Avian predators are less abundant during periodical cicada emergences, but why?

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Abstract. Despite a substantial resource pulse, numerous avian insectivores known to depredate periodical cicadas (*Magicicada* spp.) are detected less commonly during emergence years than in either the previous or following years. We used data on periodical cicada calls collected by volunteers conducting North American Breeding Bird Surveys within the range of cicada Brood X to test three hypotheses for this observation: lower detection rates could be caused by bird calls being obscured by cicada calls ("detectability" hypothesis), by birds avoiding areas with cicadas ("repel" hypothesis), or because bird abundances are generally lower during emergence years for some reason unrelated to the current emergence event ("true decline" hypothesis). We tested these hypotheses by comparing bird detections at stations coincident with calling cicadas vs. those without calling cicadas in the year prior to and during cicada emergences. At four distinct levels (stop, route, range, and season), parallel declines of birds in groups exposed and not exposed to cicada calls supported the true decline hypothesis. We discuss several potential mechanisms for this pattern, including the possibility that it is a consequence of the ecological and evolutionary interactions between predators of this extraordinary group of insects.

Key words: Breeding Bird Survey; Brood X; Magicicada *spp.; periodical cicadas; population cycles; predator satiation.*

INTRODUCTION

Resource pulses have been increasingly recognized as a dynamic with important implications for both the ecology and evolution of consumers (Ostfeld and Keesing 2000, Yang et al. 2008). One of the most spectacular known pulses is that caused by the emergence in eastern North American hardwood forests of periodical cicadas (*Magicicada* spp.), whose dynamics have been the subject of scientific inquiry for nearly 350 years (Oldenburg 1666). Divided into developmentally synchronized, temporally isolated cohorts known as broods (Fig. 1), each of which is composed of three to four sympatric species, periodical cicada nymphs develop 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 approximately one month. During these brief periods above ground, periodical cicadas can be among the most abundant of all forest insects, achieving densities of 2.6×10^6/ha (Lloyd and

Dybas 1966*a*), enough to have a significant effect on host tree growth (Karban 1980, Koenig and Liebhold 2003) and nutrient cycling both in the forest floor (Whiles et al. 2001, Yang 2004) and local streams (Menninger et al. 2008). Furthermore, adults are large, nontoxic, easily captured, and readily consumed by both avian and mammalian predators (Stephen et al. 1990, Krohne et al. 1991, Williams and Simon 1995), making it unsurprising that emergences have significant effects on populations of numerous avian predators (Koenig and Liebhold 2005).

Surprisingly, the most common impact among insectivorous birds seems to be a reduction in numbers during emergence years, despite the pulse of a readily available food source. Of the 24 potential or known avian predators investigated by Koenig and Liebhold (2005) using data from the North American Breeding Bird Survey (BBS), only two, the Yellow-billed (*Coccyzus americanus*) and Black-billed (*C. erythropthalmus*) Cuckoo, were apparently attracted to periodical cicada emergence events and thus more abundant during emergences than the preceding year. Of the remaining 22 species, 16 were less abundant during emergence
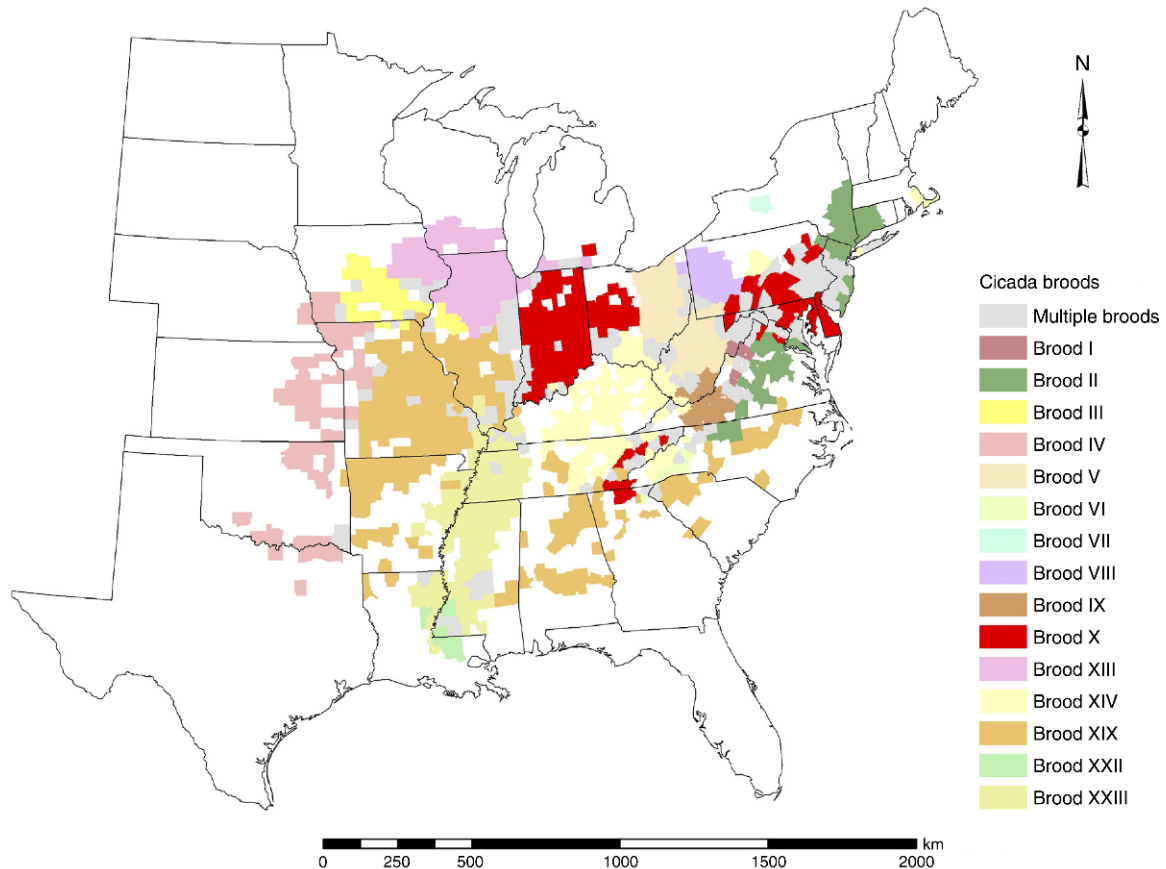
Fig. 1.   The range of periodical cicada (*Magicicada* spp.) broods in the USA (based on Marlatt [1907] and Simon [1988]); the disjunct range of Brood X is in red.

years than the year before, with five being significantly so (Red-headed Woodpecker, *Melanerpes erythrocephalus*; Northern Cardinal, *Cardinalis cardinalis*; Common Grackle, *Quiscalus quiscula*; Brown-headed Cowbird, *Molothrus ater*; and House Sparrow, *Passer domesticus*). Here, we investigated these five species along with seven other species that experienced declines of at least 3% from the year prior to emergences (year −1) to emergence years (year 0): American Kestrel (*Falco sparverius*), Red-bellied Woodpecker (*Melanerpes carolinus*), Blue Jay (*Cyanocitta cristata*), American Crow (*Corvus brachyrhynchos*), Tufted Titmouse (*Poecile carolinensis*), White-breasted Nuthatch (*Sitta carolinensis*), and Brown Thrasher (*Toxostoma rufum*).

   We considered three hypotheses for the lower number of detections of these birds during emergence years. The first hypothesis (the "detectability" hypothesis) is that lower detection is a direct result of the loud mating calls of cicadas, which can reach 800 dynes/cm^2 (Simmons et al. 1971). Second, the loud mating calls could repel birds, driving them into areas with fewer cicadas because of disruption to the bird's normal communication (the

"repel" hypothesis, proposed by Simmons et al. 1971). Third, bird numbers may be regionally lower in emergence years, even to some extent outside the range of cicadas, for reasons unrelated to the current cicada emergence event (the "true decline" hypothesis). All three hypotheses are consistent with the pattern shown by Koenig and Liebhold (2005) of fewer detections during the breeding season within the range of emergent broods.

   We tested these hypotheses using data on bird populations separated into sites where cicadas were locally abundant (C) vs. sites where they were not (NC). For two of the tests, comparisons were based on the fact that, within a given brood, periodical cicada densities are characteristically patchy, with large numbers of adults aggregating in some locations but virtually absent in others (Rodenhouse et al. 1997).

   Each of the three hypotheses predicts a different pattern of bird detections between C and NC groups. If measured declines are an artifact of detectability, then no decline should be evident for NC groups (Fig. 2a). If measured declines are due to birds being repelled from
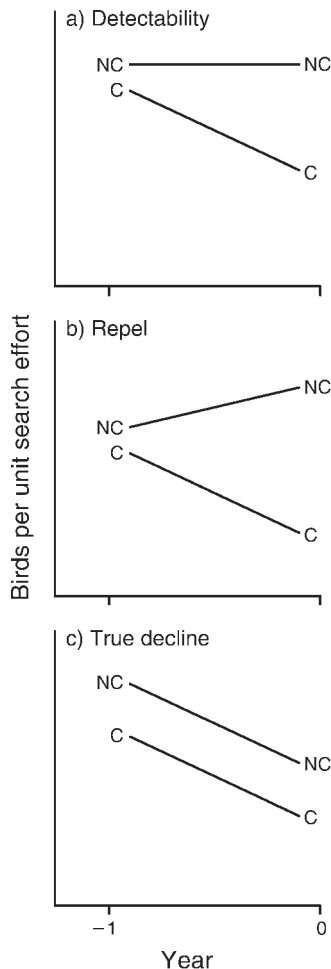
FIG. 2. The three hypotheses and their predictions vis-à-vis sites with (C) and without (NC) audible cicadas in the year prior to (year −1) and during (year 0) cicada emergences. In all cases, the key prediction is with respect to how densities of birds in NC sites change from year −1 to year 0; there is no prediction with respect to relative densities in NC vs. C sites since this may reflect habitat differences or other unrelated factors. (a) Dectectability hypothesis: Birds are present but less detectable due to cicada calling; no difference between C and NC sites is predicted. (b) Repel hypothesis: Birds are locally repelled by cicada calls; birds in NC sites may be augmented by birds repelled from nearby C sites. (c) True decline hypothesis: Birds are at lower densities during emergence years regionally for reasons unrelated to the emergence, and thus no difference in declines of birds between C and NC sites is predicted.

areas with cicadas, then nearby NC groups are predicted to show an increase (Fig. 2b), the magnitude of which will depend on the distance repelled birds move from affected areas. Finally, if the overall abundance of birds is regionally lower during cicada emergence years, then both C and NC groups should show parallel declines (Fig. 2c).

As in Koenig and Liebhold (2005), we used BBS data for these comparisons, but took advantage of a program implemented in 1987 and 2004 to have BBS volunteers record whether calling cicadas were present at each survey stop along routes within the range of Brood X (Fig. 1). This allowed us to compare C and NC groups that were spatially separated at three levels (stop, route, and range). As a fourth comparison, we used data for the same 12 species of birds during the winter prior to emergences from the National Audubon Society's Christmas Bird Counts (CBC). This allowed us to test the hypotheses with data seasonally removed from any direct influence of emergences.

METHODS

BBS surveys are conducted once a year during the breeding season (May and June) and consist of standardized three-minute observations at a series of 50 stops located 0.8 km apart along a road transect done in the same order each year (Bystrack 1981). At each stop, observers record all birds seen or heard during 3-min observations. Data, which are available from USGS (*available online*),[5] were used only when the same observer conducted surveys in both year −1 and the associated year 0, a procedure that eliminated a small proportion (<10%) of the data. Within the range of Brood X during both the 1987 and 2004 emergences, the number of stops at which cicadas were heard calling was reported and divided into three abundance categories: none (no chorusing heard), low (chorusing audible at 1–10 stops), and high (chorusing at >10 stops). In addition, during the 2004 survey, observers recorded the individual survey stops where cicadas were heard calling, allowing us to divide stops into those where cicadas were and were not heard calling.

CBC data are gathered from circles 24 km in diameter and take place each winter on a single day within a three-week period between 14 December and 5 January. Because the number of people involved in these surveys is highly variable, the number of birds counted is standardized for effort by dividing by the number of "party hours" (Bock and Root 1981). In order to match the BBS data, data from areas within periodical cicada Brood X were analyzed for the two winters prior to the 1987 and 2004 emergences (the winters of 1986–1987 and 2003–2004) along with the winters immediately preceding those years (1985–1986 and 2002–2003).

At each level (stop, route, range, and season), we compared the observed patterns of bird detections to those predicted by the three hypotheses (Fig. 2). For the BBS analyses we only included routes or stops that had birds of the target species present in year −1, the rationale being that the hypothesis being tested was not whether birds were more or less abundant during emergences, but rather why birds declined in abundance during emergence events. Because a decline was not

possible unless birds had been detected the year before, we restricted analyses to sites where birds had been detected in year −1.

For each of the 12 species of birds, the number of individuals counted during the surveys in each of the years considered was log-transformed ($\log(x + 1)$) to help meet the assumptions of normality. We first tested for a significant decline both among sites where cicadas were and were not present using Wilcoxon matched-pairs tests so as to confirm that a decline was observed. Next we performed linear mixed-effects models in which the difference in birds counted in year −1 vs. year 0 was the dependent variable, bird species was included as a random effect, and whether the stops or surveys were located where cicadas were present (C) or not (NC) was the fixed effect. We then calculated the proportion of routes or stops showing a decline for each species for both C and NC surveys, testing for differences in the proportion of declining routes using Fisher exact tests.

At the smallest spatial scale (the stop-level analysis), we compared the change in abundance between year −1 and year 0 at individual BBS stops with (C) vs. without (NC) calling cicadas during the 2004 emergence. Depending on the species, between 4 and 49 surveys met the necessary criteria for comparing stops that did and did not report cicada calls. For route-level comparisons, we separated routes within the range of Brood X into those where cicadas were recorded during at least one stop (C) and those where they were not recorded at any stops (NC) in both the 1987 and 2004 emergence years. The majority of surveys (90% of 61) were only done during one of the two emergence events. When data were available for both events ($N = 6$), values were averaged as long as cicadas were either heard or not heard during both ($N = 5$); on the one route where this was not the case, the two surveys were included separately. This provided a total of 62 comparisons between routes of which 29 reported no audible cicadas, 14 reported "low" cicadas, 16 reported "high" cicadas, and three reported "low" cicadas during one emergence and "high" cicadas during the second emergence.

At the range level, we used the known range of Brood X (Fig. 1) to separate routes into those that were within the range of Brood X (C, $N = 92$) and those outside of, but within 50 km, the range of Brood X (NC, $N = 98$). Analyses were conducted both including routes outside the range of Brood X, but overlapping another cicada brood and excluding routes overlapping a second cicada brood.

At the season level, we compared relative abundances between year −1 and year 0 from BBS surveys conducted during the breeding season when cicadas were present (C) with similarly located CBC surveys conducted the previous winter when cicadas were absent (NC). We compared the previous rather than the following winter to avoid capturing potential post-cicada-emergence

increases (Koenig and Liebhold 2005). As before, we performed a linear mixed-effects model in which the difference in birds counted in year −1 vs. year 0 was the dependent variable, bird species was a random effect, and whether the data were from the BBS (C) or CBC (NC) surveys was the fixed effect. We then calculated the proportion of surveys exhibiting a decline for each species, testing for differences in the proportion of declining routes using Fisher exact tests.

All analyses and statistics were performed in R 2.10.0 (R Development Core Team 2009). P values ≤ 0.05 are considered statistically significant.

Results

Stop-level test

No routes for American Kestrels met our criteria for inclusion in this analysis. For the remaining species, there was a range of four (Red-headed Woodpeckers) to 52 (Northern Cardinals) routes. Averaged across the 12 species, the proportion of stops showing declines from year −1 to year 0 was 62.5% and 56.6% for C and NC stops, respectively. Both declines were significantly greater than 0 by Wilcoxon matched-pairs tests ($P < 0.001$), and there was no significant difference between the declines in the linear mixed-effects model (effect size $= -1.55 \pm 1.16$ [mean $\pm$ SE], t value $= -1.34$, df $= 616$, $P = 0.18$; Fig. 3a). Note that there were considerably more stops where cicadas were not recorded (NC), resulting in more bird detections overall. Comparing species individually, there was no significant difference for any of the species in the probability of declines between the two categories of stops (Appendix: Table A1).

Route-level test

The mean probability of a decline within the range of Brood X for routes where cicadas were (C) and were not (NC) audible was 53.7% and 50.4%, respectively. Although the declines were significant among the C routes (Wilcoxon matched-pairs test, $P < 0.001$) and not among the NC routes ($P = 0.10$), there was no significant difference between them in a mixed-effects model in which the two categories of audible cicadas (low and high) were combined (effect size $= -0.072 \pm 0.049$, t value $= -1.46$, df $= 638$, $P = 0.14$; Fig. 3b). Results were similar if the two categories were kept separate (results not presented). Considering the 12 species individually, only the American Kestrel exhibited a significantly greater decline among routes where cicadas were audible (Appendix: Table A2).

Range-level test

The overall probability of a decline for routes within the range of Brood X (C) compared to outside, but within 50 km of Brood X (NC) was 56.1% and 50.4%, respectively. These declines were significant for both C and NC sites, whether we excluded broods outside the
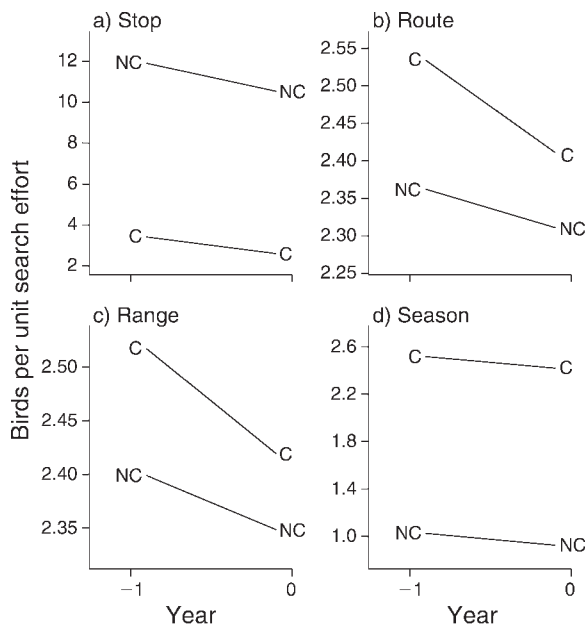
FIG. 3. Overall results of tests comparing the mean number of birds counted in year −1 and year 0 in (a) stops where cicadas were present (C) vs. stops within the same BBS (Breeding Bird Survey) route where they were not (NC); (b) routes where cicadas were audible (C) vs. routes where they were not (NC) (Brood X routes only); (c) routes within the range of Brood X (C) vs. routes outside of but within 50 km of Brood X (NC); and (d) Breeding Bird Survey (BBS) routes (C) vs. CBC routes (NC) within the range of Brood X. Only BBS surveys where at least one bird of the target species was counted in year −1 are included. Although the absolute values differ, the mean declines from year −1 to year 0 are not significantly different between C and NC sites in any of the four tests (see *Results*).

range of Brood X but overlapping a second brood (C sites, $P < 0.001$; NC sites, $P = 0.02$) or not (both $P < 0.001$). In the mixed-effects model the differences between C and NC sites was not significant (overlapping broods excluded, effect size = -0.044 ± 0.026, t value = 1.69, df = 1856, $P = 0.09$; overlapping broods included, effect size = -0.023 ± 0.023, df = 2406, t value = -0.99, $P = 0.32$; Fig. 3c). Analyses comparing each of the 12 species separately indicated no significant differences in the probability of declines for any of the species except American Crows, which suffered significantly greater declines within compared to outside the range of Brood X (Appendix: Table A3).

Season-level test

Within the range of Brood X, the overall probability of a decline for BBS surveys conducted when cicadas were emergent (C) was 56.1% compared to 59.5% for winter CBC surveys when no cicadas were present (NC). Both these declines were significant with a Wilcoxon matched-pairs test (both $P < 0.001$), but were not significantly different from each other (effect size = 0.002

$\pm$ 0.027, t value = 0.06, df = 1665, $P = 0.96$; Fig. 3d). Analyses comparing each of the 12 species separately revealed five species where there was a significant difference between the probability of a decline in the BBS vs. the CBC data (Appendix: Table A4). However, three of these five differences were in the direction of there being a higher, rather than lower, probability of a decline in the CBC (NC) data.

DISCUSSION

A number of insectivorous bird species appear to exhibit unexpectedly lower abundances during periodical cicada emergences (Koenig and Liebhold 2005). Four tests comparing detections of birds exposed (C) and not exposed (NC) to abundant local cicada populations found generally significant but statistically indistinguishable declines in both groups. These parallel declines support the hypothesis that a true decline in birds is coincident with, but not directly related to, the local periodical cicada emergence event (Fig. 2). In particular, the presence of declines in the CBC data confirms that reductions occur by the winter prior to emergences and are not due to some statistical artifact in the BBS data.

While statistically indistinguishable differences between C and NC groups are evidence supporting the "true decline" hypothesis (Fig. 1c), the possibility that lower detectability or some degree of repelling may be playing a role is suggested by the slightly (albeit not significantly) greater declines observed among C compared to NC groups in three of the analyses (stop, route, and range). Among analyses of individual species, American Kestrels exhibited a significantly greater probability of decline among C routes in the route-level and season-level analyses, while American Crows exhibited significantly greater probability of decline among C routes in the range-level and season-level analyses (Appendix). Countering these results were three species (Brown-headed Cowbird, Northern Cardinal, and Brown Thrasher) that were significantly more likely to exhibit declines in the CBC data (NC) than in the BBS data (C).

The first of these results, that of American Kestrels in the route-level analysis, found only 33.3% of routes declining among NC routes vs. 70.8% declining among C routes (Appendix: Table A2). As such, this was the only statistically significant result matching the prediction of the hypothesis that birds were possibly repelled by cicadas and thus more abundant in routes where cicadas were not audible. At the range-level analysis, American Crows also stood out as exhibiting particularly large and significantly greater declines among C routes (Appendix: Table A3). The cause of this is unclear, but as noted by Koenig and Liebhold (2005), the American Crow, with its loud calls and large body size, is an unlikely candidate for a species that would be

potentially overlooked due to cicada calling. Alternatively, we suggest that this result may have been at least partly due to the effects of West Nile virus, a pathogen particularly devastating to American Crows that spread through the range of Brood X between 1999 and 2001 (Hochachka et al. 2004, LaDeau et al. 2007, Koenig et al. 2010), and thus may have differentially affected declines, which were particularly high between 2003 and 2004 (when 75.9% of 54 routes declined) compared to 1986 and 1987 (when 58.9% of 73 routes declined) (Fisher exact test, $P = 0.058$).

Why do so many bird species decline in numbers during years of periodical cicada emergences if the declines are unrelated to the calling or local abundance of the cicadas themselves? We can think of two general possibilities. First is that emergences are concordant with some ecological interaction causing the declines, such as impacts on tree health, abundance of other insect prey, or some other effect of the resource pulse generated by emergences such as the attendant increase in cuckoo populations. The latter is particularly intriguing to the extent that North American cuckoos, although typically not brood parasites, have been recorded engaging in interspecific brood parasitism during years of particularly high insect food abundance (Nolan and Thompson 1975, Hughes 1999). The problem with all these hypotheses is determining how any of them would similarly influence populations of birds living outside the direct influence of cicada emergences, either because of geography (in the range-level test), spatial variation in cicada populations (in the stop-level and route-level tests), or season (in the season-level test). Nonetheless, these are probably not the only important ecological factors that are affected by cicada emergences, and it is possible that one or more of them may have effects on avian populations extending both seasonally and geographically beyond what one might intuitively expect.

A second possibility for the avian declines is that they are the consequence of population processes initiated by previous emergence events that have long-lasting demographic consequences on bird populations extending beyond the areas where cicadas are abundant (Koenig and Liebhold 2005). This hypothesis is consistent with recent studies demonstrating that periodical cicada emergences constitute a resource pulse large enough to significantly influence nutrient flux (Whiles et al. 2001, Yang 2004) and tree growth (Karban 1980, Koenig and Liebhold 2003), despite the fact that emergences are characteristically spatially heterogeneous, being locally abundant in some places and virtually absent a short distance away (Williams and Simon 1995). Indeed, Koenig and Liebhold (2005) previously documented population influences of cicada emergences lasting as long as 4–7 years post-emergences in some species and significantly increased spatial synchrony among popu-

lations of birds up to 250 km apart within the range of the same cicada brood. Thus, periodical cicada emergences have effects on bird populations that extend relatively far geographically and can be detected years after emergence events.

We know of no mechanism that would result in population declines occurring exactly 13 or 17 years after emergence events, as predicted by this hypothesis. Thus, additional analyses are clearly desirable. For example, if emergences instigate long-term population cycles in bird populations, we would minimally expect to see a marked increase in abundance of cicada predators following emergence years. This was indeed the case: Of the 12 species included in the analyses here, 11 increased in abundance from emergence years (year 0) to year 1 (binomial test, $P = 0.006$), increasing an average ($\pm$SE) of 8.1% $\pm$ 1.7% (Koenig and Liebhold 2005).

We have shown that a series of insectivorous birds that would be expected to capitalize and be attracted to a pulse of large, nontoxic insects, instead are present in lower density during periodical cicada emergences for reasons apparently unrelated to the emergence events themselves. These trends presumably result in lower overall avian predation pressure on cicadas during emergence events than would otherwise be expected. Although additional analyses are needed to confirm the mechanism causing these patterns, particularly intriguing is the potential for this discovery to provide a partial ecological resolution of the "cicada problem" that has plagued evolutionary biologists for nearly 350 years (Oldenburg 1666, Lloyd and Dybas 1966a, b, Williams and Simon 1995).

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APPENDIX

Results of the analyses for individual species (*Ecological Archives* E092-065-A1).