Consequently, an investigator's definition of foraging variables may influence both the strength and validity of the conclusions. Secondly, in many studies, foraging modes and microhabitat utilization are examined throughout a season with little attention given to potential, but important, changes in foraging behaviors that occur within and between seasons. Investigators recently have reported substantial variation in behavior both between (e.g., Alatalo 1980, Hutto 1981b, Greenberg 1987b) and within seasons (e.g., Saether 1982; Carrascal 1984; Carrascal and Sanchez-Aguado 1987; Hejl and Verner, this volume). As a result, combining data over several field seasons or even over a single season may lead to biased results and conclusions.

Our objective was to determine the adequacy of "traditional" variables as used in studies of avian foraging mode and microhabitat to describe responses of birds to an outbreak of cicadas. Any conclusions would necessarily take into account variation within seasons and between seasons due to the presence or absence of cicadas.

METHODS

Two study sites in Washington Co., Arkansas, were used: an upland hardwood forest adjacent to hayfields, located northeast of Durham, and an area adjacent to

TABLE 1. SUMMARY OF DIFFERENCES DURING 1985 AND 1986 FOR THE SIX FORAGING VARIABLES AMONG THE THREE PERIODS FOR THE FOUR BIRD SPECIES STUDIED. ALL VARIABLES WERE TESTED USING LIKELIHOOD CHI-SQUARED TESTS, EXCEPT FOR ABSOLUTE HEIGHT, FOR WHICH A KRUSKAL-WALLIS TEST WAS USED. EMPTY CELLS SIGNIFY $P > 0.05$, * = $0.01 < P < 0.05$, ** = $0.001 < P < 0.01$, *** = $0.0001 < P < 0.001$, **** = $P < 0.0001$

Species	Year	Relative height	Relative position	Foraging mode	Canopy	Absolute height	Substrate
Red-eyed Vireo	1985	***	***	***		****	
	1986			*	***	**	**
Tufted Titmouse	1985	***	*	*	***	****	***
	1986	****			***	****	
Blue-gray Gnatcatcher	1985			****			
	1986	****		****		****	*
Acadian Flycatcher	1985						
	1986		***			****	

the north and west banks of Lake Wilson on the outskirts of Fayetteville. Dominant trees at the Durham site were post oak (*Quercus stellata*) and black oak (*Q. velutina*), shagbark hickory (*Carya ovata*), and eastern redcedar (*Juniperus virginiana*). Dominant trees in upland hardwood forests that surround Lake Wilson were post and black oaks, shagbark and black (*C. texana*) hickories, and winged elm (*Ulmus alata*). Over one million adult cicadas emerged within the forest on the 16 ha study site near Durham during the emergence year (K. G. Smith unpubl.).

Foraging data were collected by one person (Kellner) during spring and summer of 1985 and 1986. Each field season was divided into three periods: 15 April to 10 May (I), 10 May to 10 June (II), and 11 June to 31 July (III). Those periods represented times before, during, and after which adult cicadas were superabundant in 1985.

Data were recorded on only actively hunting birds that attacked prey frequently. Birds that engaged in long, uninterrupted bouts of singing or that were in the company of fledglings were ignored. Once sighted, a foraging bird was followed until lost from sight. Thus, data consist of sequences of observations on individual birds as they searched for and attacked prey. The following variables were noted for each foraging bout: height in meters, relative height (upper, middle, or lower crown, in equal thirds), place in canopy (overstory or understory), relative horizontal position in the crown (inner, middle, or outer, in equal thirds), substrate on which birds were located (branch, twig, trunk, or leaf). Foraging moves, as defined by Robinson and Holmes (1982), were: (1) glean, an attack by a perched bird toward prey that also was perched; (2) hover, an attack in flight toward perched prey; (3) sally, an attack in flight toward flying prey; (4) probe, an attack by a perched bird on prey located beneath the substrate's surface. Although data were collected on a wide variety of species, here we focus on two species that were observed consuming cicadas, Tufted Titmice (*Parus bicolor*) and Red-eyed Vireos (*Vireo olivaceus*), and two species that were not observed consuming cicadas, Acadian Flycatchers (*Empidonax virescens*) and Blue-gray Gnatcatchers (*Poliophtilla caerulea*).

We compared foraging behavior among the three periods within and between years, allowing detection

of foraging differences within each period for each species. We randomly selected approximately one third of the observations for each species and used those subsamples in all statistical analyses. This was done in an attempt to obtain independent samples; however, we realize that this method does not guarantee independence of observations. Likelihood ratio Chi-squared or Fisher's exact tests were used to test for differences for variables with discrete or continuous data, while tests involving height, the only continuous variable, were done using Kruskal-Wallis or Wilcoxon tests. Differences were considered to be statistically significant at $P \leq 0.05$. We also used Schoener's (1970) similarity index to compare foraging behavior of each species between consecutive periods and between the same period in consecutive years.

RESULTS

WITHIN-YEAR COMPARISONS

If cicadas were responsible for variation in foraging behavior among periods, more differences among periods should occur in 1985 than 1986 and those differences would be due to changes in behaviors of vireos and titmice but not flycatchers and gnatcatchers. We found that comparisons between periods within a year were significantly different in 24 of 48 cases (Table 1); however, within-year variation was not restricted to 1985 (the year cicadas were present) for any species. Tufted Titmice showed more significant variations in behavior in 1985 than 1986, but Red-eyed Vireos, which also consumed cicadas, exhibited about the same amount of variation during each year. Acadian Flycatchers and Blue-gray Gnatcatchers both had more within-year variations during 1986, the non-cicada year.

If cicadas were responsible for significant differences in behavior, we would expect shifts in foraging between periods I and II and between periods II and III in 1985, but not in 1986. Titmice exhibited shifts in substrate use that followed that pattern (Table 2). However, shifts most

TABLE 2. PERCENT OF OBSERVATIONS WITHIN EACH CATEGORY AND NUMBER OF OBSERVATIONS FOR THE FORAGING VARIABLES LISTED FOR THE FOUR SPECIES OF BIRDS DURING THE THREE SAMPLING PERIODS IN 1985 AND 1986

Species Year	Period	Relative height			Relative position			Foraging mode				Canopy			Substrate					
		Lower	Middle	Upper	N	Inner	Middle	Upper	N	Glean	Hover	Sally	Probe	N	Over	Under	N	Branch	Twig	N
Red-eyed Vireo																				
1985	I	78	9	13	32	38	34	28	32	89	11	0	0	9	100	0	32	42	58	36
	II	22	29	49	41	15	15	70	41	70	30	0	0	10	100	0	41	33	67	36
	III	28	18	54	257	29	19	61	256	34	66	0	0	96	98	2	261	24	76	378
1986	I	46	16	38	132	27	20	53	132	56	44	0	0	41	82	18	133	40	60	111
	II	36	23	41	375	23	19	58	369	56	44	0	0	103	93	7	394	24	76	338
	III	34	22	44	173	23	17	60	172	39	61	0	0	59	91	9	196	24	76	147
Tufted Titmouse																				
1985	I	11	39	50	56	71	11	18	56	92	8	0	0	39	100	0	56	41	59	56
	II	36	28	36	36	56	6	39	36	81	15	2	2	58	100	0	38	63	37	35
	III	39	30	31	74	49	10	41	73	66	19	2	13	62	91	9	76	30	70	73
1986	I	23	15	62	34	26	18	56	34	71	0	0	29	7	100	0	36	56	44	32
	II	62	16	22	131	33	21	46	131	79	10	1	10	61	90	10	142	42	58	107
	III	18	41	41	17	53	13	33	15	50	21	0	29	14	76	24	21	25	75	16
Blue-gray Gnatcatcher																				
1985	I	49	26	25	65	23	28	48	64	38	24	38	0	37	97	3	66	28	72	58
	II	36	26	38	114	32	21	47	114	39	52	9	0	156	97	3	126	18	82	103
	III	35	32	32	68	19	16	65	69	22	68	10	0	135	96	4	71	20	80	66
1986	I	28	19	53	171	19	21	60	172	55	35	10	0	51	93	7	182	9	91	150
	II	44	20	36	313	19	13	68	320	33	50	12	0	127	91	9	356	15	85	251
	III	26	28	46	161	23	14	63	164	20	57	23	0	106	94	6	200	7	93	127
Acadian Flycatcher																				
1985	II	44	34	22	32	42	18	39	33	11	83	6	0	18	89	11	36	42	58	33
	III	54	19	27	154	47	8	45	153	3	90	7	0	245	80	20	167	29	71	133
	II	58	18	24	149	42	21	37	150	5	88	7	0	198	73	27	169	27	73	116
1986	III	68	16	16	68	37	7	56	68	3	85	12	0	61	74	26	90	24	76	66

TABLE 3. MEAN FORAGING HEIGHT, STANDARD DEVIATION, AND SAMPLE SIZE (N) FOR THE FOUR SPECIES OF BIRDS DURING EACH SAMPLING PERIOD IN 1985 AND 1986

Species	Period	1985			1986		
		\bar{X}	SD	N	\bar{X}	SD	N
Red-eyed Vireo	I	10.1	0.34	31	5.6	0.16	129
	II	7.9	0.72	10	6.2	0.10	361
	III	7.0	0.12	255	6.2	0.13	179
Tufted Titmouse	I	11.6	0.42	52	6.9	0.24	32
	II	5.4	0.45	37	6.1	0.15	131
	III	5.0	0.29	67	3.8	0.49	21
Blue-gray Gnatcatcher	I	5.9	0.39	56	6.0	0.17	167
	II	6.4	0.22	111	5.8	0.13	291
	III	6.5	0.20	71	5.3	0.15	169
Acadian Flycatcher	II	4.5	0.40	32	4.5	0.17	155
	III	3.9	0.17	150	3.2	0.20	83

often occurred between periods I and II, with fewer shifts between periods II and III, in both years suggesting that behaviors tend to change early in the breeding season regardless of cicadas.

The overall pattern of within-year variation is difficult to interpret. Foraging behaviors varied dramatically among periods for each of the six variables we quantified, but no trend was apparent among species. Foraging variables sometimes exhibited significant variation between periods during one year, while exhibiting little variation during another year (Tables 2 and 3). Similarly, within each year, variables often exhibited significant variation between periods for one or more species, but not for all species. Several species did exhibit significant variation between periods for the same variables in 1985 and 1986. However, in all cases save one, significant variation during one year did not follow the same pattern in the following year.

An examination of average similarity indices revealed that, in general, species foraged more similarly across the three periods in 1986 than in 1985. Tufted Titmice were the only exception and foraged more similarly in 1985 than 1986 (Table 4). In 1985, foraging differed more between periods I and II than between periods II and III for all species. No obvious trends in foraging similarities emerged during 1986. This evidence indicates that the three periods differed more in 1985 than 1986. However, this is not evidence that cicadas influenced foraging behavior because trends in foraging similarity were exhibited by the two species that did not consume cicadas, but not by titmice.

BETWEEN-YEAR COMPARISONS

Comparing foraging behavior observed within the same period of both years for each species

revealed significant differences in 29 of 66 tests (Table 5). Examining only the number of significant differences, no consistent pattern emerged that would suggest cicadas influenced foraging behavior. No species exhibited more variation between 1985 and 1986 in period II than in I or III. In addition, flycatchers and gnatcatchers exhibited almost as much variation between period II of 1985 and 1986 as did titmice and vireos. Overall, species exhibited substantial variability between each pair of periods indicating that these species are capable of great plasticity for the six variables we quantified, even when comparing similar periods between years.

If cicadas were responsible for significant between-year differences, we would expect significant differences to occur between years for period II and not to occur between years for either periods I or III for those species that ate cicadas. In addition, we would not expect a similar pattern for the two species that did not eat cicadas. Comparing period II for vireos, only one significant difference was found (Table 5). Vireos foraged significantly higher in 1985 than in 1986, perhaps in response to the presence of cicadas in the upper portions of trees. However, vireos also foraged higher during both periods I and III in 1985 (Table 3). Gnatcatchers also foraged significantly higher in 1985 during both periods II and III. Titmice exhibited three significant differences in foraging behaviors that may have resulted from exploitation of cicadas (Table 5), foraging more in upper crowns and inner portions of trees and on branches during the cicada emergence (period II in 1985). Those differences were consistent with our expectations for titmice actively seeking cicadas which are known to concentrate in upper portions of trees and are most abundant along the main trunk and branches to-

TABLE 4. SIMILARITY INDICES FOR EACH SPECIES COMPARING FORAGING BEHAVIORS BETWEEN PERIODS FOR EACH YEAR

Species Period	1985						1986					
	Relative height	Relative position	For-aging mode	Canopy	Sub-strate	\bar{X}	Relative height	Relative position	For-aging mode	Canopy	Sub-strate	\bar{X}
Red-eyed Vireo												
I × II	0.44	0.73	0.81	1.00	0.91	0.78	0.90	0.95	1.00	0.89	0.84	0.92
II × III	0.89	0.95	0.64	0.98	0.91	0.87	0.98	0.98	0.83	0.98	1.00	0.95
Tufted Titmouse												
I × II	0.75	0.80	0.89	1.00	0.78	0.84	0.60	0.90	0.81	0.90	0.86	0.81
II × III	0.95	0.94	0.85	0.91	0.67	0.86	0.56	0.80	0.70	0.86	0.83	0.75
Blue-gray Gnatcatcher												
I × II	0.87	0.92	0.71	1.00	0.90	0.88	0.83	0.92	0.81	0.98	0.94	0.90
II × III	0.94	0.82	0.83	0.99	0.98	0.91	0.82	0.95	0.85	0.98	0.92	0.90
Acadian Flycatcher												
II × III	0.85	0.90	0.66	0.91	0.87	0.84	0.90	0.81	0.95	0.99	0.97	0.92

ward the center of trees. This pattern was not exhibited by any other species during period II, nor did titmice exhibit similar shifts during other periods.

If cicadas influenced foraging behavior, we would expect foraging similarities to be lowest between years for period II for the two cicada consumers, but not for the two non-consumers. However, in both years, a seasonal trend toward increasing foraging stereotypy existed from period I through period III for all species (Table 6).

DISCUSSION

We found substantial within- and between-year variation for all species that we studied, limiting

our conclusions regarding the influence of cicadas on foraging titmice and vireos. Similar within- and between-year variation in foraging behavior of birds has been documented by others (e.g., Alatalo 1980, Rabenold 1980, Hutto 1981b, Wagner 1981b, Saether 1982, Carrascal 1984) and may be widespread, making it impossible to pool data over seasons or years. More importantly, unexplained seasonal or yearly variation may make conclusions concerning relationships between species (e.g., Root 1967, Rice 1978, Robinson 1981) or sexes (e.g., Williamson 1971, Bell 1982, Holmes 1986) more tenuous. Consequently, it is important that researchers direct attention toward discovering causes of seasonal and yearly variation in foraging behavior.

TABLE 5. SUMMARY OF DIFFERENCES FOR THE SIX FORAGING VARIABLES WITHIN SAMPLING PERIODS BETWEEN 1985 AND 1986 FOR THE FOUR BIRD SPECIES STUDIED. ALL VARIABLES WERE TESTED USING LIKELIHOOD CHI-SQUARED TESTS, EXCEPT ABSOLUTE HEIGHT, FOR WHICH A KRUSKAL-WALLIS TEST WAS USED, AND PLACE IN CANOPY FOR RED-EYED VIREOS IN THE PRECICADA AND CICADA PERIODS, FOR WHICH FISHER'S EXACT TEST WAS USED. EMPTY CELLS SIGNIFY $P > 0.05$, * = $0.01 < P < 0.05$, ** = $0.001 < P < 0.01$, *** = $0.0001 < P < 0.001$, **** = $P < 0.0001$

Species	Period	Relative height	Relative position	Foraging mode	Canopy	Absolute height	Foraging substrate
Red-eyed Vireo	I	***	*	*	***	****	
	II					****	
	III				***	****	***
Tufted Titmouse	I	*	***	*		****	
	II	*	*		*		*
	III						
Blue-gray Gnatcatcher	I	****		***			***
	II		***		*	*	
	III			*		****	*
Acadian Flycatcher	II				*		
	III					*	*

TABLE 6. SIMILARITY INDICES FOR EACH SPECIES COMPARING FORAGING BEHAVIORS BETWEEN YEARS FOR EACH PERIOD

Species Period	Relative height	Relative position	Foraging mode	Canopy	Substrate	\bar{x}
Red-eyed Vireo						
I	0.68	0.76	0.67	0.82	0.98	0.78
II	0.86	0.97	0.86	0.93	0.91	0.91
III	0.90	0.97	0.95	0.93	1.00	0.95
Tufted Titmouse						
I	0.76	0.55	0.71	1.00	0.85	0.77
II	0.74	0.78	0.92	0.90	0.79	0.83
III	0.79	0.93	0.82	0.85	0.95	0.87
Blue-gray Gnatcatcher						
I	0.72	0.89	0.72	0.96	0.81	0.82
II	0.92	0.79	0.95	0.94	0.97	0.91
III	0.87	0.96	0.87	0.98	0.87	0.91
Acadian Flycatcher						
II	0.84	0.98	0.68	0.84	0.85	0.84
III	0.86	0.89	0.95	0.94	0.95	0.92

Several factors may account for seasonal and yearly variation in foraging behavior of birds. First, yearly variation in weather may influence patterns of plant phenology, which, in turn, may influence abundance and availability of arthropods (see Hejl and Verner, this volume). Second, spring migration results in population fluctuations that may influence availability of arthropods, or influence territorial behavior of residents, ultimately resulting in changes in foraging behavior of birds. Third, stage in the breeding cycle will influence foraging behavior of parent birds (e.g., Morse 1968).

Part of our inability to discern the influence of periodical cicadas on foraging behavior may also have resulted from our perspective of microhabitat. Like most researchers, we followed MacArthur (1958) in our definitions and analysis of microhabitat variables. This approach considers a host of mostly discrete variables that are

analyzed as separate entities. For example, relative height is analyzed separately from all other variables including relative position. However, there is no reason to assume that a bird's behavior at a particular relative position is not influenced by its relative height. Interactions of this nature between variables could be determined through use of log-linear models (Fienberg 1977). In addition, there is no reason to assume a bird's view of microhabitat consists of discrete compartments (e.g., relative height and relative position as in this paper) and an attempt should be made to redefine microhabitat on a continuous scale. For example, relative height could be defined as a ratio of a bird's absolute height to the total height of the tree in which it is foraging. A similar ratio could be used to describe relative position. Such designations could always be converted back into traditional discrete categories.

We assumed that presence of cicadas would cause a significant change in foraging behaviors of forest birds (see also Hutto, this volume). Perhaps we did not document such a change because cicadas were numerous throughout the study area and birds were able to consume them without shifting microhabitat use. It is also possible that we would have seen a greater effect had we analyzed variables that characterize speed, direction, and distance moved by foraging birds. Morton (1980a) found that such variables were often superior to microhabitat parameters in distinguishing between species. Hutto (this volume) also discussed that notion, contending that changes in food resources (i.e., arthropods) were reflected by changes in foraging movements of insectivorous birds.

ACKNOWLEDGMENTS

R. Hutto, H. Recher, and S. Robinson reviewed the manuscript and provided helpful comments. J. Birdsey provided assistance in the field and K. Golden assisted in data processing. We thank M. Cassidy for kindly allowing us to conduct our research on his property. This research was supported by a grant from the National Science Foundation (BSR 84-08090).