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Avian Predation Pressure as a Potential Driver of Periodical Cicada Cycle Length

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ABSTRACT: The extraordinarily long life cycles, synchronous emergences at 13- or 17-year intervals, and complex geographic distribution of periodical cicadas (*Magicicada* spp.) in eastern North America are a long-standing evolutionary enigma. Although a variety of factors, including satiation of aboveground predators and avoidance of interbrood hybridization, have been hypothesized to shape the evolution of this system, no empirical support for these mechanisms has previously been reported, beyond the observation that bird predation can extirpate small, experimentally mistimed emergences. Here we show that periodical cicada emergences appear to set populations of potential avian predators on numerical trajectories that result in significantly lower potential predation pressure during the subsequent emergence. This result provides new support for the importance of predators in shaping periodical cicada life history, offers an ecological rationale for why emergences are synchronized at the observed multiyear intervals, and may explain some of the developmental plasticity observed in these unique insects.

Keywords: *Magicicada*, periodical cicadas, periodicity, population cycles, predator satiation.

Introduction

Periodical cicadas (*Magicicada* spp.) have the longest life span of any insect. Sufficiently spectacular as to be noted by early American colonists (Oldenburg 1666), 15 different “broods”—single-aged, mostly nonoverlapping cohorts that develop asynchronously with other populations—are currently known, each of which is composed of three or four coexisting species (Marlatt 1907; Simon 1988; Williams and Simon 1995). Satiation of aboveground predators has been considered the most important driver of the synchronous emergences observed in this system since studies in the nineteenth century demonstrated the potential for avian predators to extirpate populations induced

to emerge out of phase with the main brood present in a region (Marlatt 1907; May 1979).

The factors driving the extraordinary length of periodical cicada cycles has proved more elusive. Various hypotheses have been proposed, including interactions with long-lived parasitoids (Lloyd and Dybas 1966a, 1966b), belowground intra- or interspecific competition (Bulmer 1977; Grant 2005), and avoidance of hybridization (Cox and Carlton 1988), the latter of which has been found theoretically to be facilitated by cycles that are prime-numbered years in length (Goles et al. 2000; Webb 2001; Tanaka et al. 2009; Yoshimura et al. 2009). Despite this plethora of ideas, no empirical basis for 13- or 17-year cycles has previously been detected (Grant 2005; Lehmann-Ziebarth et al. 2005).

We investigated the interaction between periodical cicada emergences and the combined estimated potential predation pressure of 15 avian species that have been shown to be affected by periodical cicada emergences, either because population counts were significantly related to years since emergence in statistical models or because populations changed significantly the year before or the year after emergences (table 1; Koenig and Liebhold 2005). Rather than focusing on the bird populations per se, here we estimate the potential predation pressure of those bird populations on cicadas and, in particular, how it is related to the periodical cicada cycle.

Material and Methods

Data on relative avian population sizes over a 45-year period (1966–2010; this extends the data used by Koenig and Liebhold [2005] by 8 years) were obtained from the North American Breeding Bird Survey (<http://www.pwrc.usgs.gov/bbs/>). We included all 15 species (out of the 24 insectivorous species examined initially by Koenig and Liebhold [2005]) whose populations had previously been shown to be affected by periodical cicada emergences,

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Table 1: Bird species included in the analyses

Species	Scientific name	Mean body mass (g)
Yellow-billed cuckoo	<i>Coccyzus americanus</i>	64.0
Black-billed cuckoo	<i>Coccyzus erythrophthalmus</i>	51.1
Red-headed woodpecker	<i>Melanerpes erythrocephalus</i>	71.6
Red-bellied woodpecker	<i>Melanerpes carolinus</i>	61.7
Blue jay	<i>Cyanocitta cristata</i>	86.8
American crow	<i>Corvus brachyrhynchos</i>	448.0
Brown-headed cowbird	<i>Molothrus ater</i>	43.9
Common grackle	<i>Quiscalus quiscula</i>	113.5
Northern cardinal	<i>Cardinalis cardinalis</i>	44.7
House sparrow	<i>Passer domesticus</i>	27.7
Northern mockingbird	<i>Mimus polyglottos</i>	48.5
Gray catbird	<i>Dumetella carolinensis</i>	36.9
Brown thrasher	<i>Toxostoma rufum</i>	68.8
Tufted titmouse	<i>Baeolophus bicolor</i>	21.6
Wood thrush	<i>Hylocichla mustelina</i>	47.7

Note: Included are insectivorous species whose populations exhibit evidence of being affected by periodical cicada emergences based on previous analyses (Koenig and Liebhold 2005).

either because population counts were significantly related to years since emergence in general linear models or because populations had changed significantly in the year before or the year after emergences. For each species, we calculated mean numbers of birds (untransformed) counted at each Breeding Bird Survey route, after detrending within routes to eliminate long-term trends. We then summed detrended numbers of birds for each of the 15 species in each year, weighting species values by their estimated field metabolic rate (where field metabolic rate = $10.5 \times (\text{mean body mass})^{0.681}$; Nagy 2005), under the assumption that depredation of cicadas will be related to each species's total metabolic rate.

Sites were matched to the emergences of specific cicada broods by means of a geographic information system and brood boundaries based on county-level maps (Marlatt 1907; Simon 1988), after which data were standardized by year of the cicada life cycle. That is, within sites, we averaged values for each avian species during year 0 (emergence year), year 1, year 2, and so on, through either year 12 (within the range of 13-year broods) or year 16 (within the range of 17-year broods). Values were then standardized to a mean of 0 and a standard deviation of 1, so that each site was weighted equally, and averaged across all sites within the range of periodical cicada broods. Results were determined for birds living within the ranges of 13- and 17-year broods separately and were restricted to sites that fell within the nonoverlapping range of a single brood. Only sites with data for a complete cycle were included. Sample sizes (number of sites) were $N = 238$ (17-year broods) and $N = 138$ (13-year broods).

Differences in mean estimated potential predation pressure relative to the local cicada life cycle were tested with

repeated-measures general linear models. Statistical significance was based on linearly independent pairwise comparisons among the estimated marginal means and was performed in SPSS (SPSS 1999). Values were divided by their standard errors for plotting.

Results

For both 13- and 17-year broods, estimated potential predation pressure was significantly depressed during emergence years (fig. 1). In the years between emergences, potential predation pressure within the range of 13-year broods exhibited a numerical increase immediately after emergences, followed by a crash in year 4. Values again dipped in year 10 and during the thirteenth (emergence) year. Within the range of 17-year broods, potential predation pressure following emergences underwent a single long, slow increase peaking in year 12, after which it declined, reaching a nadir in the seventeenth (emergence) year.

Three explanations for the significantly low predator populations recorded during emergence years include (1) birds are less detectable because of the high densities and loud mating calls of cicadas; (2) cicada calls impair normal communication and drive birds away from emergence areas (Simmons et al. 1971); and (3) low numbers are the consequence of long-lasting demographic processes initiated by the previous emergence event (Koenig and Liebhold 2005). Prior analyses specifically testing these alternatives indicate that avian populations are also reduced during emergence years in populations located within the geographic range of broods, but in areas where cicadas are not chorusing, thus rejecting the first two hypotheses and

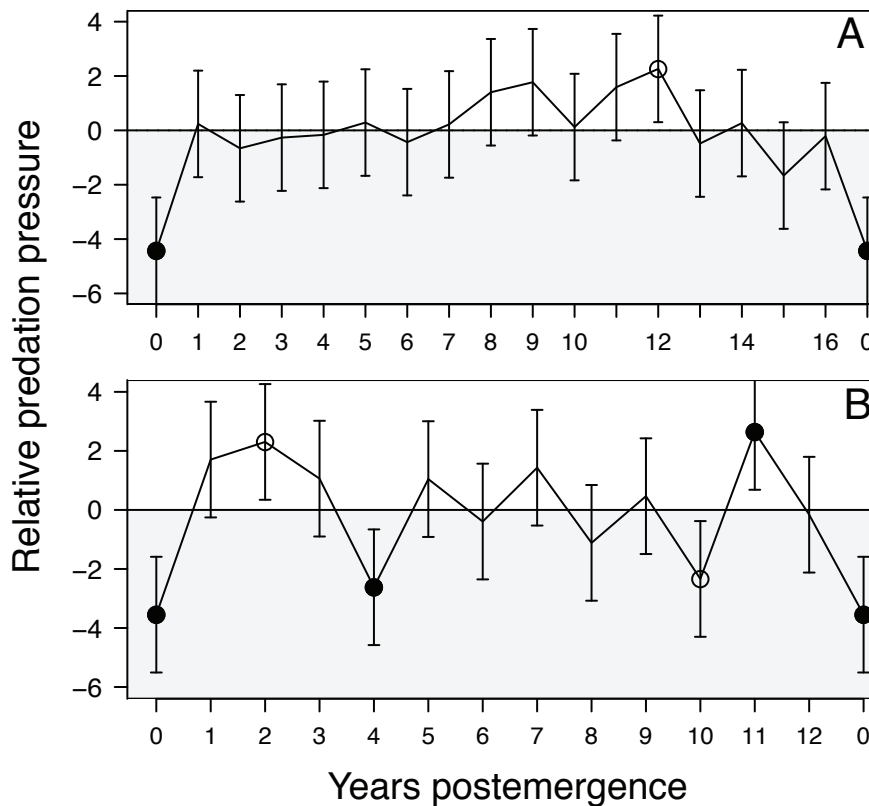


Figure 1: Mean (± 2 SE) estimated potential predation pressure on periodical cicadas during each year of the 13- or 17-year life cycle, based on 15 bird species whose populations were related to the periodical cicada cycle (table 1; Koenig and Liebhold 2005): A, 17-year broods; B, 13-year broods. In both panels, the Y-axis plots deviations (in SE) from the overall mean, and values are averaged across all years of data. Year 0 (emergence year) is plotted at both the beginning and the end of the cycle. Circles represent statistically significant values (open: $P < .05$; filled: $P < .01$).

providing support for the hypothesis that low predation pressure is due to factors initiated during the prior, rather than current, emergence (Koenig et al. 2011).

Discussion

Predator satiation by periodical cicadas has long been thought to play a key role in causing periodicity and maintaining population synchrony of periodical cicadas (Lloyd and Dybas 1966*b*; May 1979; Itô 1998; Hayes 2004). Our results confirm that avian populations do not (or are unable to) track emergences by either maintaining high populations in between emergences—a key assumption of at least one prior model of periodical cicada periodicity (Hoppensteadt and Keller 1976)—or increasing their populations in anticipation of the abundant prey base available during (and only during) emergence events. More surprising is the finding that potential predation pressure on cicadas is significantly reduced during emergence years. That these years of low predation pressure coincide with

cicada emergences suggests that predator satiation, besides being an important synchronizing factor, may play a role in the evolution of cycle length by instigating a multiyear numerical response in bird populations that ultimately benefits adult cicada survival.

Given their lack of defenses against avian predators (Williams and Simon 1995), it is clearly advantageous for cicadas to emerge when potential predation is relatively low. Furthermore, individuals in 13-year broods that fail to emerge on schedule would benefit by delaying emergence by 4 years, when potential predation pressure will have declined from the increase it experienced after emergence (fig. 1*B*). The patterns of potential predation pressure indicated by our results thus offer an ecological rationale for at least some of the developmental plasticity observed in periodical cicadas, in particular the recently documented 4-year-delayed emergences that have been hypothesized to be the evolutionary mechanism by which new broods form (Marshall et al. 2011).

Periodical cicada emergences have previously been

shown to create a significant resource pulse influencing nutrient flux (Whiles et al. 2001; Yang 2004), plant and tree growth (Karban 1980; Koenig and Liebhold 2003; Yang 2004), small mammals (Krohne et al. 1991; Marcello et al. 2008; Vendegrift and Hudson 2009), and both long-term population size and spatial synchrony of bird populations (Koenig and Liebhold 2005). Results reported here extend those findings, suggesting that the extraordinary life cycle of periodical cicadas may “engineer” bird populations in a way that keeps them from tracking emergences, not by their extreme length or as a consequence of being prime numbered, but rather by setting bird populations on a trajectory such that the subsequent emergence coincides with reduced predation pressure.

The mechanism by which this is accomplished is unknown, and indeed it seems remarkable that bird densities could be influenced more than a decade later by a single, relatively short-lived event. One possible explanation comes from work demonstrating that emergences cause substantial pulsed enrichment of forest soils, with both corresponding direct effects belowground and indirect effects aboveground (Yang 2004). That such resource pulses can have long-lasting effects cascading through communities is now well established (Jones et al. 1998; Ostfeld and Keesing 2000), although no previous system has been suggested to have effects lasting as long as those found here. Another possibility is that numerical interactions with alternative avian prey species, such as foliage-feeding caterpillars, several of which exhibit regular multiyear cycles (Myers 1988), might mediate the long-term changes in bird populations that are driving the patterns found here.

Clearly, many mysteries remain regarding periodical cicada biology (Hayes 2004). Although considerable progress has been made in recent years investigating the patterns of speciation (Cooley et al. 2001) and the evolutionary history (Yoshimura 1997; Grant 2005) of this group, much remains to be discovered concerning how modern-day ecological factors affect periodical cicada populations. Results shown here suggest that avian predators—long thought to be key to synchronizing emergence events—may play a key role in several of the difficult-to-explain life-history features of these extraordinary insects. The role of other ecological factors, including predation by small mammals, parasites, and reductions in forest productivity in emergence years, remain to be examined empirically.

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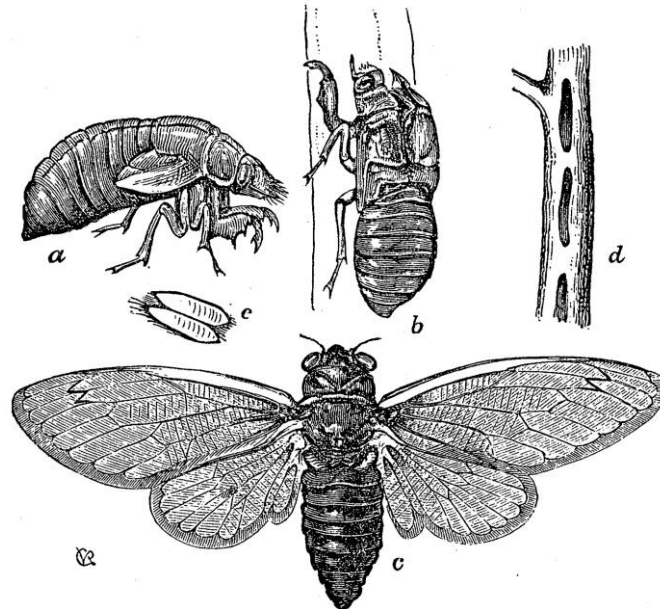
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The Seventeen-year Cicada and Pupa.

a, Pupa; b, the same after the adult has escaped through the rent in the back; c, the winged fly; d, the holes in which the eggs (e) are inserted. From "Injurious and Beneficial Insects" by A. S. Packard Jr. (*American Naturalist*, 1873, 7:524–548).