

EFFECTS OF PERIODICAL CICADA EMERGENCES ON ABUNDANCE AND SYNCHRONY OF AVIAN POPULATIONS

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Abstract. We used 37 years of North American Breeding Bird Surveys to test for effects of periodical cicada (*Magicicada* spp.) emergences on the abundance and spatial synchrony of 24 species of avian predators in hardwood forests of the eastern United States. Fifteen (63%) of the bird species exhibited numerical changes in abundance apparently associated with emergences of the local periodical cicada brood, and intraspecific spatial synchrony of bird abundance was significantly greater between populations sharing the same cicada brood than between populations in the ranges of different broods. Species exhibited at least four partially overlapping temporal patterns. (1) Cuckoos (*Coccyzus* spp.) occurred in high numbers only during emergence years and subsequently declined in abundance. (2) Red-bellied Woodpeckers (*Melanerpes carolinus*), Blue Jays (*Cyanocitta cristata*), Common Grackles (*Quiscalus quiscula*), and Brown-headed Cowbirds (*Molothrus ater*) increased significantly 1–3 years following emergences and then declined. (3) Red-headed Woodpeckers (*Melanerpes erythrocephalus*), American Crows (*Corvus brachyrhynchos*), Tufted Titmice (*Baeolophus bicolor*), Gray Catbirds (*Dumetella carolinensis*), and Brown Thrashers (*Toxostoma rufum*) were found in significantly low numbers during emergence years, underwent significant numerical increases in the following year, and then stabilized. (4) Wood Thrushes (*Hylocichla mustelina*), Northern Mockingbirds (*Mimus polyglottos*), Northern Cardinals (*Cardinalis cardinalis*), and House Sparrows (*Passer domesticus*) exhibited significantly deviant population numbers 1–2 years prior to emergences, below the long-term mean in the first two species and above the long-term mean in the latter two. These results suggest that the pulses of resources available at 13- or 17-year intervals when periodical cicadas emerge have significant demographic effects on key avian predators, mostly during or immediately after emergences, but in some cases apparently years following emergence events.

Key words: bird populations; Breeding Bird Survey; eastern North America; hardwood forests; *Magicicada*; periodical cicadas; predation; predator satiation; pulsed resources; spatial synchrony.

INTRODUCTION

The ecosystem importance of pulsed resources that occur as episodic events at long, multiyear intervals has recently begun to be appreciated as more long-term studies have documented the ecological consequences of pulsed phenomena (Ostfeld and Keesing 2000). Such pulses can have cascading effects as the relatively large amount of energy made ephemerally available makes its way both up and down the food chain (Pace et al. 1999). Widespread examples include mast-fruiting by seed-bearing trees and various kinds of insect and rodent outbreaks.

A particularly dramatic pulsed phenomenon is the emergence of periodical cicadas of the genus *Magicicada* in hardwood forests of eastern North America (Yang 2004). These insects exhibit one of the most extraordinary life cycles of any insect. Nymphs de-

velop underground for either 13 or 17 years, after which adults emerge from the ground and climb into the canopy, where they feed, mate, oviposit on twigs, and die, all within a period of 3–4 weeks. Several weeks later, first-instar nymphs hatch from the eggs, descend to the forest floor, burrow into the soil, and start the process once again. Such periodicity is rare, and of known periodical species, no others come close to matching the cycle length of *Magicicada* (Heliövaara et al. 1994).

Periodical cicada populations are divided into developmentally synchronized, temporally isolated cohorts known as broods, each composed of three or four sympatric species. Populations of 12 of these broods require 17 years to complete development, whereas three broods require 13 years (Williams and Simon 1995, Marshall and Cooley 2000). Over most of their range, broods are allopatric; thus all individuals at a given location generally emerge synchronously during the same year.

Emphasizing the potential significance of emergences is the fact that periodical cicadas are among the most

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abundant of all forest insects, reaching 2.6×10^6 cicadas/ha (Lloyd and Dybas 1966a, b, Karban 1980). Adults are large, nontoxic, easily captured, and readily consumed by a variety of predators (Dybas and Davis 1962, Lloyd and Dybas 1966b, Williams and Simon 1995). This combination of abundance, lack of natural defenses, and extraordinary synchrony within a region can result in periodical cicadas being consumed in large numbers during emergences; predators, in turn, have been observed to annihilate small populations of periodical cicadas (Marlatt 1907, Alexander and Moore 1958). In contrast, predators are generally unable to consume more than a fraction of the periodical cicadas during emergences when cicadas are abundant (Karbon 1982, Williams et al. 1993). These results support the widely held assumption that much of the life-history evolution of periodical cicadas has been driven by predator satiation, and that their extraordinarily long life cycle has evolved to escape the numerical responses of predators (Williams and Simon 1995).

Periodical cicada adults have an immediate negative impact on the radial growth of host trees, depressing growth of hardwoods on a regional scale by ~4% in emergence years (Koenig and Liebhold 2003). However, the carcasses of dead adult cicadas, present in large numbers in emergence years, provide a significant nutrient resource pulse to forest soils, increasing microbial biomass and nitrogen availability (Yang 2004). Given this pulse of energy and nutrients, one would expect that important "bottom-up" effects in the form of higher populations of predators would be relatively easy to detect. Surprisingly, this has not proven to be the case. Although numerous species have been observed eating periodical cicadas, we are aware of only a handful of studies reporting demographic effects of periodical cicadas on potential predators, none of which has reported effects outside of emergence years.

Three of these studies have been on birds. Nolan and Thompson (1975) reported several apparent differences in the breeding of Yellow-billed and Black-billed Cuckoos (for scientific names, see Table 1) in southern Indiana, USA, during an emergence of Brood X, including increased numbers of nests, earlier breeding, and larger clutches. More quantitatively, Anderson (1977) compared reproduction in House Sparrows (*Passer domesticus*) and European Tree Sparrows (*Passer montanus*) near St. Louis, Missouri, USA in 1972 during emergence of Brood XIX with four non-emergence years, finding significantly larger clutch sizes and shorter interclutch intervals in European Tree Sparrows and significantly higher fledging success and increased nestling body mass in House Sparrows during the emergence year. Strehl and White (1986) studied Red-winged Blackbirds (*Agelaius phoeniceus*) during an emergence of Brood XXIII in southern Illinois, USA, and reported several differences including increased nestling body mass and survival compared to non-emergence years.

We are aware of only one study that has addressed the effects of periodical cicada emergences on a non-avian taxon. Krohne et al. (1991) studied small mammals in west-central Indiana during an emergence of Brood X and found no apparent effect on white-footed mice (*Peromyscus leucopus*), but a fourfold increase in the numbers of short-tailed shrews (*Blarina brevicauda*).

Here we take a new approach to the challenge of detecting demographic effects of pulsed periodical cicada emergences on avian populations. Using avian census data from the North American Breeding Bird Survey, we matched sites with appropriate cicada brood emergence years to explore effects of emergences on regional abundance of 24 bird species known or likely to eat periodical cicadas. Our working hypothesis was that periodical cicadas are an important pulsed resource that is likely to have strong "bottom-up" consequences for their communities, and that the long-term, regional data provided by the Breeding Bird Survey would yield considerably more power to detect those consequences than the approaches to this issue used in previous studies.

METHODS

The North American Breeding Bird Survey (BBS) consists of a series of censuses performed once a year in the spring. Each census consists of a 3-minute observation at a series of 50 stops 0.8 km apart along a road transect (Bystrack 1981). We downloaded surveys performed for the 37 breeding seasons from 1966 to 2002, inclusive (*available online*).⁴ From these, we extracted data for 24 species of terrestrial birds (Table 1) that are known or likely (based on size, distribution, and diet) to eat periodical cicadas. Thus, our analyses were exploratory in that they included species for which there exist no prior published data regarding their propensity to eat cicadas. We expected a priori that populations of at least some species that we tested would not exhibit any relationship to periodical cicada emergences.

Each BBS site was matched to the local cicada brood based on county-level maps of brood distributions (Marlatt 1907, Simon 1988) using a geographical information system. In order to eliminate complications arising from areas of apparent sympatry among different broods, data from the few counties with records of two or more broods or with low-density emergences were discarded. Thus, only BBS sites unambiguously located within the range of a single brood of periodical cicadas emerging in abundant densities were included in the analyses. In total, 356 sites were used; 127 of these were within the range of 13-year cicada broods and 229 were within the range of 17-year broods (Fig. 1). However, not all sites yielded data for analyses of

⁴ (<http://www.mbr-pwrc.usgs.gov/bbs/bbs2002.html>)

TABLE 1. Species of birds and number of Breeding Bird Surveys (BBS) used in the analyses.

Species	Scientific name	Code	No. surveys within range of cicada broods		References†
			13-year	17-year	
American Kestrel	<i>Falco sparverius</i>	AMKE	92	215	Riis (1940)
Black-billed Cuckoo	<i>Coccyzus erythrophthalmus</i>	BBCU	33	203	Riis (1940); Nolan and Thompson (1975)
Yellow-billed Cuckoo	<i>Coccyzus americanus</i>	YBCU	127	228	Riis (1940); Nolan and Thompson (1975)
Red-headed Woodpecker	<i>Melanerpes erythrocephalus</i>	RHWO	122	166	Howard (1937); Riis (1940)
Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	RBWO	127	224	
Red-eyed Vireo	<i>Vireo olivaceus</i>	REVI	126	225	Kellner et al. (1990)
Blue Jay	<i>Cyanocitta cristata</i>	BLJA	127	229	Riis (1940); Karban (1982)
American Crow	<i>Corvus brachyrhynchos</i>	AMCO	127	229	Riis (1940)
Carolina Chickadee	<i>Poecile carolinensis</i>	CACH	113	114	
Tufted Titmouse	<i>Baeolophus bicolor</i>	TUTI	127	223	Kellner et al. (1990)
White-breasted Nuthatch	<i>Sitta carolinensis</i>	WBNU	102	225	
Wood Thrush	<i>Hylocichla mustelina</i>	WOTH	127	215	Karban (1982)
American Robin	<i>Turdus migratorius</i>	AMRO	126	229	Howard (1937); Karban (1982)
Gray Catbird	<i>Dumetella carolinensis</i>	GRCA	123	228	
Northern Mockingbird	<i>Mimus polyglottos</i>	NOMO	126	202	
Brown Thrasher	<i>Toxostoma rufum</i>	BRTH	127	229	
European Starling	<i>Sturnus vulgaris</i>	EUST	126	229	Howard (1937); Riis (1940); Karban (1982)
Eastern Towhee	<i>Pipilo erythrophthalmus</i>	EATO	126	218	
Northern Cardinal	<i>Cardinalis cardinalis</i>	NOCA	127	229	
Red-winged Blackbird	<i>Agelaius phoeniceus</i>	RWBL	127	229	Strehl and White (1986); Steward et al. (1988)
Common Grackle	<i>Quiscalus quiscula</i>	COGR	126	229	Howard (1937); May (1979); Karban (1982)
Brown-headed Cowbird	<i>Molothrus ater</i>	BHCO	127	229	Howard (1937); Riis (1940)
Baltimore Oriole	<i>Icterus galbula</i>	BAOR	100	222	
House Sparrow	<i>Passer domesticus</i>	HOSP	127	228	Howard (1937); Riis (1940); Anderson (1977)

† References are listed for those species known to eat periodical cicadas or whose demography has been shown to be affected by periodical cicada emergences.

all species, and thus sample sizes were often smaller than these values (Table 1).

Data were manipulated as follows. First, we log-transformed the number of birds counted during each year of the survey ($\log[\text{number of birds counted} + 1]$) in order to help equalize variances and normalize the data. Given the short duration of most of the time series (mean = 26 years) relative to the length of the cicada cycles, using anything besides a linear regression to remove long-term trends was not feasible. Thus, we detrended each site \times year series using a linear regression and then standardized to mean = 0 and SD = 1. For each year, we then determined the length of time since the last emergence of the coincident cicada brood (YEAR). YEAR varied from 0 (an emergence year) to 12 or 16 years, depending on whether the local brood was a 13-year or 17-year form. However, in order to combine populations living within the ranges of 13-year and 17-year broods, we analyzed the four years

prior to emergences (YEAR -4 to YEAR -1, corresponding to YEAR 9 to YEAR 12 for populations within the range of 13-year broods and YEAR 13 to YEAR 16 for populations within the range of 17-year broods), the emergence year (YEAR 0), and the eight years following emergences (YEAR 1 to YEAR 8).

For analyses testing for overall effects of emergences, we calculated the mean standardized population size for all values of YEAR within a series. That is, if the BBS data for a particular species \times site series encompassed two emergence years (for example, 1973 and 1990 for a survey conducted within the range of Brood XIII), we averaged the standardized population abundance estimates for those two years. This procedure yielded a single set of population estimates for each species \times site series. Only sites for which at least one survey was performed for all years of the appropriate cicada brood cycle were included in the analyses.

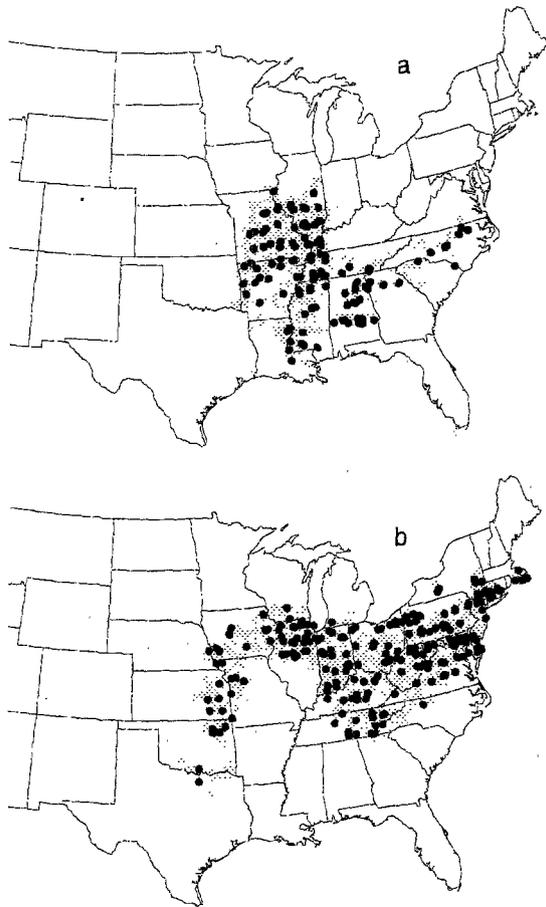


FIG. 1. The eastern United States, showing in gray the geographic range of (a) 13-year and (b) 17-year periodical cicada broods. Black circles represent localities of Breeding Bird Surveys used in the analyses.

Differences in the mean population size of each species vis-à-vis YEAR were tested with SPSS (1999) using repeated-measures general linear models. Statistical significance was based on linearly independent pairwise comparisons among the estimated marginal means. We also specifically targeted the effect of emergences on population size by statistically comparing size in YEAR -1 with that in YEAR 0, and YEAR 0 with that in YEAR 1, using paired mean standardized population values (one set for each species \times site data set) and Wilcoxon signed-ranks tests.

Analyses of spatial synchrony (Bjørnstad et al. 1999, Koenig 1999, Liebhold et al. 2004) were performed by calculating the Pearson correlation coefficient between the log-transformed and detrended population estimates of each bird species, comparing time series from all sites in a pairwise fashion. All years of data were used. Contrasts were then made first by binning pairs according to the geographic distance separating sites (<100 km, 100 to <250 km, 250 to <500 km, 500 to

<1000 km, and 1000–2500 km), and then according to whether pairs of sites were within the range of the same brood of periodical cicadas or within the range of different cicada broods. For each distance category, the mean distance was equalized between within- and between-brood sites by randomly eliminating between-brood sites relatively far apart until the means were the same. Among sites not sharing the same brood, pairwise comparisons between different broods of the same periodicity (both 13-year or both 17-year) and those of different periodicity (13-year vs. 17-year) were combined. For estimates of the overall influence of cicadas on avian synchrony, we averaged the mean correlation coefficients of sites within and between the range of cicada broods for each distance category across species and tested for significance between the within- and between-brood values with paired Wilcoxon signed-ranks tests.

RESULTS

Population abundance.—Of the 24 species considered, 12 (50%) exhibited significant differences ($P \leq 0.05$) among years based on the general linear models and 13 (54%) exhibited significant differences between YEAR -1 and YEAR 0, YEAR 0 and YEAR 1, or both (Table 2). Ten of 12 (83%) species significant by the general linear models also exhibited a significant change in abundance between emergence years and the year following emergences. Altogether, 15 (63%) of the species exhibited numerical changes in abundance, apparently associated with emergences of the local periodical cicada brood.

Plots of the estimated marginal means vs. years to or since emergence for these 15 species suggest at least four major patterns (Fig. 2). See Table 1 for all scientific names. The first, exhibited by the two cuckoos (Fig. 2a, b), involved population abundances that jumped to significantly high levels in emergence years and subsequently declined to average, and by YEAR 5 below-average, values. In both cases, the declines following emergence were supported by the strong increase in birds counted in YEAR 0 compared to YEAR -1 and subsequent highly significant decrease in birds counted in YEAR 1 compared to YEAR 0, with the changes being >40% for the Black-billed and 17% for the Yellow-billed Cuckoo (Table 2). The two species declined an average of 29.4% from YEAR 0 to YEAR 1.

In the second pattern, exhibited by the Red-bellied Woodpecker (Fig. 2c), Blue Jay (Fig. 2d), Common Grackle (Fig. 2e), and Brown-headed Cowbird (Fig. 2f), populations were average or below average in the year prior to emergences and increased in YEAR 1 to values that were significantly above the long-term mean. Abundance then remained significantly above average in all species, except the Common Grackle, through YEAR 2 and, in the case of the Blue Jay, through YEAR 3, after which they declined to average

TABLE 2. Results of repeated-measures, general linear models (one for each species), number of birds counted in years during and following cicada emergences, and percentage change in bird counts.

Species	Years since emergence†			No. birds counted‡ (mean ± SE)			Change in bird count (%)	
	F	df	P	Year prior to	Emergence	Year following	YEAR -1	YEAR 0 to
				(YEAR -1)	year	emergence		
American Kestrel	1.3	12,295	0.21	0.83 ± 0.07	0.78 ± 0.06	0.80 ± 0.06	-5.4	+2.0
Black-billed Cuckoo	2.7	12,221	0.002	0.47 ± 0.05	0.70 ± 0.08	0.40 ± 0.05	+46.7***	-41.9**
Yellow-billed Cuckoo	4.0	12,343	<0.001	4.81 ± 0.29	5.64 ± 0.27	4.69 ± 0.26	+17.3	-16.9***
Red-headed Woodpecker	1.8	12,276	0.04	2.48 ± 0.20	2.15 ± 0.18	2.54 ± 0.20	-13.5*	+18.2***
Red-bellied Woodpecker	2.4	12,339	0.005	5.51 ± 0.28	5.15 ± 0.27	5.65 ± 0.29	-6.6	+9.7***
Red-eyed Vireo	0.8	12,339	0.61	9.57 ± 0.69	9.48 ± 0.69	9.27 ± 0.65	-0.9	-2.2
Blue Jay	3.9	12,343	<0.001	14.08 ± 0.49	12.99 ± 0.44	14.54 ± 0.50	-7.8	+12.0***
American Crow	3.8	12,344	0.001	32.74 ± 0.91	29.87 ± 0.84	32.78 ± 0.96	-8.8	+9.7***
Carolina Chickadee	1.5	12,215	0.14	5.55 ± 0.31	5.89 ± 0.30	6.08 ± 0.35	+6.0	+3.3
Tufted Titmouse	1.2	12,337	0.28	8.74 ± 0.35	8.47 ± 0.34	8.78 ± 0.35	-3.0	+3.6*
White-breasted Nuthatch	0.7	12,315	0.79	1.63 ± 0.10	1.56 ± 0.10	1.73 ± 0.12	-4.5	+10.7
Wood Thrush	2.4	12,330	0.006	8.65 ± 0.46	8.57 ± 0.46	8.58 ± 0.44	-0.9	+0.1
American Robin	1.2	12,343	0.31	42.62 ± 1.43	43.66 ± 1.47	44.42 ± 1.43	+2.4	+1.7
Gray Catbird	1.9	12,338	0.03	7.81 ± 0.43	7.63 ± 0.45	8.24 ± 0.46	-2.4	+8.0***
Northern Mockingbird	2.2	12,315	0.012	14.02 ± 0.77	14.43 ± 0.79	14.41 ± 0.76	+2.9	+0.2
Brown Thrasher	1.8	12,344	0.05	4.80 ± 0.19	4.35 ± 0.17	4.64 ± 0.18	-9.4	+6.6*
European Starling	1.2	12,343	0.28	73.09 ± 3.21	74.53 ± 3.42	74.23 ± 3.27	+2.0	-0.4
Eastern Towhee	0.7	12,332	0.77	8.68 ± 0.44	8.54 ± 0.45	8.47 ± 0.41	-1.7	-0.8
Northern Cardinal	1.0	12,344	0.46	26.15 ± 0.80	25.45 ± 0.77	26.15 ± 0.86	-2.7*	+2.8
Red-winged Blackbird	1.6	12,344	0.09	91.38 ± 4.67	94.76 ± 5.51	95.29 ± 5.34	+3.7	+0.6
Common Grackle	2.4	12,343	0.005	85.54 ± 5.07	76.16 ± 3.42	85.01 ± 4.04	-11.0*	+11.6**
Brown-headed Cowbird	2.3	12,344	0.008	12.95 ± 0.52	11.85 ± 0.46	13.38 ± 0.55	-8.5**	+12.9***
Baltimore Oriole	0.6	12,310	0.86	3.80 ± 0.24	3.86 ± 0.24	3.81 ± 0.25	+1.6	-1.4
House Sparrow	1.6	12,343	0.09	82.68 ± 4.51	79.07 ± 4.27	76.88 ± 3.92	-4.4*	-2.8

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

† Between-subjects effects, including four years prior to emergence (YEAR -4) to eight years after emergence (YEAR 8).

‡ Values listed are the mean numbers of individuals counted during the surveys.

§ Significance from paired Wilcoxon signed-ranks tests comparing mean YEAR -1 to YEAR 0 and YEAR 0 to YEAR 1 values for each species × site series.

levels. The mean percentage increase in population numbers counted in YEAR 1 compared to YEAR 0 in these four species ranged between 9.7% and 12.9%, averaging 11.6% (Table 2).

The third pattern, shown by the Red-headed Woodpecker (Fig. 2g), American Crow (Fig. 2h), Tufted Titmouse (Fig. 2i), Gray Catbird (Fig. 2j), and Brown Thrasher (Fig. 2k), again involved a significant increase in numbers between YEAR 0 and YEAR 1, but in contrast to the prior group, started during emergence years with populations significantly below the overall mean. Numbers subsequently fluctuated around the long-term mean values, with the exception of significantly high abundance of American Crows in YEAR 8. The mean percentage increase in population size between YEAR 0 and YEAR 1 in these five species ranged from 3.6% to 18.2% and averaged 9.2% (Table 2).

The fourth pattern included four species whose unifying feature was that they exhibited population numbers significantly different from the long-term mean prior to emergences. Values were significantly below average in YEAR -2 in the Wood Thrush (Fig. 2l) and in YEAR -1 in the Northern Mockingbird (Fig. 2m), whereas they were significantly above average in YEAR -2 in the Northern Cardinal (Fig. 2n) and in YEAR -1 in the House Sparrow (Fig. 2o). In both

of these latter species, populations decreased significantly between YEAR -1 and emergence years (YEAR 0).

Population synchrony.—Mean spatial synchrony of the bird species was generally fairly low, with $r < 0.10$ for all but one (98%) of the correlations in the <100 km distance class (Table 3). Nonetheless, synchrony was significantly greater than zero for 25 of 40 (63%) comparisons within the <100 km distance category and for 12 of 40 (30%) in the 100 to <250 km distance category (Table 3). Few values were significant at the larger distance categories, and these are not considered further. Within the <100 km distance category, 18 of 24 (75%) species were significant when comparing populations sharing the same cicada brood, whereas only 7 of 24 (29%) species were significant across cicada broods (Fisher exact test, $P = 0.002$).

Across species, comparisons were made for all 24 bird species and for only the 15 species that, based on the results in Table 2, exhibited significant differences in population abundance, apparently related to periodical cicada emergences. Results for both groups of species indicated that mean spatial synchrony was greater for all distance categories among sites within the range of the same cicada brood. Differences were statistically significant for the 100 to <250 km dis-

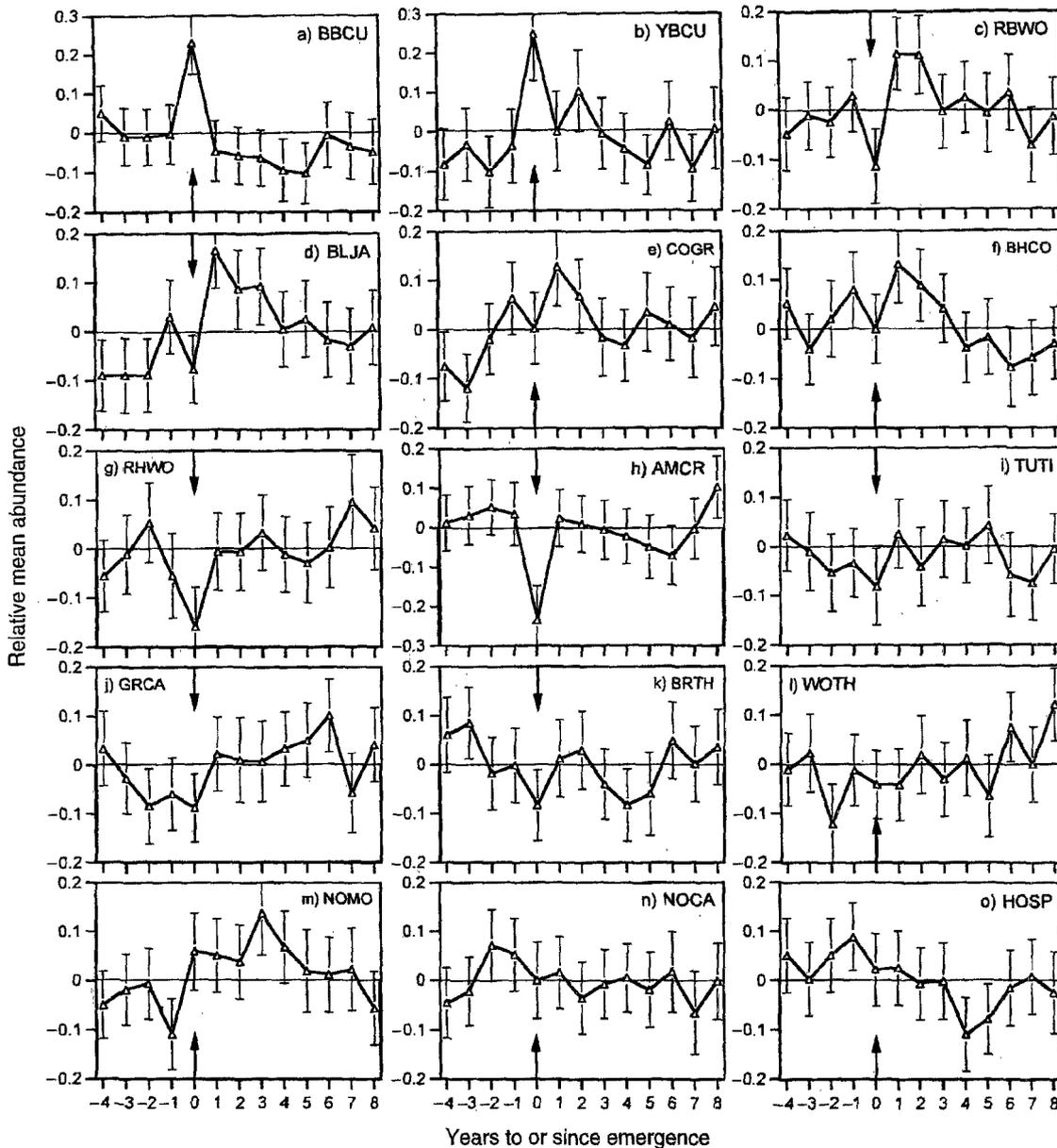


FIG. 2. Standardized population abundance (mean and 95% confidence interval) vs. years since cicada emergence (YEAR -4 to YEAR 8) for the 15 bird species whose populations during these years were significantly related to years since emergence in a general linear model, or whose populations changed significantly in the year before or year after emergences (Table 2). Values are plotted in reference to emergences of the local periodical cicada brood; arrows designate emergence years (YEAR 0). For species codes and sample sizes, see Table 1.

tance class using all species, and for both the <100 km and 100 to <250 km distance classes using only the 15 species apparently influenced by cicada emergences (Fig. 3). Among these latter species, synchrony between sites <100 km apart sharing the same brood was, on average, 42.7% greater than between sites a similar distance apart but not sharing the same cicada brood.

DISCUSSION

These results provide strong observational evidence that periodical cicada emergences have significant effects on populations of a variety of key avian predators. Of the 24 bird species considered, 12 (50%) yielded significant evidence that population abundance varied over the length of the cicada cycle; 13 (54%) exhibited

TABLE 3. Spatial synchrony, correlation coefficient r (mean \pm SD), of bird populations located within vs. between cicada broods for sites <100 km and sites 100–250 km apart.

Species	Sites <100 km apart†			Sites 100–250 km apart†		
	Between brood	Within brood	Difference (%)‡	Between brood	Within brood	Difference (%)‡
American Kestrel	-0.016 \pm 0.027	0.020 \pm 0.017	[+]	0.008 \pm 0.019	0.017 \pm 0.018	+113
Black-billed Cuckoo	0.039 \pm 0.037	0.052 \pm 0.021	+33	0.035 \pm 0.024	0.023 \pm 0.020	-34
Yellow-billed Cuckoo	0.083 \pm 0.026	0.137 \pm 0.016	+65	0.066 \pm 0.018	0.094 \pm 0.017	+42
Red-headed Woodpecker	0.066 \pm 0.027	0.057 \pm 0.019	-16	0.027 \pm 0.020	0.038 \pm 0.019	+41
Red-bellied Woodpecker	0.037 \pm 0.027	0.050 \pm 0.017	+35	0.009 \pm 0.020	0.022 \pm 0.019	+144
Red-eyed Vireo	0.066 \pm 0.028	0.031 \pm 0.017	-53	0.018 \pm 0.020	0.025 \pm 0.018	-39
Blue Jay	0.016 \pm 0.024	0.048 \pm 0.016	+200	0.010 \pm 0.021	0.026 \pm 0.017	+160
American Crow	0.047 \pm 0.027	0.036 \pm 0.018	-23	0.012 \pm 0.019	0.024 \pm 0.018	+100
Carolina Chickadee	0.042 \pm 0.036	0.048 \pm 0.021	+14	0.019 \pm 0.027	0.019 \pm 0.024	0
Tufted Titmouse	0.060 \pm 0.027	0.083 \pm 0.017	+38	0.039 \pm 0.020	0.051 \pm 0.018	+31
White-breasted Nuthatch	0.031 \pm 0.018	0.031 \pm 0.018	0	0.018 \pm 0.020	0.009 \pm 0.019	-50
Wood Thrush	0.045 \pm 0.025	0.049 \pm 0.018	+9	0.033 \pm 0.020	0.035 \pm 0.018	+6
American Robin	0.078 \pm 0.028	0.067 \pm 0.018	-14	0.031 \pm 0.020	0.037 \pm 0.019	+19
Gray Catbird	0.052 \pm 0.025	0.036 \pm 0.017	+31	0.006 \pm 0.019	0.016 \pm 0.018	+167
Northern Mockingbird	0.053 \pm 0.025	0.083 \pm 0.018	+57	0.055 \pm 0.019	0.055 \pm 0.019	0
Brown Thrasher	0.007 \pm 0.028	0.041 \pm 0.016	+486	0.008 \pm 0.020	0.015 \pm 0.018	+88
European Starling	0.078 \pm 0.027	0.045 \pm 0.017	-42	0.010 \pm 0.020	0.022 \pm 0.018	+120
Eastern Towhee	0.068 \pm 0.028	0.043 \pm 0.017	-37	0.014 \pm 0.020	0.015 \pm 0.018	+7
Northern Cardinal	0.032 \pm 0.026	0.059 \pm 0.016	+84	0.023 \pm 0.021	0.018 \pm 0.019	-22
Red-winged Blackbird	0.029 \pm 0.029	0.077 \pm 0.018	+166	0.034 \pm 0.019	0.049 \pm 0.018	+44
Common Grackle	0.030 \pm 0.028	0.065 \pm 0.017	+117	0.021 \pm 0.020	0.037 \pm 0.018	+76
Brown-headed Cowbird	0.045 \pm 0.024	0.038 \pm 0.017	-16	0.016 \pm 0.019	0.023 \pm 0.018	+44
Baltimore Oriole	0.096 \pm 0.028	0.039 \pm 0.018	-59	0.012 \pm 0.020	0.022 \pm 0.018	+83
House Sparrow	0.021 \pm 0.027	0.069 \pm 0.017	+229	0.047 \pm 0.020	0.044 \pm 0.018	-6

Note: Species in boldface are those with significant differences indicated by repeated-measures general linear models or by a significant change in abundance just before or just following emergences (Table 2).

† Mean distance between within- and between-brood sites equalized. Values in boldface are significantly greater than zero ($P < 0.05$) based on randomization tests.

‡ Percentage increase (+) or decrease (-) from between-brood value to within-brood value. This was not calculated for the one case in which the between-brood value was negative.

significant change in numbers just prior to or immediately following emergences (Table 2). Spatial synchrony was generally low in these data, matching earlier results analyzing spatial synchrony in California land birds using the BBS data by Koenig (1998). Nonetheless, synchrony was greater between sites within the range of the same cicada brood than between sites the same distance apart, but within the range of different broods.

That some species exhibited no significant effects related to periodical cicada emergences is not surprising. For example, Red-eyed Vireos were included on the basis of having been observed eating periodical cicadas by Kellner et al. (1990), even though these authors subsequently detected no changes in foraging behavior in this species during a cicada emergence. Other species such as Carolina Chickadees and White-breasted Nuthatches were included solely on the basis of being plausible cicada predators. Given the exploratory nature of the analyses, it is particularly impressive that populations of over half (63%) of the species analyzed appeared to be significantly influenced by cicada emergences. Of those not obviously affected, based on the population analyses, at least one, the Red-winged Blackbird, was apparently influenced in terms of increased spatial synchrony (Table 3). Including this species, only eight of the 24 (33%) species tested

(American Kestrel, Red-eyed Vireo, Carolina Chickadee, White-breasted Nuthatch, American Robin, European Starling, Eastern Towhee, and Baltimore Oriole) yielded no evidence (in terms of either their population numbers vis-à-vis cicada emergences, or higher spatial synchrony between populations sharing the same periodical cicada brood) that cicada emergences had any detectable effect on their population ecology.

It is also noteworthy that the changes in bird abundances associated with cicada emergence detected here represent regional increases over most or all of the geographic range of cicada broods. Although there is evidence that insect outbreaks can synchronize bird populations over short distances (Jones et al. 2003), this is the first report of geographically widespread changes in avian populations due to pulses in insect abundance. The changes are particularly remarkable, considering that the areas over which they were detected most likely contained considerable variation in adult cicada abundance during the year of emergence.

The apparent effects of cicada emergences on the avian species varied. Several bird species exhibited a numerical increase following emergences. Of the 10 species for which significant differences were detected from YEAR 0 to YEAR 1, values in YEAR 1 significantly increased from those in emergence years in eight species (Table 2), indicating a positive numerical

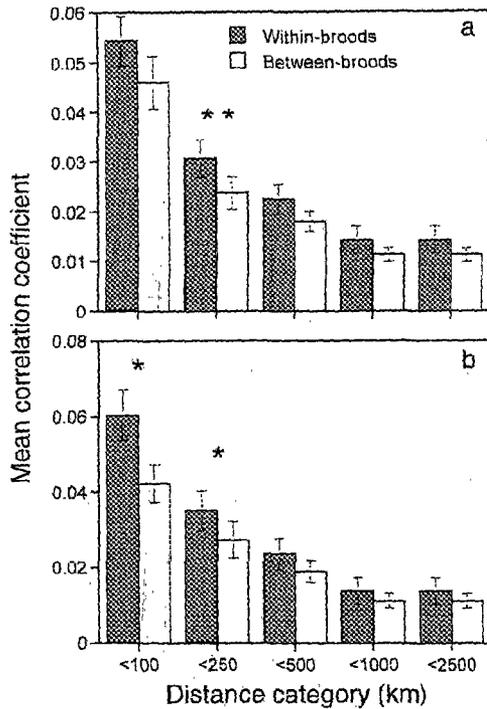


FIG. 3. Spatial synchrony, r (mean \pm SE), between sites within the range of the same periodical cicada brood ("within broods") and between sites within the ranges of different broods ("between broods") divided into five categories according to the distance between sites for (a) all 24 bird species considered and (b) only the 15 bird species exhibiting significant differences by at least one of the analyses summarized in Table 2. Within- and between-brood means were compared using Wilcoxon signed-ranks tests; significant differences are indicated by the asterisks (* $P < 0.05$; ** $P < 0.01$).

increase presumably attributable to high survivorship or reproductive success enjoyed during emergence years. The increase in counts of these eight species ranged up to 18.2% and averaged $10.0\% \pm 4.7\%$ (mean \pm SD). These beneficial effects of emergences were usually unambiguous only in YEAR 1, but in the case of the Blue Jay, numbers remained significantly high ($P < 0.05$) for three years following emergences (Fig. 2d). Prior studies, just discussed, suggest that these numerical responses are most likely to be a consequence of increased reproductive success during emergence years, including larger clutch size, more nesting attempts, and increased nestling survival. Offspring resulting from such increased reproduction may survive for years and, assuming that they exhibit some general site fidelity, would then potentially result in mean population numbers significantly above the long-term mean for several years following the emergence event itself.

In contrast, numbers of the two cuckoo species significantly increased during, and decreased subsequent

to, emergences (Table 2, Fig. 2a, b). The most likely explanation for this finding is that individuals of these two Neotropical migrants are attracted to areas of cicada emergences, thus resulting in relatively high populations in emergence years, followed by average or slightly below-average numbers in subsequent years. Presumably, numbers decline following emergences as returning migrants are attracted away from a particular site to other regions, including those where other cicada broods are emerging. This hypothesis is supported qualitatively by prior studies that have generally found that these cuckoos are drawn to insect outbreaks (Bent 1940, Hamilton and Hamilton 1965, Nolan and Thompson 1975, Hughes 1999, 2001).

A second dimension along which species differed was in their relative numbers during emergence years. In the case of the two cuckoos, the large populations found in emergence years (Fig. 2a, b) are again most likely due to birds being attracted to regions where emergences are taking place. It is less clear why populations of four species (Northern Cardinal, Common Grackle, Brown-headed Cowbird, and House Sparrow) declined from YEAR -1 to YEAR 0 (Table 2) and why abundances of seven species (Red-bellied Woodpecker, Blue Jay, Red-headed Woodpecker, American Crow, Tufted Titmouse, Gray Catbird, and Brown Thrasher) were significantly below the long-term average during emergence years (Fig. 2c, d, g-k). We can think of three possible explanations for this finding. The first is that these species avoid regions where emergences are taking place, either because of the cicadas themselves or because of some secondary factor such as the relatively large numbers of cuckoos attracted to such areas. This latter factor would be particularly intriguing if Black-billed and Yellow-billed Cuckoos, which are apparently attracted to cicada emergences, were somehow detrimental to the other species. However, because neither species of cuckoo is parasitic and all of the several species of birds exhibiting low numbers during emergence years are known to eat cicadas (Table 1), this hypothesis seems unlikely.

A second possibility is that the noise generated by cicadas during emergences may have made it more difficult to hear these species during surveys, thus resulting in relatively few birds being counted. Although possible, it seems unlikely that this problem would differentially affect the woodpeckers or American Crows, all three of which have loud, raucous calls that are at least as easily detected as calls of the other species for which relatively low numbers during emergence years were not found. The relatively high numbers of the cuckoo species detected during emergence years also counter the predictions of this hypothesis.

A third hypothesis is that the low population size of these species found during emergence years is not directly due to the ongoing emergence event, but rather is an indirect effect held over from the *prior* emergence event 13 or 17 years earlier. Although this hypothesis

is speculative, it is worth considering that the primary adaptive benefit of the extraordinary life cycle of periodical cicadas is presumably to decrease predation on adults (Lloyd and Dybas 1966b, Hoppensteadt and Keller 1976, Bulmer 1977, May 1979, Karban 1982, Williams and Simon 1995, Itô 1998), and that this goal would be most effectively achieved if the cicada life cycle not only eliminated the opportunity for predators to track cycles, but also initiated a long-term population cycle in predators themselves that culminated in relatively low numbers 13 or 17 years later, when the next emergence took place.

However, even with the data considered here, it appears that the demographic consequences of emergences may persist for several years, and are detectable both in the abundance and population synchrony of a large percentage of the terrestrial avifauna. In the case of the Blue Jay, this takes the form of relatively high numbers 1–3 years post-emergence (Fig. 2d). In the case of at least the two cuckoos, high numbers either during or just after emergences are followed by declining populations and relatively low numbers 4–7 years post-emergence (Fig. 2a, b). These results indicate that, at least in some species, the effects of cicada emergences are detectable years after the event itself. The large pulse of microbial biomass and nitrogen potentially provided by cicada carcasses to forest soils following emergences provides a plausible mechanism for such persistent “bottom-up” effects (Yang 2004).

These results are surprising, to the extent that prior studies have generally failed to detect evidence that cicada emergences affect the behavior or demography of other species in their communities. For example, a detailed study of an emergence of brood XIX in the Ozarks found little change in the foraging behavior of insectivorous birds attributable to the emergence (Kellner et al. 1990), and the emergence failed to result in any detectable ecological release among other arthropod prey within the forest (Stephen et al. 1990). This same study estimated that periodical cicadas contributed <1% to the total nutrient flux of the ecosystem (Wheeler et al. 1992), although higher densities of cicadas can clearly represent much higher nutrient fluxes (Yang 2004).

More recently, Koenig and Liebhold (2003) found the effects of periodical cicadas on growth of the oaks on which they feed to be significant during emergence years, decreasing radial growth by 4% on a regional scale. This “top-down” effect of cicada emergences is modest compared to the “bottom-up” effect on avian predators found here, where emergences were followed by increases in populations of eight bird species by an average of 10.1%, and decreases in the two cuckoo species by an average of 29.4%.

Also significant were the effects of periodical cicada emergences on spatial synchrony. Although synchrony was generally low, it was nonetheless significantly greater than zero in the majority (75%) of bird species

between sites <100 km apart when comparing sites sharing the same cicada brood. Such sites were 43% more synchronous, on average, than sites within the range of different broods, when comparing the 15 species that otherwise provided some evidence of being influenced by cicada emergences (Fig. 3). Spatial synchrony previously has been documented in a variety of avian populations (Small et al. 1993, Ranta et al. 1995a, b, Koenig 1998, 2001a, b, Paradis et al. 2000, Bellamy et al. 2003, Jones et al. 2003), where it has, in many cases, been attributed to synchronous fluctuations in the availability of food, including insects. Although other factors, particularly environmental synchrony (the Moran effect), may in many cases be an important synchronizing force (Hudson and Cattadori 1999, Koenig 2002, Liebhold et al. 2004), the results found here support the hypothesis that food can be responsible for a significant fraction of observed synchrony in at least some avian populations.

In summary, periodical cicada emergences are a pulsed resource with significant consequences both to their hosts down, and to their predators up, the food chain. Clearly, emergences should be taken into account when measuring and interpreting long-term trends of several of the most common bird species within the range of periodical cicadas, because observed trends are likely to be driven, at least in part, by emergences and their ecological aftermath.

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