vol. 201, no. 5 the american naturalist may 2023

Natural History Note

Periodical Cicada Emergences Affect Masting Behavior of Oaks

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Submitted June 4, 2022; Accepted November 3, 2022; Electronically published March 24, 2023

abstract: Oaks (*Quercus* spp.) are masting species exhibiting highly variable and synchronized acorn production. We investigated the hypothesis that periodical cicadas (*Magicada* spp.), well known to have strong effects on the ecosystems in which they occur, affect acorn production of oaks through their xylem feeding habits as nymphs, the oviposition damage they inflict as adults during emergences, or the nutrient pulse resulting from the decomposition of their bodies following breeding. We found negative effects on acorn production during emergence years and the year following emergences and enhanced acorn production 2 years after emergence. We also found evidence indicating a significant effect of cicada emergences on spatial synchrony of acorn production by trees growing within the range of the same cicada brood compared with different broods. These results demonstrate that periodical cicadas act as a trophic environmental "veto" depressing acorn production during and immediately following emergences, after which the nutrient pulse associated with the cicada's demise enhances oak reproduction.

Keywords: acorn production, masting behavior, oak reproduction, periodical cicadas, resource pulses, superimposed epoch analysis.

Introduction

The drivers of variable and synchronized seed production by forest trees, known as mast-fruiting or masting behavior, have been of interest for more than 50 years (Kelly and Sork 2002; Koenig 2021). Evolutionarily, the ultimate factors involved in masting are generally thought to be a combination of predator satiation and pollination efficiency (Janzen 1971; Isagi et al. 1997), with a smaller role for the possibility that seed production tracks disturbances that enhance subsequent seed survival (Vacchiano et al. 2021). Ecologically, the proximate mechanisms driving masting primarily include environmental constraints on resources and pollination and weather cues (Pearse et al. 2016; Bogdziewicz et al. 2020). Notable among potential constraints affecting resources are environmental "vetoes" that reduce reproduction in some years, thereby synchronizing reproduction and potentially driving masting behavior (Bogdziewicz et al. 2018*b*, 2019). Environmental vetoes are generally thought to be weather related, but other external events can potentially restrict reproduction and affect masting as well.

One such external factor that is sufficiently large-scale and geographically broad, both as a potential environmental veto and in its effects on nutrients, is the emergences of periodical cicadas (*Magicicada* spp.) in eastern and midwestern North America. These insects exhibit a unique life cycle lasting 13 or 17 years, nearly all of which is spent underground as nymphs feeding on roots, often of oaks (*Quercus* spp.). Following the final nymphal molt, adults emerge from the soil to mate, feed, and oviposit on twigs and then die after a period of 3–4 weeks (Lloyd and Dybas 1966*a*, 1966*b*; Simon et al. 2022). Several weeks later, first-instar nymphs hatch, drop to the forest floor, and begin their long period of root feeding underground until the next emergence 13 or 17 years later.

Periodical cicadas are among the most abundant forest insects, achieving densities up to 2.6×10^6 cicadas ha^{-1} (Lloyd and Dybas 1966*a*, 1966*b*; Karban 1980), which, at an average mass of ~1.16 g (Karban 2014), is potentially more than 3,000 kg ha^{-1}. Such tremendous productivity, in conjunction with their synchrony, has been associated with a significant decrease in radial growth of their host trees during or shortly after emergence (Karban 1980, 1982; Koenig and Liebhold 2003; Speer et al. 2010). This effect could be due to either xylem feeding by last-instar nymphs before emergence or damage inflicted on trees by adults ovipositing during emergence. Emergences have also been found to result in significant effects on avian predator populations (Koenig and Liebhold 2005) and, because of the pulse of nitrogen resulting from the decaying carcasses of adult cicadas, have significant bottom-up effects on the

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American Naturalist, volume 201, number 5, May 2023. © 2023 The University of Chicago. All rights reserved. Published by The University of Chicago Press for The American Society of Naturalists. https://doi.org/10.1086/723735

ecosystems in which they occur (Wheeler et al. 1992; Yang 2004).

Although periodical cicadas have been shown, both empirically and experimentally, to have strong effects on the vegetative growth of their host trees, previous experimental work failed to detect an effect of introducing cicada eggs on acorn production by scrub oak (*Quercus ilicifolia*; Karban 1985). Here, employing a different approach, we test the hypothesis that periodical cicada emergences have significant effects on acorn production of oaks, which are typical masting species (Koenig et al. 1994; Koenig and Knops 2002; Bogdziewicz et al. 2018*a*) that often synchronize reproduction over large geographic areas (Koenig and Knops 2013; Koenig et al. 2017). We hypothesized that root xylem feeding by nymphs, twig xylem feeding by adults, or the oviposition damage inflicted during their short emergence period might act as an environmental veto negatively affecting the acorn crop just before, during, or immediately after emergences (Smith and Linderman 1974; Cook et al. 2001). We further hypothesized that the nutrient pulse resulting from decomposing cicada carcasses might be sufficiently large to enhance resource availability and result in a positive lagged effect on acorn production within several years following an emergence (Yang 2004).

Spatial synchrony of some oak species can be on the scale of hundreds of kilometers, driven largely by the environmental effects of weather influencing the resources that the trees can invest in acorn production (Koenig and Knops 2013; Koenig et al. 2017). With this in mind, we also investigated the hypothesis that cicada emergences affect spatial synchrony of acorn production by altering the resources available to the trees on which they feed as nymphs and oviposit as adults. Specifically, we tested whether these effects enhanced synchrony between pairs of masting time series co-occurring within the range of the same cicada brood (and thus where emergences occur in the same year) compared with time series within the range of different cicada broods (and thus where emergences occur in different years).

Material and Methods

Although periodical cicadas feed on a variety of broadleaved deciduous trees (Dybas and Lloyd 1974; White 1980), we focused on oaks (*Quercus* spp.), for which the most data were available. Seed production (masting data) was obtained from three sources: the recently compiled MASTREE+ time series of plant reproduction (Hacket-Pain et al. 2022), the time series of plant reproduction compiled by Pearse et al. (2017, 2020), and a set of additional time series from Virginia and Maryland courtesy of T. Fearer (personal communication). Duplicates were removed, but otherwise, series were used as provided; that is, we used both data that were attributable to a specific species and data reported generally for *Quercus* spp., thus potentially combining multiple oak species.

We compiled a total of 84 data sets within the range of a cicada brood, each encompassing at least 6 years and with data taken during at least one emergence year. Data included 10 species of oaks (*Q. alba*, *Q. borealis*, *Q. coccinea*, *Q. marylandica*, *Q. montana*, *Q. palustris*, *Q. prinus*, *Q. rubra*, *Q. stellata*, and *Q. velutina*), 20 sites potentially involving multiple species in the white oak subgenus *Leucobalanus*, 20 sites potentially including multiple species in the red oak subgenus *Erythrobalanus*, and seven sites including oak species not identified to species or subgenus. Of the data with subgenus noted, 36 data sets were “1-year” species that mature acorns in a single season (typically of the subgenus *Leucobalanus*) and 41 were “2-year” species that mature acorns in two seasons (typically of the subgenus *Erythrobalanus*; Mohler 1990). The number of years of data ranged from 6 to 28, with a mean (±SD) of 15.1 ± 7.5 years. Overall, the range of years encompassed by the data was from 1936 to 2009. All data were quantitative; that is, they provided interval or ratio-level data on the number of acorns counted or found in traps.

We standardized each time series between 0 (for the least productive crop year in the series) and 100 (for the most productive), following Koenig and Knops (2000). We refer to these as the “scaled” acorn crop. Mean scaled values can be considered the mean percentage of the maximum observed acorn crop. This procedure allowed time series to be combined for analysis, regardless of the units used in the survey.

Each time series was matched to the local cicada brood using a geographical information system (ArcGIS, Redlands, CA) to overlay crop series coordinates onto county-level maps of brood distributions (Marlatt 1907; Simon and Lloyd 1982; fig. 1). Counties with apparent sympatry of more than one brood or with low-density emergences were eliminated from the analyses. Acorn crop time series were spread across six different 17-year cicada broods and one 13-year brood.

We tested for the effects of periodical cicada emergences on acorn production using superimposed epoch analysis, a technique used previously to examine the effects of periodical cicada emergences on radial tree growth and bird populations (Koenig and Liebhold 2003, 2005) and commonly used in the geophysical sciences (Linblad 1978; Kelly and Sear 1984). On the basis of our hypotheses, we limited discussion to the period from 2 years before emergence (year −2) to 4 years after emergence (years 1–4). Results for all years are provided in figure A1.

We first matched years to the life cycle of the co-occurring cicada brood. Then we calculated the mean (±95% confidence interval) scaled acorn crop from sites within the range of each cicada brood for the emergence

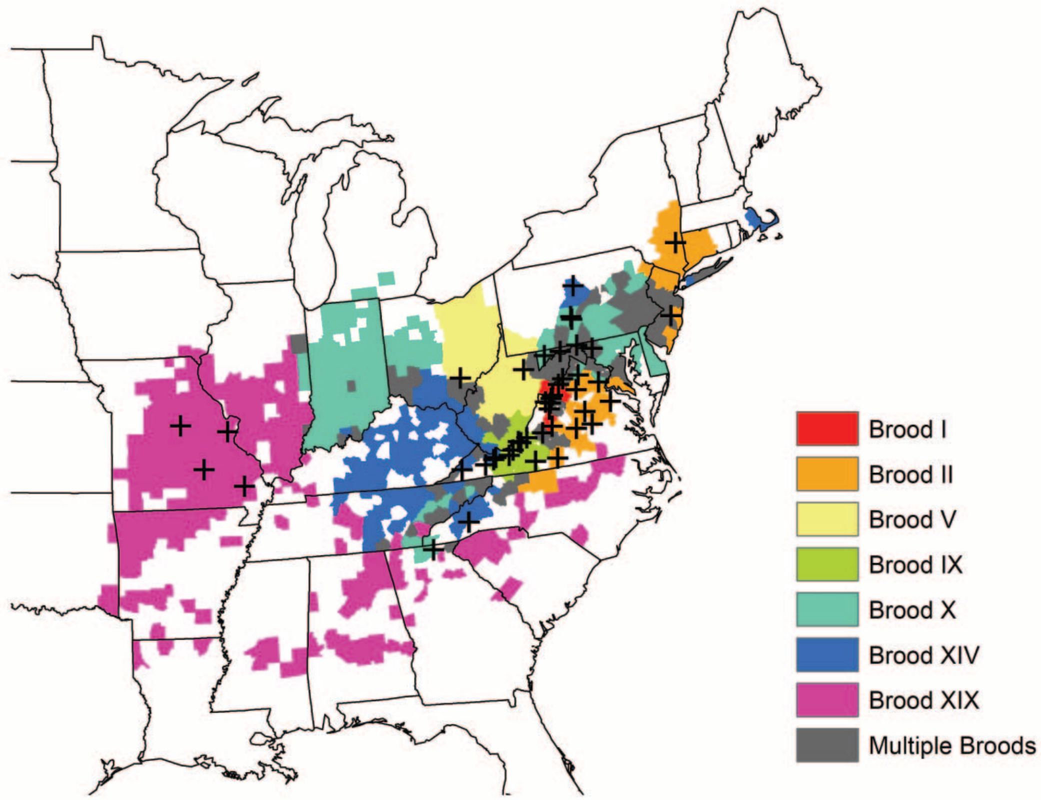

Figure 1: Geographic distribution of periodical cicada broods used or referred to here. Sites for which acorn production was available are marked with plus signs. Broods I–XIV are 17-year broods, and brood XIX is a 13-year brood. Adapted from Marlatt (1907) and Simon and Lloyd (1982).

year of the brood. For each emergence (i.e., epoch) year *i*, we also compiled the mean acorn crops for the other six (i.e., non-*i*) emergence years and tested for differences from the mean acorn crop of all 7 years included in the analysis using nonparametric Wilcoxon paired signed rank tests. We also tested for different effects depending on developmental time of the oaks by conducting analyses that included 1- and 2-year species of oaks separately under the assumption that the effects on acorn production would potentially be delayed in the latter given the longer developmental period of their acorns.

Tests for the effects of periodical cicada emergences on spatial synchrony of acorn production were made by calculating Pearson correlation coefficients between each pair of masting series for which at least 6 years overlapped (Koenig 1999; Liebhold et al. 2004). Correlation coefficients were then divided into those for which the two series were within the range of the same cicada brood (within brood) and those within the range of different cicada broods (between brood) and were further divided into categories depending on the geographic distance between sites. Five distance categories were used: sites <100, 100–250, 250–500, 500–750, and 750–1,000 km apart. No within-brood data were available for either the 250–500-km category or the 750–1,000-km category. Wilcoxon signed rank tests were used to compare the difference between within- and between-brood correlation coefficients. All analyses were conducted in R (ver. 4.1.2; R Core Team 2021).

Results

Data for acorn production included between 55 and 71 time series, depending on the emergence year. (Few data sets included data for all of the years of a cicada cycle, and thus not all data sets were included in the analysis of any given cycle year.) Results indicated that acorn crops in the emergence year (year 0) and immediately after emergence (year 1) were significantly smaller than the mean acorn crop, while crops in year 2 were significantly larger than the mean (fig. 2). There was no significant difference between the overall mean acorn crop and crops in the 2 years before emergence or in years 3 and 4 after emergence. This was also true for most subsequent postemergence years, with the exceptions of years 5, 8, and 12, each of which was smaller than the overall mean (fig. A1).

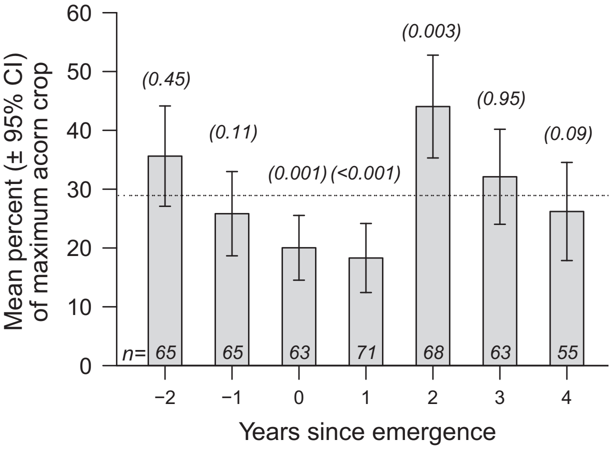

Figure 2: Histogram of mean percentage (±95% confidence interval) of the maximum scaled acorn crop as a function of years since emergence (years −2 to 4) of the local periodical cicada brood. *P* values from Wilcoxon paired signed rank tests are in parentheses above the bars; sample size (*n* = number of data sets) for each emergence year is listed inside each bar. The dotted line is the mean acorn crop across the 7 years included in the analysis.

One hypothesis for the negative effect on acorn production lasting 2 years is that the effect in year 0 is primarily on the 1-year species that mature acorns the same year while the effect in year 1 is primarily on oaks that mature their acorns in 2 years. We tested this by conducting parallel analyses comparing acorn production in years −2 to 4 for 1- and 2-year species of oaks separately. Contrary to the prediction, the main negative effect on 1-year species was in year 1, while the main negative effect on the 2-year species was in year 0 (fig. 3).

There was no significant difference between within- and between-brood pairwise correlations for sites <100 km apart or for sites 100–250 km apart in the spatial synchrony analyses. There was, however, a significant difference between the within- and between-brood correlations at sites 500–750 km apart (fig. 4). All within-brood values in this distance class came from the geographically extensive brood II (fig. 1). Restricting the analysis to pairwise comparisons that involved brood II, the difference was still substantial but not statistically significant (mean ± SE; within-brood correlation coefficient = 0.47 ± 0.10; between-brood correlation coefficient = 0.20 ± 0.11; Wilcoxon test, $P = .09$).

Discussion

Periodical cicada emergences have previously been found to have significant effects on radial growth of the cicadas' tree hosts in several studies (Karban 1980, 1982; Koenig and Liebhold 2003; Speer et al. 2010), although two other studies reported no significant effects (Cook et al. 2001; Clay et al. 2009) and a recent experimental study adding cicada carcasses to the soil found no effect on leaf nutrients or growth of young sycamores (*Platanus occidentalis*; Setälä et al. 2022). Our results extend the effects of cicada emergences to acorn production of oaks. Like the effects on growth, however, such effects may be variable, as suggested by the earlier unsuccessful attempt to detect an effect of periodical cicada emergences on acorn production by young scrub oaks (Karban 1985).

Our results supported the hypothesis that periodical cicada emergences have strong effects on masting behavior, both as a trophic veto negatively affecting seed production during and just after emergence years and by enhancing resource availability and acorn production several years following emergences. Regarding the environmental veto, resource depletion potentially caused by twig xylem feeding by the cicada brood during emergences and the girdling and killing of twigs in tree crowns by cicada adults while ovipositing (Smith and Linderman 1974; Rodenhouse

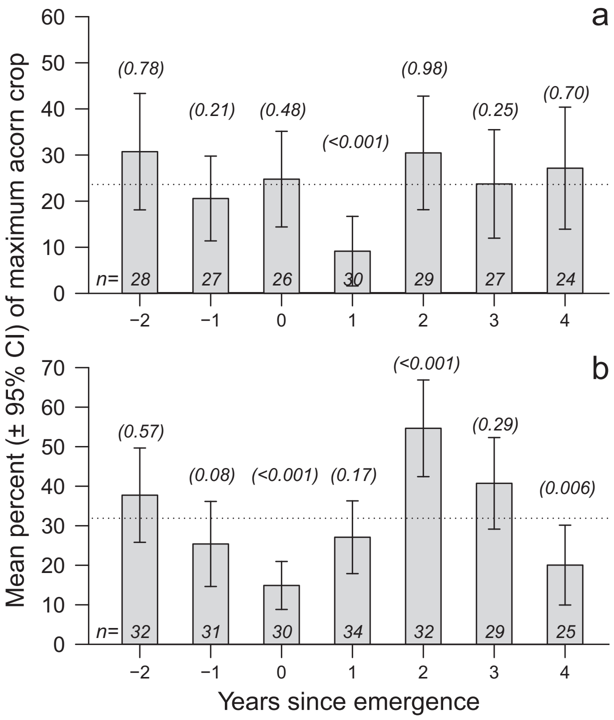

Figure 3: Histogram of mean percentage (±95% confidence interval) of the maximum scaled acorn crop as a function of years since emergence (years −2 to 4) of the local periodical cicada brood. *a*, Oaks that mature acorns in 1 year only (1-year species). *b*, Oaks that mature acorns in 2 years only (2-year species). *P* values from Wilcoxon paired signed rank tests are in parentheses above the bars; sample size (*n* = number of data sets) for each emergence year is listed inside each bar. The dotted line is the mean acorn crop across the 7 years included in the analysis.

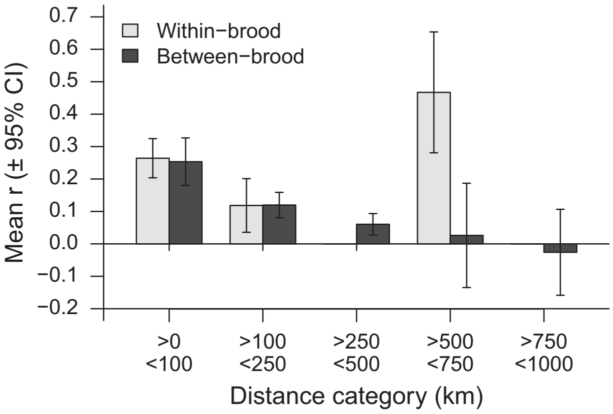

Figure 4: Mean (±95% confidence interval) correlation coefficient (synchrony) between sites as a function of five nonoverlapping distance categories, divided into sites sharing the same brood (within brood) versus sites hosting different broods (between brood). There were no within-brood sites 250–500 or 750–1,000 km apart. Only the difference between within-brood synchrony and between-brood synchrony at sites 500–750 km apart was significant (Wilcoxon test, $P < .001$).

et al. 1997; Cook et al. 2001) was associated with decreased acorn production both during emergence years and the following year (years 0 and 1). This 2-year effect could be a consequence of cicadas having a sufficiently negative effect on the oaks that it takes 2 years for their productivity to recover. Alternatively, it could be that the effect lasts only 1 year, affecting 1-year oak species during emergence years and 2-year oak species the subsequent year. Analyses separating 1- and 2-year species failed to support this latter hypothesis.

Our results do not discriminate between the effects of twig xylem feeding by adults and the oviposition damage inflicted by adults. They do, however, fail to support a significant effect of belowground xylem feeding by nymphs, as this would be likely to depress resources in the years immediately before emergence. However, given the poor nutritional value of xylem sap (McCutcheon et al. 2009) and the well-documented effects of oviposition damage (Williams and Simon 1995), it is reasonable to conclude that xylem feeding has only a minor effect on the energy budget of the trees and that our results are primarily due to oviposition damage by adults, despite this effect not always having been found to be significant (Cook and Holt 2002; Flory and Mattingly 2008).

As for the effect of emergences on nutrients, the resource pulse provided by the decaying carcasses of cicadas after emergence (Wheeler et al. 1992; Yang 2004) was associated with a positive lagged effect on acorn production in year 2. Although the absolute degree of enhancement of resources is unknown, the pulse plausibly affected stored resources and could potentially affect subsequent seed production of the trees, as predicted by the resource budget model of masting behavior (Isagi et al. 1997; Satake and Iwasa 2000; Crone and Rapp 2014). Significant negative effects observed in three subsequent postemergence years (years 5, 8, and 12; fig. A1) were not predicted and remain unexplained.

Because of cicadas' potential effects on resources, we anticipated that spatial synchrony of acorn production by trees growing within the range of the same cicada brood would be greater than between trees subject to different cicada broods (and thus experiencing the effects of emergences in different years). Results supported this prediction but only among trees 500–750 km apart. Given that within-brood values for this comparison were due entirely to sites within the range of a single brood (brood II), this result should be interpreted cautiously.

Koenig and Liebhold (2003) found significant coherence of periodical cicada life cycles (for both 13- and 17-year broods) with periodicities of radial tree ring growth of oaks. Interestingly, the effects on radial growth matched those found here for acorn production both in year 0 (both effects negative) and in year 2 (both effects positive; table 1), consistent with a lack of a trade-off between these life history traits (Knops et al. 2007). Furthermore, Koenig and Liebhold (2005) found significantly greater spatial synchrony among populations of potential avian predators of cicadas living within the range of the same cicada brood compared with different broods separated by distances up to 250 km. Along with the results reported here, these findings indicate that the life cycle of periodical cicadas affects spatial synchrony of multiple components of the ecosystem, including, possibly, reproduction of oaks.

Trees require resources to produce seeds. Our results indicate that periodical cicada emergences are an exogenous factor that affects the resources available to oaks in ways that influence acorn production, both negatively during and immediately following emergences—a trophic

Table 1: Comparison of the effects of periodical cicada emergence year on acorn production and the radial growth of oaks

Emergence year	Effect on acorn production	Effect on radial growth
−2	NS	Negative
−1	NS	NS
0	Negative	Negative
1	Negative	NS
2	Positive	Positive
3	NS	NS
4	NS	NS

Note: Effect on acorn production from this study; effect on radial growth of oaks from Koenig and Liebhold (2003). The significant effects on radial growth are based on trees within the range of 13-year broods only.

veto—and positively 2 years following emergences. These effects confirm the essential role of resources in masting but do not discriminate among the various ways that resources may affect such behavior (Pearse et al. 2016).

One notable aspect of these data is that seed production was almost certainly measured independently of, and most likely without knowledge of, the life cycle of the co-occurring periodical cicada brood. There is therefore no reason to expect bias in the data. On the contrary, periodical cicada populations are typically highest in forest edges and sparse in continuous closed-canopy forests (Lloyd and White 1976). To the extent that some of the acorn crop time series used here may have been collected in areas without large populations of cicadas, the effects reported here are likely conservative.

The life cycle of periodical cicadas involves many perplexing evolutionary and ecological problems that will no doubt continue to elicit interest for at least another 350 years (Oldenburg 1666; Hayes 2004). That emergences of these insects have significant, and in some cases long-lasting, ecological consequences on the ecosystems in which they occur is clear, however. Our results add reproduction of oaks to the previously detected long-lasting effects of emergences on other ecosystem functions, including avian populations, tree growth, and nutrient cycling, and support an essential role of resources, in this case influenced by an insect in the food chain, in masting behavior. Future studies will no doubt continue to add to the ecological consequences of these extraordinary insects.

Acknowledgments

We thank Todd Fearer for sharing his acorn production data and Andrew Hacket-Pain and the other members of the MASTREE+ group who helped update the seed production database from which much of the data used here were derived. The manuscript was improved by the comments of Dave Kelly, Andreas Wion, and an anonymous reviewer. A.M.L. acknowledges support from grant EVA4.0 (CZ.02.1.01/0.0/0.0/16_019/0000803) financed by the Czech Operational Programme, Science, Research, and Education and by the USDA Forest Service. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US government.

Statement of Authorship

W.D.K. conceptualized the study, performed the analyses, and wrote the first draft of the manuscript. J.M.L., I.S.P., and W.D.K. helped assemble the masting database. A.M.L. merged the masting data with the cicada brood data. All authors read, commented on, and helped revise the manuscript.

Data and Code Availability

The data used in the analyses have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.9w0vt4bk2; Koenig et al. 2022).

APPENDIX

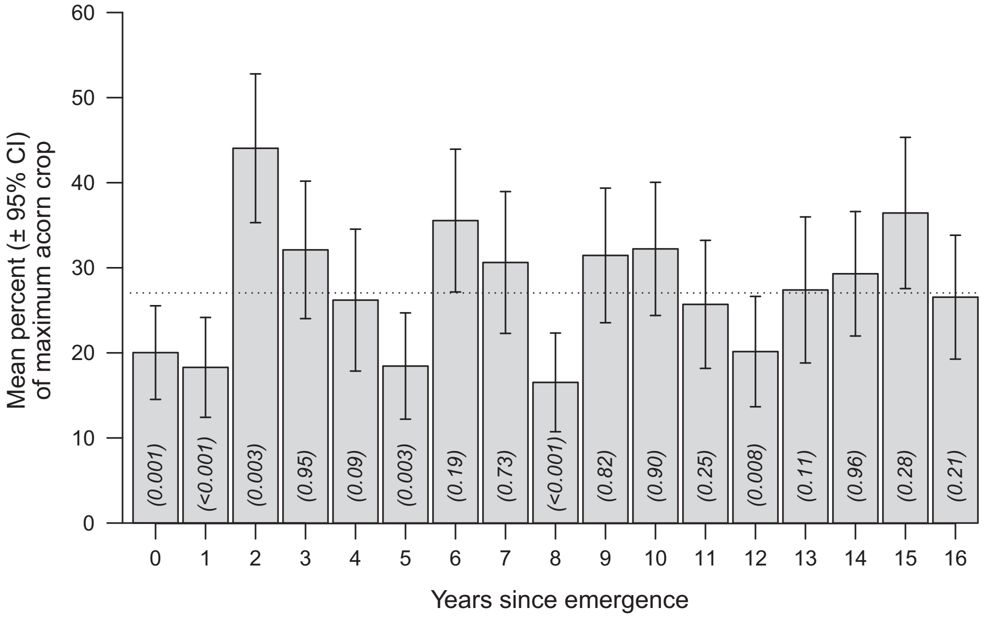

Figure A1: Histogram of mean (±95% confidence interval) of the maximum scaled acorn crop as a function of all years since emergence (years 0–16) of the local periodical cicada brood. Data include 17-year broods only. The dotted line is the mean acorn crop across all 17 years included in the analysis. *P* values are given in parentheses. Years 0, 1, 5, 8, and 12 are significantly smaller than the overall mean; only year 2 is significantly larger than the overall mean (Wilcoxon signed rank tests).

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Natural History Editor: Edmund D. Brodie III