

BIRD PREDATION ON PERIODICAL CICADAS IN OZARK FORESTS: ECOLOGICAL RELEASE FOR OTHER CANOPY ARTHROPODS?

FREDERICK M. STEPHEN, GERALD W. WALLIS, AND KIMBERLY G. SMITH

Abstract. Population dynamics of canopy arthropods were monitored in two upland forests in the Arkansas Ozarks during spring and summer of 1984–1986 to test whether the emergence of adult 13-year periodical cicadas on one site during late spring in 1985 would disrupt normal patterns of bird predation on canopy arthropods, resulting in ecological release for those prey populations. Canopy arthropods on foliage of oak, hickory, and eastern redcedar were sampled weekly beginning in June 1984, and April 1985 and 1986, and continuing through August in all years. We classed arthropods into four broad guilds based on foraging mode (chewers, suckers, spiders, and lepidopterous larvae) and expressed densities as number of individuals per kg of foliage sampled. Two-way analysis of variance revealed no significant treatment effects for densities of chewing, sucking, or lepidopteran larval guilds. A significant interaction of mean density between sites among years was detected for the spider guild, but not when cicadas were present, indicating that ecological release did not occur. We trace the development of the notion that bird populations are capable of affecting prey population levels, and discuss those ideas in light of our results, which suggest that birds have little impact upon their arthropod prey in Ozark forests.

Key Words: Arkansas; canopy arthropods; ecological release; guilds; insect sampling; *Magicicada*; Ozarks; periodical cicadas; predation.

One of the most predictable events in nature is emergence of periodical cicadas (Homoptera: Cicadidae: *Magicicada*). Unavailable to above-ground consumers for long periods (either 13 or 17 years), they become superabundant for about 6 weeks as adults, while they reproduce, then die (Marlatt 1907). Densities may approach 3 million/ha (Dybas and Davies 1962) and emergences are regarded as a classic example of predator swamping (Lloyd and Dybas 1966a, b). Periodical cicadas apparently contain no noxious compounds (Brown and Chippendale 1973) and have only limited anti-predatory behaviors (Steward et al. 1988a) and during their emergences become a highly desirable prey for many bird species (Marlatt 1907, 1908; Forbush 1924; Beamer 1931; Allard 1937; Howard 1937; Leonard 1964; Nolan and Thompson 1975; Anderson 1977; Best 1977; Karban 1982; Murphy 1986; Strehl and White 1986; Steward et al. 1988a; Kellner et al., this volume). Indeed, predation is generally assumed to have been a driving force in the evolution of the life cycle (Lloyd and Dybas 1966b, May 1979, Karban 1982).

Given that most forest birds in the Ozarks eat adult periodical cicadas when they are available, what is the effect of prey switching behavior by birds on populations of the normal canopy arthropod prey? In particular, do normal prey items experience a type of "ecological release," whereby populations expand greatly as a result of a decrease in avian predation pressure owing to the appearance of a superabundant prey?

Emergence of 13-year periodical cicadas

(*Magicicada tredecim* Walsh and Riley, *M. tredecassini* Alexander and Moore, and *M. tredecula* Alexander and Moore; Brood XIX, Simon 1979) in northwestern Arkansas in 1985 afforded us an opportunity to test this idea. We sampled canopy arthropods during pre-emergence (1984), emergence (1985), and post-emergence (1986) summers on two study sites, one on which cicadas emerged in 1985 and another nearby where they did not.

STUDY AREAS AND METHODS

We used anecdotal records of emergences of 13-year periodical cicadas from Brood XIX (Simon 1979) from 1959 and 1972 in northwestern Arkansas to locate study areas during 1984. Cicada chorusing had been notable at certain farms adjacent to the White River, near Durham, Washington County (L. O. Warren and R. Watson, pers. comm.), and examination of favored tree species revealed substantial twig scars (Marlatt 1907) from 1972. Digging among roots of scarred trees yielded vertical pre-emergence tunnels, which cicada nymphs construct up to one year before emergence (Cory and Knight 1937). A 16 ha study site (Cassidy) was established here as the cicada site. Another 16 ha site (Tillery) located 3.5 km to the east served as the control site.

The Cassidy site was more xeric than the Tillery site and was on a predominantly west-facing slope, meeting a pasture adjacent to the White River. Both locations were similar in tree species composition, with a wide variety of hardwoods characteristic of Ozark upland forests (Moore 1972), including a predominance of oaks (*Quercus* spp.) and hickories (*Carya* spp.), plus abundant eastern redcedar (*Juniperus virginiana* L.). Those three taxa were sufficiently numerous and distributed

within both sites so that they were selected as sample trees for the canopy arthropod study.

Arthropod sampling

Each site was divided into a grid consisting of 100, 0.16 ha (40 × 40 m) subplots. Data were collected weekly from 1984 through 1986. Sampling began in June 1984 and in April of 1985 and 1986, approximately coincident with appearance of new foliage, and continued through August in all three years of study.

The sampling regime varied slightly each year, as refinements were made to optimize efficiency. In 1984, eight subplots were randomly selected on each site: four along the perimeter of each site and four in the interior. Within those subplots, two crown heights (<10 m and >10 m) were sampled on each of the three tree taxa. Each week, 48 samples (8 subplots × 3 tree taxa × 2 crown heights) were taken, resulting in 1008 samples. In subsequent years, high and low crown heights were merged into one lower mid-crown sample, as we detected no significant differences in arthropod populations as a function of height in 1984. Analyses of 1984 data in this paper used only the 504 lower crown samples, as they were most similar in height to all subsequent samples.

The number of subplots was increased in 1985 to 16 at the control and 24 at the cicada site for a total of 2400 samples. Sampling in 1986 was similar to the previous year, but one week shorter, resulting in 2244 samples.

All sampling was conducted in morning to minimize variation in insect movement within the crown (e.g., Holmes et al. 1978). Each sample unit consisted of three terminal branches from a tree cut with a pole pruner, and dropped into an attached muslin bag. We attempted to standardize each branch cutting to sample similar amounts of foliage for each species through time. Foliage consisted of leaves, petioles, and small twigs (larger stems were clipped and discarded). All foliage was immediately placed into a paper bag (ca. 30 × 17 × 30 cm), which was folded and stapled closed. Bags were returned to the laboratory, weighed to determine wet weight of foliage biomass, then frozen overnight to kill all arthropods. The next day, foliage was shaken, and all stem and leaf surfaces carefully examined. Total arthropod wet weight was measured and specimens were held for identification in 70% ethyl alcohol.

Multiple methods of sampling may be required to properly sample entire canopy arthropod communities (Cooper 1989, Morrison et al. 1989). Methods such as pole pruning miss actively flying insects, while techniques that do catch fliers (e.g., sticky traps) usually do not sample non-flying arthropods, such as spiders and caterpillars. We assumed that potential cicada predators would prey primarily on non-fliers. We also hypothesized that arthropod populations may not be immediately "released" but perhaps release would be best reflected in subsequent immature populations. We assumed that foliage collection maximized catch of immatures, a consistent majority of non-active flying adults, and spiders.

Guild selection

Arthropods were identified to order and, where possible, to family. Size of each specimen was estimated

as small (<6 mm), medium (≥6 and <19 mm), or large (≥19 mm). Specimens were categorized into four guilds based loosely on feeding behavior: (1) chewing insect guild, containing all families in orders Lepidoptera and Orthoptera, sawfly families in the order Hymenoptera, and families Chrysomelidae, Scarabaeidae and Curculionidae in the Coleoptera; (2) sucking insect guild, containing all families in orders Homoptera and Thysanoptera, plus families Aradidae, Berytidae, Coreidae, Miridae, Pentatomidae, Scutelleridae, Tingidae, and Thyreocoridae in the order Hemiptera; (3) spider guild, containing all spiders; and (4) medium to large lepidopterous larval guild, a subgroup of the chewing insect guild.

Not all taxa collected are included in our guilds. Choices for guild membership were made to incorporate the two main phytophagous insect feeding types, plus the large, entirely entomophagous, arachnid group. Medium to large lepidopteran larvae (a relatively large-sized and flightless food resource) were examined separately, as they form a common food for insectivorous birds of the forest canopy (Holmes et al. 1979c). Other authors, working with similar canopy arthropod data, have demonstrated that choice of taxa in guild formation can significantly influence results (Stork 1987; Cooper et al., this volume). We are aware that the feeding guilds we specified are broad, but their taxonomic composition remained relatively constant between cicada and non-cicada sites.

Data analyses

We summarized data in two ways: (1) numbers of individuals/sample unit; and (2) numbers of arthropods standardized by kg of tree foliage sampled, calculated by dividing number of individuals by weight of foliage. Exploratory data analysis indicated that most variables were not normally distributed and that mean/variance ratios were not stable. Because most standardized variables approximated a negative binomial or Poisson distribution, for all analyses of variance a square root transformation was used after 3/8 was added to each value, a process that stabilizes the variance of a Poisson distribution regardless of the mean (Anscombe 1948). Standardized data reported in tables are untransformed means, presented with associated sample sizes and standard errors of the mean.

The General Linear Models procedure in SAS (SAS 1982) was used for analysis of variance, with Tukey's mean separation tests ($P \leq 0.05$) where appropriate. Two-way analysis of variance was used to test for differences in mean densities between sites and among years, and, more importantly, to determine if any significant site-year interactions existed. Although arthropod levels could change from year to year and from site to site for many reasons, a significant site-year interaction would suggest that presence of periodical cicadas may have affected population dynamics of other canopy arthropods in 1985. To determine if significant interactions were due to changes between sites in 1985, differences in mean arthropod densities between sites in 1984 and in 1986 were tested against those from 1985 using t-tests (the CONTRAST option in GLM).

We considered two primary factors in categorizing data for further analysis: (1) expression of relative arthropod abundance in a manner that reduces bias as-

sociated with variation in size of sample units, and (2) combination of arthropod taxa into appropriate groups for further analysis.

RESULTS

FOLIAGE ANALYSIS AND EXPRESSION OF ARTHROPOD ABUNDANCE

Weight of canopy foliage collected/sample (combined over site, month, and year) varied significantly with tree taxa, and averaged 86.9, 75.1, and 52.6 g for cedar, hickory, and oak, respectively. Amount of foliage collected/sample varied with seasonal phenology: foliage weight of cedar and oak increased as the season progressed, and foliage weight of hickory increased from April to May then remained constant (Table 1). On average, foliage samples collected from the Cassidy site were significantly heavier than those taken at Tillery.

Mean numbers of arthropods collected/sample varied as a function of host tree (Table 2). Mean numbers for chewer and spider guilds were similar in cedar and hickory, but chewers were higher and spiders were lower on oak. Medium to large lepidopterans and sucking insects were least abundant on cedar, with larger numbers on hickory and oak, particularly for members of the sucking insect guild.

Different interpretations of guild abundance among tree species can be made, however, depending on whether or not one uses mean numbers/sample unit or mean numbers/kg of foliage sampled. For example, chewing and sucking insect guilds had significantly different numbers/kg of foliage for each tree taxon, with lowest density on cedar, a greater density on hickory, and the highest on oak (Table 2). On average, more cedar than hickory foliage was collected (Table 1); yet, number of chewers/sample unit was not significantly different between those two tree taxa. However, significant differences are evident when numbers of chewers are expressed per kg of host foliage. We conclude that expression of numbers within guilds on the basis of kg of foliage sampled is more appropriate for valid comparisons among trees, sites, seasons, and years.

GUILD DENSITIES

Approximately 165 taxa were recorded from 5148 samples. In the chewing insect guild, comparison of average numbers/kg of foliage combined over tree taxa and months revealed significant differences among years and between sites (Table 3); however, analysis of variance did not reveal a significant site-year interaction.

Cassidy consistently had a lower average density of chewing insects than Tillery. Densities were similar for 1984 and 1985 on both sites.

TABLE 1. FOLIAGE WEIGHT ANALYSIS BY TREE TAXA AND SITE. DATA ARE NUMBERS OF SAMPLES, MEAN GRAMS OF FOLIAGE, PLUS OR MINUS STANDARD ERROR OF THE MEAN, SEPARATED BY TREE TAXA OR SITE OVER ALL YEARS^a

	April			May			June			July			August			Overall means		
	N	\bar{X}	SE	N	\bar{X}	SE	N	\bar{X}	SE	N	\bar{X}	SE	N	\bar{X}	SE	N	\bar{X}	SE
Cedar	136	76.7	2.29 A ^b	383	76.1	1.51 A	360	83.3	1.74 B	456	89.1	1.69 C	380	102.1	1.95 D	1715	86.9	0.85
Hickory	136	62.3	2.79 A	384	78.5	1.60 B	360	75.2	1.54 B	455	75.0	1.47 B	380	76.3	1.49 B	1715	75.1	0.74
Oak	136	25.3	1.09 A	384	47.1	1.06 B	360	48.8	1.06 B	456	54.2	1.10 C	380	69.8	1.29 D	1716	52.6	0.60
Cassidy site	216	60.5	2.48 A	719	68.8	1.21 B	624	72.1	1.35 BC	815	76.7	1.27 C	660	85.8	1.40 D	3034	74.7	0.64
Tillery site	192	48.3	2.04 A	432	64.6	1.37 B	456	65.0	1.31 B	552	67.0	1.25 B	480	78.5	1.43 C	2112	67.0	0.66

^a Comparison of means between each month, as well as overall means between Cassidy and Tillery, are all significantly different ($P < 0.05$).

^b Means and se's of the combined tree taxa across each row followed by the same letter are not significantly different ($P < 0.05$).

TABLE 2. COMPARISON OF MEAN NUMBERS/SAMPLE UNIT VS. MEAN NUMBERS/KG OF HOST FOLIAGE FOR THE FOUR ARTHROPOD GUILDS ON EACH OF THE TREE TAXA SAMPLED

	Cedar		Hickory		Oak	
	\bar{X} ^a	SE	\bar{X}	SE	\bar{X}	SE
Chewers						
Numbers	1.12	0.04 A	1.21	0.05 A	1.38	0.05 B
No./kg	13.99	0.49 A	19.14	0.86 B	31.00	1.17 C
Medium & Large Lepidoptera						
Numbers	0.16	0.01 A	0.38	0.02 B	0.34	0.02 B
No./kg	1.47	0.13 A	5.53	0.32 B	7.33	0.45 B
Suckers						
Numbers	0.75	0.04 A	3.16	0.14 B	3.26	0.16 B
No./kg	9.34	0.52 A	45.53	1.88 B	60.49	2.50 C
Spiders						
Numbers	1.62	0.05 A	1.58	0.05 A	1.16	0.06 B
No./kg	20.68	0.74 AB	23.38	0.76 A	22.55	1.03 B

^a Means across each row followed by the same letter are not significantly different, based on analysis of transformed data ($P < 0.05$). Number of samples for each mean calculated equals 1716.

Chewers increased in 1986 at Cassidy, as would be expected if populations were released in the year following cicada emergence. However, a similar increase occurred at Tillery, negating the idea of a treatment effect at Cassidy.

Lepidopteran larval densities (Table 3) were different from chewers. Lepidopteran larvae were about twice as common in 1984 on Tillery compared to Cassidy. A small, non-significant increase at Cassidy and decrease at Tillery occurred in 1985, and the density at Tillery still was significantly greater than at Cassidy in 1985. A slight increase occurred at Cassidy in 1986, but this site was still less than Tillery. No significant site-year interaction was found, suggesting that periodical cicadas had no impact on population dynamics of medium and large lepidopteran larvae.

Sucking insect densities were substantially higher in 1984 than in either of the two succeeding years (Table 3). Cause of the decline was unknown, but occurred in a similar manner on both sites. Average density of sucking insects was significantly different between the two sites in two of three years, 1985 and 1986. Although means shown in 1985 are close, ANOVA of the transformed data indicated slightly higher densities at Tillery. If cicadas affected bird foraging and alternate prey, one would expect a significant site-year interaction as a result of the cicada emergence, but such an interaction was not found. Comparisons produced highly significant differences among years, but patterns of change (i.e., decrease in density in 1985, which carried forward to 1986) were the same for both sites, which is not compatible with the concept of a treatment effect.

Spider populations were denser at Tillery than Cassidy (Table 3). However, magnitude of density change on each site varied among years, resulting in a significant site-year interaction. Differences in mean population densities between sites were 24 in 1984, about 11 in 1985, and 14.3 in 1986. Using the CONTRAST option in PROC GLM, we found a significant change between mean densities in 1984 and 1985, but not between 1985 and 1986. This difference was not due to more spiders on the Cassidy site during cicada emergence, as spider densities were lowest then. We further analyzed the spider data to discover if a site-month interaction existed during 1985. A changing relationship in mean numbers between sites in months during and after cicada emergence could support the ecological release hypothesis, but none was detected. We suspect that the factors causing changes in spider populations occurred during winter of 1984–1985, thus ruling out the impact of adult cicada emergence.

DISCUSSION

TEST OF THE HYPOTHESIS

If bird predation is a significant mortality factor in dynamics of canopy arthropod populations, results of reduced predation at Cassidy when cicadas were present might be seen in two ways: (1) an immediate increase in arthropods normally preyed upon by birds; and (2) higher populations later in the same year, or during the following year, resulting in increased reproductive output and success. Such changes would not be expected on Tillery where cicadas did not emerge.

TABLE 3. MEAN DENSITY/KG FOLIAGE OF THE CHEWING INSECT, MEDIUM AND LARGE LEPIDOPTERAN, SUCKING INSECT, AND SPIDER GUILDS AT EACH STUDY SITE, AVERAGED OVER ALL TREE TAXA AND ALL MONTHS

Guild	Year	Cassidy site				Tillery site				
		N	\bar{X}	SE		N	\bar{X}	SE		
Chewing	1984	264	11.5	1.01	A ^a	240	24.1	1.94	AB	** ^b
	1985	1440	13.3	0.55	A	960	21.3	1.02	A	**
	1986	1332	23.6	1.10	B	912	33.0	1.86	B	**
Medium & Large Lepid.	1984	264	3.1	0.54	A	240	6.9	1.14	A	**
	1985	1440	4.0	0.31	A	960	5.6	0.41	A	**
	1986	1332	4.5	0.39	A	912	5.5	0.55	A	**
Sucking	1984	264	55.6	4.91	A	240	65.6	6.73	A	**
	1985	1440	34.4	2.20	B	960	36.5	2.14	B	**
	1986	1332	34.0	2.09	B	912	41.4	2.54	B	**
Spiders	1984	264	17.4	1.86	A	240	41.3	4.15	A	**
	1985	1440	12.3	0.48	B	960	23.7	0.96	C	**
	1986	1332	20.7	1.01	A	912	35.0	1.41	B	**

^a Within each guild, means among years within a site (i.e., within columns) followed by the same letter are not significantly different ($P < 0.05$).
^b Means between sites during a specific year (i.e., across rows) are all significantly different (**) ($P < 0.05$).

Another possibility considered, which might mask an ecological release resulting from changes in bird foraging patterns, was that arthropod predators could respond functionally or numerically (Holling 1959b), or both, to increases in their canopy arthropod prey. The density-dependent mortality they might cause would conceal the impact of reduced bird predation. We theorized that if that were happening, we should see significant increases in a major predator guild such as spiders (Smith et al. 1987). As evident from Table 3 and the above results, spider populations decreased in 1985 on both sites, and increased in 1986 on both sites, again suggesting that populations of spiders were changing independent of cicada emergence.

Based on the above analyses of site-year interactions, no significant treatment effects from the cicada emergence were evident for chewing, sucking, or lepidopterous larval guilds, and the significant difference found for the spider guild did not appear to be associated with the period when cicadas were present. Thus, we conclude that the hypothesized ecological release did not occur.

DO BIRDS AFFECT PREY POPULATION LEVELS?

The lack of any noticeable effect of periodical cicada emergence on the population dynamics of canopy arthropod prey leads us to consider the general effect of forest birds on canopy arthropod population dynamics. In the entomological literature, the supposition that predators can regulate populations of their arthropod prey formed the basis for the developing concepts of biological control (e.g., Smith 1939, DeBach 1964, Huffaker and Messenger 1976) and the impact of

birds on specific insects has been clearly documented in some forest habitats (e.g., Dahlsten et al. 1977, Dahlsten and Copper 1979, Torgersen and Campbell 1982, Torgersen et al. 1983). In general, birds are thought to have greater impacts at endemic rather than epidemic prey densities (reviewed in Buckner 1966), although magnitude of the impact depends on which life stage suffers the greatest predation (e.g., Smith 1985). Many studies have demonstrated that bird predation can be an important source of mortality to overwintering crop pests (e.g., MacLellan 1958, Buckner 1966, Solomon et al. 1976, Stairs 1985).

In the ecological literature, a more general consideration of interactions among trophic levels led some, particularly Hairston et al. (1960), to conclude that animals in higher trophic levels can affect the populations of organisms in lower trophic levels. While that conclusion is not without controversy, it did stimulate interest in the interactions between birds and their arthropod prey. For example, a number of studies have focused on the impact of bird predation on spider populations, concluding that bird predation is important in both tropic and temperate regions (Rypstra 1984), and that winter mortality due to bird predation can be great (Askenmo et al. 1977), birds apparently eating larger individuals (Gunnarsson 1983) of all spider species encountered (Norberg 1978).

It is well documented that some bird species are attracted to arthropod outbreaks (reviewed in Otvos 1979; Kellner et al., this volume). It is less clear, however, that at low densities, territorial forest birds can substantially impact available arthropod resources. The most widely-cited work is that of Holmes et al. (1979c), who found

a higher density of lepidopteran larvae inside exclosures designed to eliminate the effect of bird predation in a northern hardwood forest in New Hampshire. However, attempts to replicate that study in the woodlands of eastern Kansas have failed to produce any effect due to bird predation (R. Holt, unpubl.). Our bird census data (K. G. Smith et al., unpubl.) suggest that birds responded to presence of periodical cicadas by congregating in the emergence area. An effect of that might be to maintain high levels of predation on canopy arthropods despite the increased consumption of cicadas by individual birds. Our observational data, however (Steward et al. 1988a, b), indicate this did not happen. Our attempts to study bird predation on lepidopteran larvae by placing caterpillars in the canopy on the Cassidy site in 1984 failed due to heavy predation by vespid wasps (Steward et al. 1988b).

By counting cicada emergence holes in 16 1-m² plots in each of the 100 subplots and by using wing traps (see Karban 1982) to collect wings of cicadas that had been eaten by birds, we estimated that over one million adult periodical cicadas emerged on the Cassidy site during 6 May to 3 June 1985 and that birds consumed about 15% of them (Steward 1986; K. S. Williams et al., unpubl.). During that same period, sampling at Tillery yielded no adult cicadas. We suggest those differences in arthropod abundance should have been sufficient to induce a treatment effect if one were to occur.

Initially, we had concerns that high variation in canopy arthropod densities could cause difficulties in determination of treatment-induced differences between sites. However, data presented here indicate that differences associated with such variables as tree species, month, site, and year were detectable in each of the guilds studied. This lends credibility to the suggestion that our extensive sampling effort produced sample sizes sufficient to detect an effect, had treatment-induced differences been present. We conclude that forest birds in the Ozarks may not have a significant impact on the population dynamics of their arthropod prey, and that results from studies conducted in northern forests may not be generalizable to situations in southern forests (see also Rabenold 1978, 1979; Steward et al. 1988b).

ACKNOWLEDGMENTS

We thank M. Cassidy and M. Tillery for allowing this research to be conducted on their lands. We also thank the many dedicated students and staff who helped in field collection and laboratory sorting of foliage samples. We appreciate the assistance of M. Mathis and D. Goldhammer in arthropod identification, R. Sanger for computer manipulation and analysis of data, and J. E. Dunn for statistical advice. We are grateful to R. T. Holmes, C. J. Ralph, and H. Recher for their time and expertise in review of this manuscript. This study was supported, in part, by National Science Foundation grant BSR-84-08090. Published with the approval of the Director, Arkansas Agricultural Experiment Station.