E-Article

Variation in Avian Predation Pressure as a Driver for the Diversification of Periodical Cicada Broods

William L. Huffmyer,[1] Fang Ji,[1] Julie C. Blackwood,[2] Alan Hastings,[3,4] Walter D. Koenig,[5,6] Andrew M. Liebhold,[7,8] Jonathan Machta,[4,9] and Karen C. Abbott[1,*]

1. Department of Biology, Case Western Reserve University, Cleveland, Ohio 44106; 2. Department of Mathematics and Statistics, Williams College, Williamstown, Massachusetts 01267; 3. Department of Environmental Science and Policy, University of California, Davis, California 95616; 4. Santa Fe Institute, Santa Fe, New Mexico 87501; 5. Cornell Lab of Ornithology, Cornell University, Ithaca, New York 14850; 6. Hastings Natural History Reservation, University of California, Berkeley, Carmel Valley, California 93924; 7. USDA Forest Service Northern Research Station, Morgantown, West Virginia 26505; 8. Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Praha 6–Suchdol, Czech Republic; 9. Department of Physics, University of Massachusetts Amherst, Amherst, Massachusetts 01003

Submitted February 1, 2023; Accepted August 4, 2023; Electronically published January 17, 2024

Online enhancements: supplemental PDF.

ABSTRACT: Periodical cicadas live 13 or 17 years underground as nymphs, then emerge in synchrony as adults to reproduce. Developmentally synchronized populations called broods rarely coexist, with one dominant brood locally excluding those that emerge in off years. Twelve modern 17-year cicada broods are believed to have descended from only three ancestral broods following the last glaciation. The mechanisms by which these daughter broods overcame exclusion by the ancestral brood to synchronously emerge in a different year, however, are elusive. Here, we demonstrate that temporal variation in the population density of generalist predators can allow intermittent opportunities for new broods to invade, even though a single brood remains dominant most of the time. We show that this mechanism is consistent, in terms of the type and frequency of brood replacements, with the distribution of periodical cicada broods throughout North America today. Although we investigate one particularly charismatic case study, the mechanisms involved (competitive exclusion, Allee effects, trait variation, predation, and temporal variability) are ubiquitous and could contribute to patterns of species diversity in a range of systems.

Keywords: periodical cicadas, generalist predation, variable predation, periodicity, Allee effect, Leslie matrix.

Introduction

Processes like resource competition and predation are known to shape species abundances and distributions in diverse taxa (e.g., von Ende 1979; Dayton and Fitzgerald 2001; many others), yet determining causes and effects can be difficult. For systems with many species and influences, understanding how these different factors interact can be challenging. One way forward is to look for systems where the different processes are somewhat isolated, so that their individual effects can be better understood, and where boundaries between different populations are sharp, so that the network of interactions is relatively simple. One of the most dramatic examples that fits these criteria is the North American periodical cicada (*Magicicada* spp.), for which one can isolate the processes that influence brood sizes from those that determine brood boundaries (Kye et al. 2021).

Periodical cicadas spend most of their life cycles underground, feeding as nymphs before emerging en masse every 13 or 17 years to mate, oviposit, and subsequently die (Williams and Simon 1995). Local assemblages of three or four sympatric periodical cicada species, collectively known as broods, are nearly always developmentally synchronized over large spatial areas (50,000–500,000 km^2), with only a very small proportion of individuals in these locations emerging in other years (Cooley et al. 2018*a*; Simon et al. 2022). Modern-day periodical cicada broods are believed to have descended from a single ancestral population, segments of which shifted to emerge 1 year early, 4 years early, or 1 year late to form new locally dominant broods (Lloyd and Dybas 1966; Kritsky 1987; Simon et al. 2022; fig. 1). Much of this diversification has occurred relatively recently: just three populations present at the end of the last glacial

* Corresponding author; email: kcabbott@case.edu.

  https://doi.org/10.1086/728118

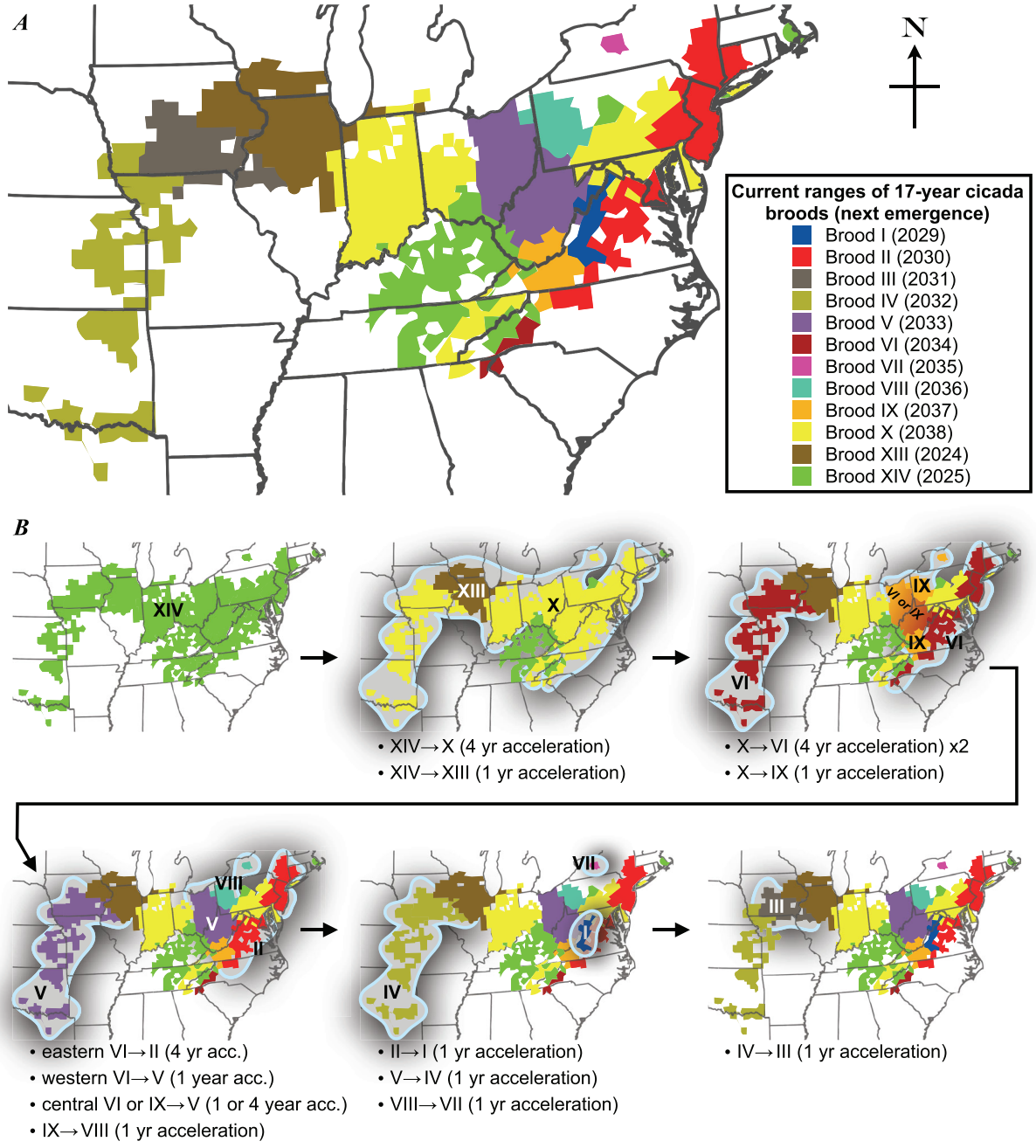

Figure 1: Modern brood map (redrawn from Liebhold et al. 2013; *A*) and Lloyd and Dybas's (1966) proposed series of replacements for 17-year cicada broods (*B*), consistent with Simon et al.'s (2022) updated scheme.

period are thought to be the ancestors of all modern 17-year and most modern 13-year cicada broods (Sota et al. 2013; Cooley et al. 2018*a*; Fujisawa et al. 2018; Du et al. 2019; Simon et al. 2022). The processes that allowed a few broods to quickly diversify into more than a dozen are unclear because the very high level of developmental synchrony observed in periodical cicada broods suggests, and field studies indicate, that there is strong selection against emerging in off years (Karban 1982; Simon et al. 2022). How then did so many new broods successfully invade and locally displace the few established broods that were dominant when the North American glaciers retreated?

Despite their unique life history, the intra- and interbrood density dependence cicadas experience is not fundamentally different from typical within- and among-population interactions. Specifically, considerable density-dependent mortality has been observed in the nymphal stage (Karban 1984), suggesting strong competition during development. The survivors then emerge to face a suite of generalist predators, especially birds, that prey on cicadas during their adult stage, creating a strong Allee effect in which predation will wipe out an emerging brood unless the population constitutes a quorum (sensu Simon et al. 2022) dense enough to satiate predators (Karban 1982; Williams et al. 1993; Sota et al. 2013). Synchronized emergence in large numbers allows broods to overcome this Allee effect (Blackwood et al. 2018; Machta et al. 2019), just as predator satiation contributes to survival in other species subject to similar Allee effects (Nagel et al. 2021).

It is curious, then, that low-density cohorts of periodical cicadas within a given brood have been observed to emerge 1 year late, 1 year early, or 4 years early, out of synchrony with the main brood (Kritsky 1987; Marshall 2001; Blackwood et al. 2018). The term "stragglers" is commonly applied to these off-year emergers, even though the phenomenon includes developmental accelerations in addition to the delays that the term suggests. The magnitude and frequency at which stragglers occur is not well understood, nor is it known why only 1- or 4-year shifts in emergence time occur (Blackwood et al. 2018; Cooley et al. 2018*a*). The presences of stragglers outside the main brood is a prerequisite for brood diversification, just as trait variance is a necessary part of phenotypic evolution (Arnold 1992). However, how a new brood, with synchronized emergence in a different year from the larger ancestral brood, can persist in the face of such strong selection against low densities remains unresolved (Simon et al. 2022).

Predators on cicadas are generalists, since they necessarily rely on alternative food sources in nonemergence years, but the impacts of dynamical feedbacks between generalist predators and their prey are not widely studied (Erbach et al. 2013). If predator densities happen to be high during a cicada emergence—due, for example, to a run of favorable weather or abundant alternative food sources—we expect cicadas to suffer particularly high mortality. The temporary increase in food availability during cicada emergence events may itself influence predator population densities. In particular, a handful of bird species has been found to exhibit numerical responses in their populations following cicada emergences (Koenig and Liebhold 2005). Individual cicadas that straggle from the main brood's emergence year lose the benefit of overcoming the Allee threshold through predator satiation, regardless of whether they accelerate or delay emergence (i.e., whether they "lead" or "lag" in the terminology of Lloyd and Dybas [1966]). Those individuals that delay, however, could suffer further consequences if predation pressure is elevated because of the generalist predators' numerical response to the previous mass emergence. On the other hand, despite the strong Allee effect, individuals that accelerate emergence avoid several years of nymphal mortality by spending fewer years developing.

In this analysis, we focus on 17-year cicadas, since their 12 modern broods are believed to have descended from just three since the end of the last glacial maximum (Fujisawa et al. 2018), making them a good case study of rapid brood diversification. We expand on a Leslie matrix model built by Blackwood et al. (2018) to investigate the problem of brood branching. Blackwood et al. (2018) developed a model that incorporated density-dependent nymphal mortality (modeled as competition), the predator's functional response, and stragglers. They found that the Allee effect imposed by the predator's functional response was often strong enough to prevent stragglers from establishing new broods. If stragglers occur commonly enough, however, they may successfully seed additional broods, particularly when interbrood density-dependent mortality is not too strong (Blackwood et al. 2018; Machta et al. 2019). Blackwood et al.'s (2018) model assumed no numerical response in predators following emergences and thus could have underestimated the challenges faced by late emergers. We build on this framework by explicitly modeling a population of generalist avian predators, including temporal fluctuations due to the numerical response to the cicada emergences and other causes, in order to ensure that barriers to new brood establishment are not artificially low in our model.

Using numerical simulations, we analyze the conditions under which a given location has a single dominant brood, undergoes succession (sequential replacements of the dominant brood), or shows brood coexistence. We find that the avian predator population density is key in determining the ability of cicada broods to invade and replace one another. In particular, temporal variation in the carrying capacity of avian predators can allow intermittent windows during which a new brood founded by stragglers can replace its parent brood. Furthermore, we show that our model can accurately replicate the number of replacements needed to explain modern brood diversity as well as the general pattern of brood replacement shown in figure 1. Our work thereby suggests a novel mechanism for brood diversification, which has remained elusive even as our ability to describe the likely pattern and timing of this diversification has improved (Simon et al. 2022).

Despite cicadas' unique life history, our model posits that their population dynamics and patterns of diversification are shaped by wholly ordinary mechanisms, including positive and negative density dependence and

temporal variation in a key quantity (here, predator carrying capacity). The lessons learned from this case study are therefore likely to translate to related questions in other taxa as well. Specifically, intermittent brood replacements are possible in our model, which typically exhibits competitive exclusion of all but the locally dominant brood, because fluctuations in predator carrying capacity cause our system to cross a bifurcation from a single-brood regime to a regime in which broods replace one another in a successional sequence (Blackwood et al. 2018). The possibility of this type of bifurcation crossing is an extremely general effect of temporal variability that has been studied in some contexts (e.g., Nelson et al. 2013) and likely applies to many more.

Methods

Model Formulation

We expand on the Leslie matrix model developed by Blackwood et al. (2018) to model the interaction between periodical cicadas and their avian predators. As in the original model, nymphal competition and stragglers (i.e., individual cicadas accelerating or delaying development) are two important components. As the specific mechanisms behind these two phenomena are not fully understood, Blackwood et al. (2018) considered different forms of straggler production and competition. Here, we build on their model of all-to-all competition (equal and symmetric competition among all larvae regardless of age) with a constant, low proportion of stragglers (a fixed, small fraction of the brood that is reassigned each year to a developmental schedule with emergence year either 1 year later or 1 or 4 years earlier than the main brood), as these assumptions are parsimonious. Because many other versions of this model produced qualitatively similar results (Blackwood et al. 2018), our central findings are robust to deviations from these specific modeling choices, as we explain below. With our model, we will examine the strengths of competition and proportions of stragglers under which brood replacement is possible and furthermore determine how generalist predators influence when replacements can occur. The components of our model are summarized in figure 2.

First, we define the cicada population density (per square meter) of each age i, where $i = 0, 1, 2, \ldots, 16$, at time t as $x_{i,t}$. Here, t has units of years. Then the vector $\mathbf{x}_t = [x_{0,t}, x_{1,t}, \ldots, x_{16,t}]^{\mathrm{T}}$ (where T is the transpose operator, indicating that this is a column vector) corresponds to the cicada population distribution at time t. For simplicity, we will focus only on the 17-year periodical cicadas in

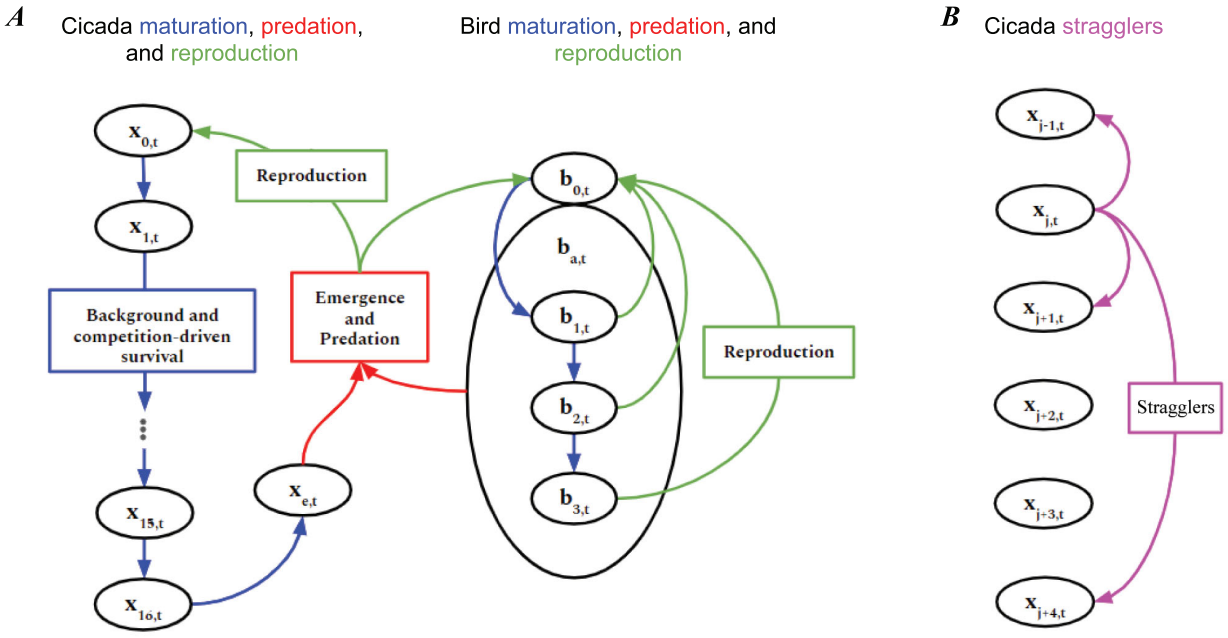

Figure 2: Schematic diagrams of the periodical cicada model with a generalist avian predator (*A*) and stragglers (*B*). In *B*, we illustrate the three possible types of stragglers (1-year delay, 1-year acceleration, and 4-year acceleration) from an arbitrary age class, *j*. In implementing the model, stragglers are modeled in this way for all age classes (although stragglers are not allowed to enter an age class younger than 0 or older than 16).

this analysis, although we expect the same principles to apply to 13-year cicadas.

Next, we define the survivorship $s_i(\mathbf{x}_t)$ of each age class i at time t based on density-independent factors and density-dependent competition within and between broods. We will assume equal competition between all broods (age classes; this is Blackwood et al.'s all-to-all competition model). Thus,

$$s_i(\mathbf{x}_t) = s\exp\left(-\sum_{j=0}^{16}\alpha x_{j,t}\right) \tag{1}$$

for every i, where $\alpha \geq 0$ is the competition coefficient and s is the empirically derived density-independent survivorship (Karban 1997; see table 1).

It is useful to denote the surviving population of adult cicadas that emerge after their final year of competition as

$$x_{e,t} = s_{16}(\mathbf{x}_t)x_{16,t}, \tag{2}$$

since these are the cicadas that interact with avian predators.

In addition to modeling the cicada population, we model a generalist avian predator population. To begin, we assume that the birds in question follow a 4-year age-structured population model, which is consistent with the life spans of the bird species that have been shown to exhibit a statistically significant numerical response following periodical cicada emergences (see the supplemental PDF, sec. S1). We define $\mathbf{b}_t = [b_{0,t}, b_{1,t}, b_{2,t}, b_{3,t}]^{\mathrm{T}}$ as the bird population density (per square meter) vector at time t. Here, we assume that the final three age classes of birds are reproductive and prey on cicadas, while the first is not reproductive and does not prey on cicadas, which is again consistent with the life history of the bird species of interest (see the supplemental PDF, sec. S1). As such, it is useful to denote

$$b_{a,t} = b_{1,t} + b_{2,t} + b_{3,t} \tag{3}$$

to be the adult bird population at time t.

Now we can begin to model some of the interactions between the periodical cicadas and their avian predators. It has been shown that the number of cicadas eaten by birds in a given year depends linearly on the number of birds present (Karban 1982), so we model the number of successful emerging cicadas that are killed by predation f in a given year t as

$$f(b_{a,t}, x_{e,t}) = \min[pb_{a,t}, x_{e,t}], \tag{4}$$

where $p \geq 0$ is the average number of cicadas killed per adult bird. The second term in the minimization results from the fact that the birds may consume, at most, the total number of emergers available in a given year; hence, the strong Allee effect.

Consequently, the proportion of emerging cicadas that are killed by birds at time t is given by

$$\frac{f(b_{a,t}, x_{e,t})}{x_{e,t}} = \frac{\min[pb_{a,t}, x_{e,t}]}{x_{e,t}}, \tag{5}$$

which we set to zero by default whenever there are no emergers, and the number of emergers killed per adult bird at time t is given by

$$\frac{f(b_{a,t}, x_{e,t})}{b_{a,t}} = \frac{\min[pb_{a,t}, x_{e,t}]}{b_{a,t}}. \tag{6}$$

Now we can construct the Leslie-style update matrix $\mathbf{L}_t$ for the cicadas, which updates at each time step. First, the

Table 1: Summary of parameters

Parameter	Definition	Value
s	Density-independent survivorship (cicadas)	.915
λ_x	Offspring per surviving adult cicada	56.18
λ_1	Fecundity of the first bird age class	1.48
$\lambda_2 = \lambda_3$	Fecundities of the second and third bird age classes	2.21
σ_0	Survival rate of the zeroth bird age class	.32
$\sigma_1 = \sigma_2$	Survival rates of the first and second bird age classes	.56
p	Average number of cicadas killed per adult bird	3,962
c	Average number of bird progeny per cicada attacked	.0001
α	Competition coefficient (cicadas)	Varies
ϕ	Proportion of cicadas that are stragglers	Varies
δ	Density dependence (birds)	Varies
K_a	Adult bird carrying capacity (function of δ, σ_i, λ_i)	Eq. (17)
$\bar{K}$	Mean adult bird carrying capacity in random walk (m^{-2})	$\approx 5.01 \times 10^{-4}$
σ_∞^2	Asymptotic variance in adult bird carrying capacity random walk	Varies
ρ	Temporal autocorrelation in adult bird carrying capacity random walk	Varies

Note: See section S1 of the supplemental PDF for parameter estimation methods.

emergers undergo competition, then predation, and finally they reproduce:

$$\mathbf{L}_t = \begin{bmatrix} 0 & 0 & \dots & 0 & s_{16}(\mathbf{x}_t)\left(1 - \dfrac{f(b_{a,t}, x_{e,t})}{x_{e,t}}\right)\lambda_x \\ s_0(\mathbf{x}_t) & 0 & \dots & 0 & 0 \\ 0 & s_1(\mathbf{x}_t) & \dots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \dots & s_{15}(\mathbf{x}_t) & 0 \end{bmatrix}. \tag{7}$$

Here, λ_x is the number of offspring per surviving adult cicada, given empirically (table 1). We follow Blackwood et al. (2018) in assuming λ_x to be density independent. This assumption is partially consistent with Karban (1981), who found that mating speed after eclosion was density independent, while female follicle number appeared density independent in one sample but positively density dependent in two others. We could account for the latter effect by making λ_x an increasing function of $x_{e,t}$, which would strengthen the Allee effect imposed by predators and further disadvantage stragglers. However, given the mixed evidence and the fact that our model already includes an Allee effect acting on emerging adults, we opt for the simpler, constant λ_x used by Blackwood et al. (2018).

The model of the cicada population also requires the straggler matrix, which we will call **D**, as in Blackwood et al. (2018). Assuming that some fixed proportion ϕ enters each of the possible off-year emergence classes (4 years early, 1 year early, or 1 year late), we define the entries of **D**, $d_{i,j}$, as follows:

$$\begin{aligned} d_{0,0} &= 1 - 2\phi, \\ d_{i,i} &= 1 - 3\phi \qquad \text{for } 1 \le i \le 12, \\ d_{i,i} &= 1 - 2\phi \qquad \text{for } 13 \le i \le 15, \\ d_{16,16} &= 1 - \phi, \\ d_{i+4,i} &= \phi \qquad \text{for } 0 \le i \le 12, \\ d_{i+1,i} &= \phi \qquad \text{for } 0 \le i \le 15, \\ d_{i-1,i} &= \phi \qquad \text{for } 1 \le i \le 16. \end{aligned} \tag{8}$$

Finally, we construct the Leslie-style update matrix for the birds, which also updates at each time t. To begin with, we introduce a general density dependence function β for the bird population, to maintain a finite equilibrium in the bird population in the absence of cicadas. We assume that density dependence is a function of the number of adult birds and has an effect on reproduction, as opposed to survival, which results in a sustained numerical response following emergences that is consistent with empirical findings:

$$\beta(b_{a,t}) = \frac{1}{1 + \delta b_{a,t}}. \tag{9}$$

Here, δ is a density dependence parameter, where $1/\delta$ is the adult bird population at which the reproductive rates of each adult bird age class are half their respective maxima. Then our update matrix for the bird population $\mathbf{M}_t$ is given by

$$\mathbf{M}_t = \begin{bmatrix} 0 & m_{1,2} & m_{1,3} & m_{1,4} \\ \sigma_0 & 0 & 0 & 0 \\ 0 & \sigma_1 & 0 & 0 \\ 0 & 0 & \sigma_2 & 0 \end{bmatrix}, \tag{10}$$

where $m_{1,i} = \lambda_i \beta(b_{a,t}) + cf(b_{a,t}, x_{e,t})/b_{a,t}$ for $i = 2, 3, 4$. Here, $\lambda_i \ge 0$ corresponds to the maximum reproduction rate of the ith bird age class, and $\sigma_i \in [0, 1]$ refers to the survival rate in similar fashion. In addition, $c \ge 0$ is the average number of additional bird progeny produced per cicada killed. Now we can write the equations that govern this model of periodical cicadas in the presence of avian predators:

$$\mathbf{x}_{t+1} = \mathbf{D}\mathbf{L}_t\mathbf{x}_t, \tag{11}$$

$$\mathbf{b}_{t+1} = \mathbf{M}_t\mathbf{b}_t. \tag{12}$$

Bird Carrying Capacity

To anchor our analysis of this model to a quantity with a clear biological interpretation, we derive the expression for the carrying capacity of the birds in the absence of cicadas. We can then study the effect of bird carrying capacity on the formation of new developmentally synchronized broods and how variation in this carrying capacity through time might produce a sequence of brood replacements consistent with figure 1. In the absence of cicadas, equation (12) reduces to the following equation for the bird population:

$$\begin{aligned} \mathbf{b}_{t+1} &= \mathbf{M}_t\mathbf{b}_t \\ &= \begin{bmatrix} 0 & \lambda_1\beta(b_{a,t}) & \lambda_2\beta(b_{a,t}) & \lambda_3\beta(b_{a,t}) \\ \sigma_0 & 0 & 0 & 0 \\ 0 & \sigma_1 & 0 & 0 \\ 0 & 0 & \sigma_2 & 0 \end{bmatrix}\mathbf{b}_t \\ &= \begin{bmatrix} 0 & \dfrac{\lambda_1}{1 + \delta b_{a,t}} & \dfrac{\lambda_2}{1 + \delta b_{a,t}} & \dfrac{\lambda_3}{1 + \delta b_{a,t}} \\ \sigma_0 & 0 & 0 & 0 \\ 0 & \sigma_1 & 0 & 0 \\ 0 & 0 & \sigma_2 & 0 \end{bmatrix}\mathbf{b}_t. \end{aligned} \tag{13}$$

The carrying capacity of this system (the total bird population at cicada-free equilibrium) is given by $K = \bar{b}_0 + \bar{b}_1 + \bar{b}_2 + \bar{b}_3 = \bar{b}_0 + \bar{b}_a$, where $\bar{\mathbf{b}}_t = [\bar{b}_{0,t}, \bar{b}_{1,t}, \bar{b}_{2,t}, \bar{b}_{3,t}]^{\mathrm{T}}$ is the nonzero solution to the following equation:

$$\bar{\mathbf{b}} = \begin{bmatrix} 0 & \frac{\lambda_1}{1+\delta\bar{b}_a} & \frac{\lambda_2}{1+\delta\bar{b}_a} & \frac{\lambda_3}{1+\delta\bar{b}_a} \\ \sigma_0 & 0 & 0 & 0 \\ 0 & \sigma_1 & 0 & 0 \\ 0 & 0 & \sigma_2 & 0 \end{bmatrix} \bar{\mathbf{b}}. \quad (14)$$

In section S2 of the supplemental PDF, we calculate this carrying capacity explicitly. The resulting carrying capacity for the entire bird population is given by

$$K = \frac{(1+\tilde{\sigma})(\tilde{\lambda}-1)}{\delta\tilde{\sigma}}, \quad (15)$$

where $\tilde{\sigma} = \sigma_0 + \sigma_0\sigma_1 + \sigma_0\sigma_1\sigma_2$ and $\tilde{\lambda} = \lambda_1\sigma_0 + \lambda_2\sigma_0\sigma_1 + \lambda_3\sigma_0\sigma_1\sigma_2$. Since only the adult birds prey on cicadas in this model, it is more useful to consider the carrying capacity of adult birds (ages 1, 2, and 3), which is

$$K_a = \frac{\tilde{\lambda}-1}{\delta}. \quad (16)$$

Carrying Capacity as a Mean-Reverting Random Walk

In addition to showing how changing the bird carrying capacity deterministically alters cicada population dynamics, we will also explicitly model the bird carrying capacity as a mean-reverting random walk to reflect natural variability in the birds' environment. Koenig and Liebhold (2013) show that bird predation pressure follows a predictable 17-year cycle in sync with cicada emergences. As such, we model the adult bird carrying capacity at each cicada generation n (where 1 generation = 17 years), K_n, as

$$K_{n+1} = K_n - (1-\rho)(K_n - \bar{K}) + \sigma_\infty\sqrt{(1-\rho^2)}\,X_n, \quad (17)$$

where $\bar{K}$ is the average adult bird carrying capacity, σ_∞^2 is the asymptotic variance of K_n, ρ is its temporal autocorrelation, and $X_n \sim \mathcal{N}(0,1)$.

After iterating equation (17), we take the absolute value of the resulting series of K_n values to avoid unrealistic negative carrying capacity values. The resulting process is a random walk with a reflecting boundary at zero. Doing so means that the actual variance and autocorrelation of the carrying capacity time series no longer equals σ_∞^2 and ρ. Nevertheless, the actual autocorrelation scales linearly with the σ_∞^2 value used in equation (17), and the actual autocorrelation scales linearly with ρ (see the supplemental PDF, sec. S3). Thus, we are safe to interpret simulations with higher σ_∞^2 as more variable and those with higher ρ as more strongly autocorrelated. Going forward, we report σ_∞^2 and ρ values rather than the true variance and autocorrelation, since these are the input parameters needed to implement our model.

Although we lack empirical estimates for σ_∞ and ρ, we can use our model to ask whether any plausible values can accurately replicate the series of replacements that could have led to the spatial distribution of distinct cicada broods observed throughout North America today.

Computational Methods

We ran each simulation for 12,002 years (706 generations), long enough for the system to equilibrate and roughly the time since the last glaciation in North America (Alexander and Moore 1962). We begin with an initial cicada population density of 100 cicadas per square meter in the first nymphal stage ($x_{0,0} = 100$) and initialize the bird population at its cicada-free equilibrium (solution to eq. [14], which has total bird population size K and adult bird population size K_a). This initial condition is tailored so that the initial Allee effects or the nymphal competition do not wipe out the cicada population within the first generation. If the initial cicada population density were lower (e.g., $x_{0,0} = 10$), then Allee effects would wipe out the entire cicada population before it can establish itself, and if it were larger (e.g., $x_{0,0} = 10{,}000$), then a combination of strong nymphal competition and predator numerical response would also wipe out the entire cicada population before it establishes itself. If we initialize the cicada population as being uniform across all possible age classes (e.g., $\mathbf{x} = [10, 10, 10, \ldots, 10]^{\mathrm{T}}$), then again provided that the total population density is not too low or too high as to result in extinction via Allee effects and nymphal competition, simulations with identical parameters converge to a unique steady state distribution.

For each simulation, we classify a brood as extinct if it is unable to overcome the Allee effect once it emerges. That is, although off-year broods will be continually repopulated by stragglers, we do not consider these broods persistent unless they have positive density after postemergence predation.

Results

Bird Carrying Capacity Fluctuations and the Establishment of New Cicada Broods

Although we were able to estimate many of the model parameters from data (table 1; for further discussion, see the supplemental PDF), several parameters remain unknown: α, the competition coefficient for the nymphal cicadas; ϕ, the cicadas' annual straggler proportion; and δ, the strength of density dependence in bird reproduction. Thus, we take a similar approach to Blackwood et al. (2018) to analyze the model's behavior across possible values of these unknown parameters so that our conclusions do

not rely on unsupported estimates. Blackwood et al. (2018) ran simulations across the straggler-competition ($\phi - \alpha$) parameter space and explored how different types of steady states arise in the cicada population. We elaborate on this analysis here by exploring that same parameter space across different values for the carrying capacity in the adult bird population, K_a (this is equivalent to looking across different values of δ, since δ is the only parameter in eq. [17] for which we lack an estimate; we discuss the results in terms of K_a, since it has a more straightforward interpretation than δ). The results are shown in figure 3. Figure 3*A* shows the different steady states that arise in the cicada population whenever we set the bird carrying capacity to somewhere within the range estimated from data (2.24×10^{-4} to 7.78×10^{-4} m^{-2}), while figure 3*B* illustrates the steady states when there is a significant reduction in bird carrying capacity (about two orders of magnitude). Comparing these two panels gives us the first indication that fluctuations in bird carrying capacities can have a large impact on cicada dynamics and the possibility for replacements.

We see in figure 3*A* and 3*B* that extinction of all broods occurs whenever competition, straggler proportion, or both are sufficiently high. Otherwise, one of several extant steady states is possible. In the parameter regions marked *C*, one brood competitively excludes all other broods (see figure 3*C* for an example of this single-brood steady state). This occurs whenever production of stragglers is sufficiently low and competition between broods is low enough to avoid extinction but high enough to suppress additional broods from establishing themselves within the same location. This steady state mimics what is seen in nature, where one brood dominates all other broods in a given location (figure 1*A*). We also see that in this region, the bird population experiences a sustained numerical response following emergences, which contributions to the suppression of late emergers and reinforces dominance of the main brood (fig. 3*D*). In the parameter regions marked *E*, and illustrated in figure 3*E*, we see the multibrood successional steady state. In this scenario, stragglers are sufficiently abundant and competition is low enough that new cohorts overcome the Allee threshold and repeatedly replace the formerly dominant brood (i.e., the identity of the brood with the greatest number of emergers in a generation changes through time). These replacements occur with a predictable frequency, which we show using green shading in figure 3*A* and 3*B*. The fourth and final steady state, depicted in figure 3*F*, corresponds to all-brood coexistence, in which competition is low enough and stragglers are common enough such that all 17 possible broods can exist together in the same location with a constant population size.

For a particular straggler proportion and competition strength (e.g., the one marked with a black circle in fig. 3*A*), reducing the bird carrying capacity results in a bifurcation where cicada broods begin to replace one another. That is, a system with straggler and competition parameters corresponding to the circle will switch from being at the single-brood steady state (fig. 3*A*) to the multibrood successional steady state (fig. 3*B*). This bifurcation suggests a possible mechanism for brood replacements and diversification. Repeated and sustained instances of traversal across this bifurcation value, driven by the predator carrying capacity varying across space and time, could allow for replacements to occur in different locations across the cicada range.

Simulations confirm that reducing the bird carrying capacity for a sufficiently long time and then returning the bird carrying capacity to its original value can result in replacement of the dominant brood and, subsequently, a return to the single-brood steady state (fig. 4*A*). Through repeated incidences of this same mechanism, allowing the bird carrying capacity to vary in time can result in a series of replacements (fig. 4*B*). This mechanism could explain how modern-day cicada broods branched off from three developmentally synchronized postglacial ancestors. Although we illustrate it with a specific example in figures 3 and 4, this key qualitative result is very general. Many alternative models of nymphal competition generate the same bifurcation (Blackwood et al. 2018), and any straggling–competition strength combination that lies in the single-brood steady state regime for some plausible bird carrying capacities and the successional regime for others would give rise to the same possibility of intermittent brood replacements with variation in the carrying capacity.

Who Replaces Whom?

Lloyd and Dybas (1966) proposed a possible series of replacements, still largely consistent with more recent work (Simon et al. 2022), to explain how the current spatial ranges of cicada broods originated (fig. 1*B*). This is by no means the only possible series of replacements (Cooley et al. 2018*a*), but it provides a starting point to answer whether the model can accurately recreate which brood has replaced which through time. Figure 1 shows 13 replacement events since divergence from the common ancestral brood, as many as 12 of which could have occurred since the last glacial maximum (i.e., the 12 replacements in brood X's lineage following the [putatively preglacial] splitting of parts of brood XIV to form X and XIII; fig. 1*B*). Clearly, other replacement schemes could get from three broods to 12 with fewer replacements per ancestral brood, so we treat 12 replacements since glaciation as the likely maximum of the range of realistic possibilities. We also treat the distribution of replacement types (1-year versus 4-year shifts in emergence year) seen in figure 1 as representative of the realistic possibilities, as it represents current understanding (Simon et al. 2022).

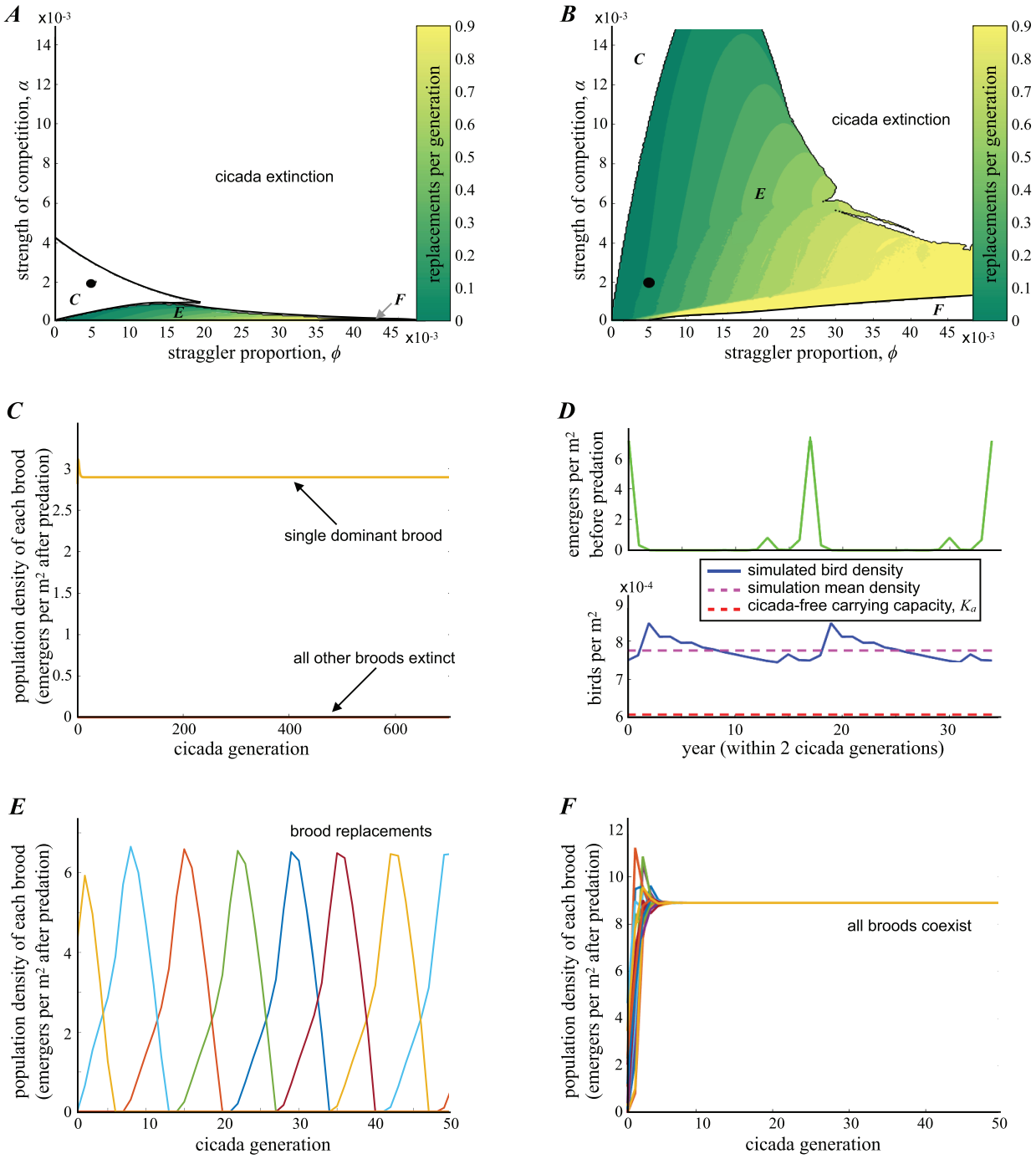

Figure 3: Steady state cicada dynamics with a constant bird carrying capacity. *A*, *B*, Straggler proportion (ϕ) versus competition (α) parameter space diagrams under the baseline adult bird carrying capacity ($K_a = 6.094 \times 10^{-4}$ m^{-2}; *A*) and a reduced adult bird carrying capacity ($K_a = 3.047 \times 10^{-5}$ m^{-2}; *B*). The regions with extant cicada populations are labeled by letters that correspond to the panel showing a representative cicada time series: *C*, the single-brood steady state; *E*, the multibrood successional steady state in which brood replacements occur; and *F*, the all-brood steady state. Bird dynamics for the single-brood steady state, showing the numerical response, are shown in *D*. In *A* and *B*, a circle at $(0.005, 0.002)$ is marked in both panels to illustrate how a drop in the bird carrying capacity can cause cicadas with this amount of stragglers and competition to switch from having a single dominant brood to exhibiting successive brood replacements.

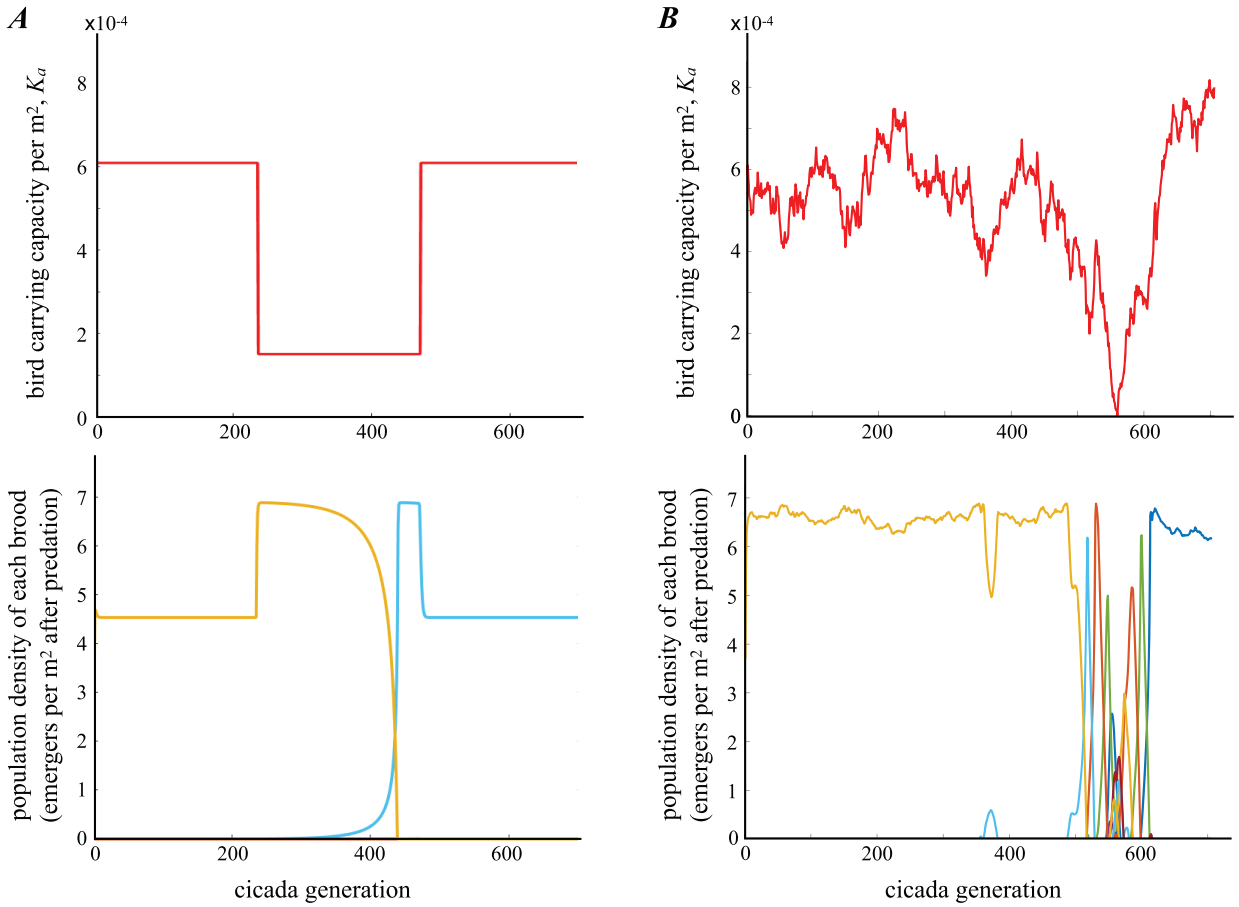

Figure 4: Illustrations of how temporary reductions in bird carrying capacity, K_a, can allow new cicada broods to establish. *A*, At a baseline carrying capacity $K_a = 6.094 \times 10^{-4}$ m^{-2}, a single cicada brood dominates. Reducing the bird carrying capacity in the middle of the simulation (to 1.506×10^{-4} m^{-2}, *top*) allows the cicada brood shown in blue to replace the previously dominant yellow brood (*bottom*). *B*, Randomly varying the bird carrying capacity according to a mean-reverting random walk ($\sigma_\infty = 5 \times 10^{-7}$, $\rho = 0.9995$) allows intermittent windows in which the bird carrying capacity dips sufficiently to allow cicada brood replacements.

Figure 5 shows good correspondence between the replacement series invoked in Lloyd and Dybas's (1966) hypothesis (orange) and those seen in simulations of our model under a variable (mean-reverting random walk) bird carrying capacity (black). Competition coefficients and straggling rates are largely unknown, but because the single-brood steady state is what we commonly observe in nature, we considered parameter combinations in and around region *C* in figure 3*A* to be generally realistic. We thus ran simulations across a 50 × 50 grid of values from $\phi = 0$ to 2×10^{-3} and $\alpha = 0$ to 4.2×10^{-3}. From these simulations, we enumerated the broods and kept track of which replaced which when in the multibrood successional steady state.

The model accurately predicts several features of the series of replacements. First, the replacements from our simulations result only from developmental accelerations, as opposed to developmental delays, which is consistent with the series of replacements proposed by Lloyd and Dybas (1966). This behavior is due to two factors. First, cohorts that delay development will suffer from an increased Allee threshold in the years following the main emergence, due to growth in the bird population driven by the main emergence event, while cohorts that accelerate development evade the predator numerical response and furthermore incite a predator numerical response that will be detrimental to subsequently emerging broods. Second, cohorts that delay development must undergo more years of competition-driven mortality, while cohorts that accelerate development will reduce this risk.

On the other hand, the model overestimates the frequency of 4-year accelerating replacements that occur

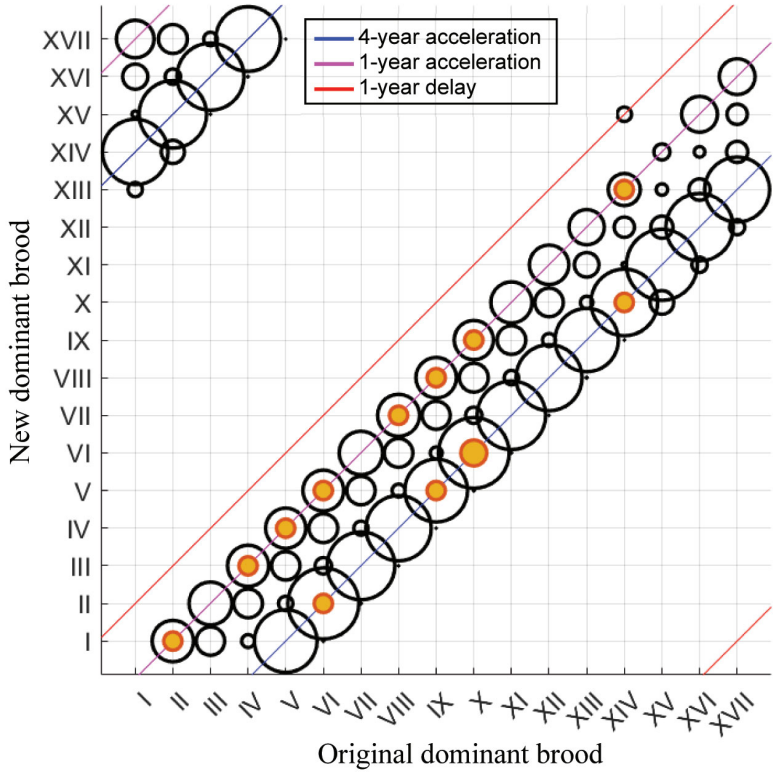

Figure 5: Who replaces whom? Circles indicate each new brood that was observed to replace a previously dominant brood in simulations (black) or Lloyd and Dybas's (1966) hypothesis (orange), with the three possible types of stragglers marked by colored lines. The size of each black circle scales with the number of times that particular replacement occurred in simulations (across a grid of (ϕ, α) values spanning $\phi = [0, 2 \times 10^{-3}]$, $\alpha = [0, 4.2 \times 10^{-3}]$). Orange circles scale (using a different scale from the black circles, to be visible on the same plot) with the frequency of each replacement in Lloyd and Dybas's (1966) proposed series of replacements (fig. 1*A*).

compared to 1-year accelerating replacements. This result likely has to do with the model's assumption that the proportion of cicadas that accelerate development by 4 years is the same as the proportion of cicadas that accelerate (or delay) development by 1 year. In reality, cicadas may be more likely to accelerate development by 1 year than 4 years (Marshall 2001), which could explain the discrepancy. Additional simulations in which 1-year shifts were twice as likely as 4-year shifts indeed showed a lower frequency of 4-year-ahead replacements (results not shown).

How Often Do Replacements Occur?

In addition to the question of whether our model can accurately replicate which brood has replaced which through time, we also wanted to compare how often replacement events occur in the model to the real-world understanding that up to 12 such replacements have occurred in the past 700 cicada generations. We have seen that the frequency of replacements depends on the strength of competition between cicadas, the proportion of stragglers, and the adult carrying capacity of the avian predators, which will in turn depend on how the predator carrying capacity changes in time. Again assuming that the competition and straggling parameters lie somewhere in the single-brood steady state region of figure 3*A*, we can then determine how the properties of the random walk (its asymptotic variance, σ^2_∞, and autocorrelation, ρ) affect the frequency of replacements as the bird carrying capacity changes through time.

Explicitly running simulations that include both the bird and the cicada populations in the presence of variable bird carrying capacity and finding the frequency of replacements is computationally expensive when done over a range of $\rho - \sigma^2_\infty$ parameter combinations. However, for a given value of competition α and straggling ϕ, we can compute the replacements per generation as a function of the bird carrying capacity (fig. S2*A*; figs. S1, S2 are available online). We therefore sampled realizations of the bird carrying capacity time series since the last glaciation and from each time series approximated the frequency of replacements (fig. S2). Although this approach is not guaranteed to produce the exact number of replacements that would

be seen in a full model simulation, it allows us to efficiently map the qualitative effects of bird carrying capacity variance and autocorrelation on brood replacement frequency (fig. 6*A*) and to identify parameter values to use in a full simulation that can serve as a proof of concept (fig. 6*B*).

Using this method, we obtained an approximate number of replacements since the last glaciation as a function of the random walk parameters (ρ and σ_∞^2) governing adult bird carrying capacity, K_a. In the brightest-yellow region in figure 6*A*, an average of 12 replacements in the time since the last glaciation is expected. One such high-replacement-rate example is shown in figure 6*B*. The darker regions of figure 6*A* further show that fewer per-ancestral-brood replacements are possible, as might be predicted by alternate replacement schemes.

Discussion

We have demonstrated that temporal variation in generalist predator population densities (due, e.g., to a variable carrying capacity and the numerical response) provides a viable mechanistic explanation for how periodical cicada broods have replaced one another and branched off from few ancestral broods, despite the general tendency for developmental synchrony within, and local exclusion among, different broods. An Allee effect and a sustained predator numerical response reinforce single-brood dominance most of the time, but a variable predator carrying capacity also allows intermittent windows for replacements to occur. These brood replacements are consistent with the order and frequency of replacements needed to create the distribution of cicada broods observed today.

Implications for Our Understanding of Cicada Brood Diversity

We demonstrated our result assuming that the strength of competition among nymphs is unaffected by their age classes. However, the precise form of density-dependent mortality in cicada nymphs is not clear (Karban 1984). Blackwood et al. (2018) considered several other forms of density dependence, ranging from competition mainly during the first two instars (or the first 3 years of a cicada's life cycle), to competitive advantage proportional to body size, to only intrabrood competition. For most forms of density dependence, Blackwood et al. (2018) found that dominant brood replacements could occur for sufficiently low levels of competition and high levels of stragglers. That is, versions of figure 3 for these other models look qualitatively similar. Consequently, the mechanism outlined in our analysis should hold for these other forms of competition provided variability in the predator's carrying capacity can again shift the cicada population in and out of the regime where brood replacements occur (as occurs for the circle marked in fig. 3*A*, 3*B*). Thus, we expect that the mechanism outlined here is robust to the form of nymphal competition and not specific to the all-to-all form modeled here. More broadly, we contend that our findings—although demonstrated through a specific case study—are generally robust against uncertainties in the model assumptions.

Despite the expansive range and unique spatial distribution of North American periodical cicadas, we have largely ignored spatial considerations in our modeling process. Instead, the spatial aspects of recolonization are treated implicitly by our model. The temporal variability in bird carrying capacity that we model can be thought of as both spatial and temporal variability, and the series of replacements observed in a model realization can be imagined as the collective set of local extinctions (Manter 1974) and replacements (Kritsky 1987) occurring throughout the cicada range (as in fig. 1*B*). Kye et al. (2021) considered Blackwood et al.'s (2018) model in two spatially adjacent broods with dispersal between them and identified dispersal and competition conditions under which brood boundaries are maintained, versus when stable brood coexistence can occur. The combination of our model with a generalist avian predator and Kye et al.'s (2021) spatial model could provide valuable insight into how dispersal, predator numerical responses, competition between cicadas, and stragglers have interacted to establish brood boundaries among distinct cicada broods originating from a single ancestral brood.

Because stragglers are poorly understood, absent adequate data from which to build a more detailed model, our study has simplified the possible forms of straggling by assuming that periodical cicadas are equally likely to accelerate development by 1 or 4 years or delay by 1 year. Our model has somewhat overestimated (with respect to Lloyd and Dybas's [1966] proposal) the frequency of 4-year accelerating replacements, a discrepancy that could be explained by different likelihoods of altering development by any of the three possibilities. Blackwood et al. (2018) also investigated the patterns that arise following isolated events that produce large numbers of stragglers. Additionally, scenarios for the origins of extant broods beyond those posited by Lloyd and Dybas (1966) have been proposed (Cooley et al. 2018*a*; Simon et al. 2022). In particular, Cooley et al. (2018*a*) suggest that periodical cicada 4-year developmental decelerations could provide a more geographically parsimonious explanation for the origins of extant broods and propose that regional climatic conditions could provide a mechanistic explanation for the varying life spans among cicada cohorts. Meanwhile, phylogenetic studies have indicated that extant cicada broods could have polyphyletic origins (Du et al. 2019). Future empirical

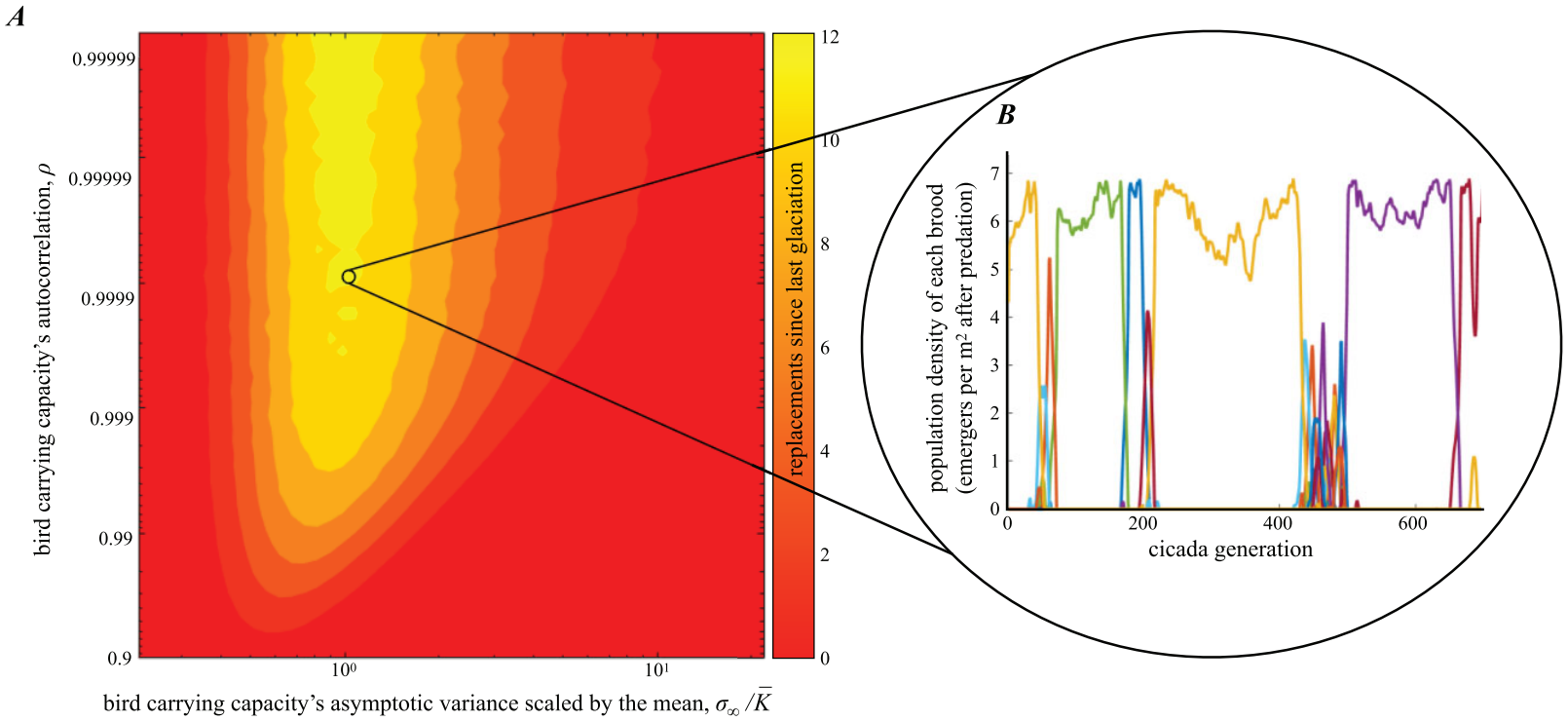

Figure 6: Expected brood replacements since last glaciation as a function of the random walk parameters (the scaled variance parameter, $\sigma_\infty/\bar{K}$, and the autocorrelation parameter, ρ). See section S3.5 of the supplemental PDF for methods. The yellow region in *A*, illustrated by the example time series in *B*, corresponds to a realistic number of replacements, per Lloyd and Dybas's (1966) hypothesis. Results are shown for $\alpha = 0.002$ and $\phi = 0.005$, and they are representative of other realistic α and ϕ values. Results in *A* were derived using the approximation method outlined in figure S2, but the realization in *B* is from a simulation of the full model.

work should investigate the precise timing, frequency, and magnitude of straggling, as well as what triggers plastic developmental responses in cicadas, for a deeper understanding of stragglers than our model allows.

The interactions between broods considered here are based on the same mechanisms as interactions between competing species and their shared predators, so our work suggests new insights into questions about intra- and interspecific interactions in general. In particular, few theoretical studies have considered the feedback between generalist predators and a focal prey species, as done here (Erbach et al. 2013). Our study also supports a recent suggestion that far-ranging generalist predators can help to stabilize food webs (Brechtel et al. 2019). In this case, the presence of a generalist predator maintains single-brood (analogous to single-species) dominance, preventing invasions by other broods. When the predator population is reduced or removed, the system becomes destabilized and invasions may occur.

Our model has, of course, excluded a plethora of other species that could interact with and prey on cicadas by modeling the periodical cicadas only in the presence of a generalist avian predator. For example, the specialist fungal pathogen *Massospora cicadina* likely imposes within-brood density dependence that is quite different from the generalist predator effects we model (Speare 1921; Cooley et al. 2018*b*). Importantly, however, the model accurately captures the dynamics of periodical cicadas in the presence of a sustained predator numerical response following emergences. Although the life span, reproductive behavior, and nature of density dependence in the predator population could be changed in the model to mimic a more diverse array of natural enemies, we believe that this relatively simple analysis sufficiently demonstrates the plausibility of the proposed mechanism.

Ultimately, whether our hypothesis for brood branching is viable depends on the frequency and spatial scale of variation in bird population densities. Future empirical work to determine whether bird carrying capacities or other demographic quantities indeed vary in such a way that could explain the series of observed cicada brood replacements would be valuable.

In addition, if differences in cicada life spans can indeed be attributed to environmental factors such as temperature (Cooley et al. 2018*a*), then since bird populations may covary with these environmental factors, investigating the feedbacks between bird and cicada populations and their environment may prove to be insightful. An alternative, although closely related, scenario to the one proposed here is that bird carrying capacities could have slowly ramped up since the last glaciation because of increasing temperatures. In such a scenario, there may have been a period when continual brood replacements were the dominant regime, followed by the current regime, where no or few replacements occur as predation has reached its current level. The spatial pattern would then be determined by exactly when different regions entered the single-brood steady state and local replacements ceased.

Broader Implications

Despite their enigmatic life history, cicada broods are subject to the same basic pressures as other populations: specifically, negative density dependence, Allee effects, and predation. Thus, although our model is cicada specific, the mechanisms it was built to evaluate are transferable to other systems. While tightly coupled specialist predator-prey pairs are a centerpiece of ecological theory, generalist predators have received far less attention. Generalist predators are typically assumed to exert relatively constant predation pressure through time (as in, e.g., Hanski et al. 1991), due to an assumed lack of a numerical response to any particular prey. We are not the first to notice that, while valid in some contexts, this is not a universally reasonable assumption (Erbach et al. 2013), and our study contributes to the small but growing catalog of examples showing the dynamical role generalist predators can play.

The mechanism that allows replacement of the dominant competitor in our model is that fluctuations in predator carrying capacity allow the cicada system to cross a bifurcation point (i.e., the example circle in fig. 3*A* and 3*B* can be in either the single-brood or the successional steady state, depending on predator carrying capacity). The idea that population dynamics can be attributed to repeated bifurcation crossing due to fluctuation in an external driver is intriguing, likely common, but little appreciated (Nelson et al. 2013; Clark et al. 2021). Virtually all ecological systems have bifurcation points that could be crossed in such a manner, so the generality of the ultimate mechanism behind brood turnover in our model would be interesting to assess in future work.

Acknowledgments

W.L.H., F.J., A.H., J.M., and K.C.A. were supported in part by the National Science Foundation (DMS-1840221). P. Thomas and D. Gurarie provided helpful comments on the manuscript.

Statement of Authorship

W.L.H. led model construction and analysis, with supervision from F.J. and K.C.A. W.L.H. wrote the originally submitted manuscript, with subsequent revisions led by K.C.A. W.D.K. provided parameter estimates. All authors

contributed to conceptualization, methods development, and review and editing of the manuscript.

Data and Code Availability

All code is publicly available on Zenodo (https://doi.org/10.5281/zenodo.8193360; Abbott 2023).

Literature Cited

Abbott, K. C. 2023. Data from: Variation in avian predation pressure as a driver for the diversification of periodical cicada broods. American Naturalist, Zenodo, https://doi.org/10.5281/zenodo.8193360.

Alexander, R. D., and T. E. Moore. 1962. The evolutionary relationships of 17-year and 13-year cicadas, and three new species (Homoptera, Cicadidae, *Magicicada*). Miscellaneous Publications of the Museum of Zoology no. 121.

Arnold, S. J. 1992. Constraints on phenotypic evolution. American Naturalist 140:S85–S107.

Blackwood, J. C., J. Machta, A. D. Meyer, A. E. Noble, A. Hastings, and A. M. Liebhold. 2018. Competition and stragglers as mediators of developmental synchrony in periodical cicadas. American Naturalist 192:479–489.

Brechtel, A., T. Gross, and B. Drossel. 2019. Far-ranging generalist top predators enhance the stability of meta-foodwebs. Scientific Reports 9:12268.

Clark, T. J., J. S. Horne, M. Hebblewhite, and A. D. Luis. 2021. Stochastic predation exposes prey to predator pits and local extinction. Oikos 130:300–309.

Cooley, J. R., N. Arguedas, E. Bonaros, G. Bunker, S. M. Chiswell, A. DeGiovine, M. Edwards, et al. 2018*a*. The periodical cicada four-year acceleration hypothesis revisited and the polyphyletic nature of Brood V, including an updated crowd-source enhanced map (Hemiptera: Cicadidae: *Magicicada*). PeerJ 6:e5282.

Cooley, J. R., D. C. Marshall, and K. B. R. Hill. 2018*b*. A specialized fungal parasite (*Massospora cicadina*) hijacks the sexual signals of periodical cicadas (Hemiptera: Cicadidae: *Magicicada*). Scientific Reports 8:1432.

Dayton, G. H., and L. A. Fitzgerald. 2001. Competition, predation, and the distributions of four desert anurans. Oecologia 129:430–435.

Du, Z., H. Hasegawa, J. R. Cooley, C. Simon, J. Yoshimura, W. Cai, T. Sota, and H. Li. 2019. Mitochondrial genomics reveals shared phylogeographic patterns and demographic history among three periodical cicada species groups. Molecular Biology and Evolution 36:1187–1200.

Erbach, A., F. Lutscher, and G. Seo. 2013. Bistability and limit cycles in generalist predator–prey dynamics. Ecological Complexity 14:48–55.

Fujisawa, T., T. Koyama, S. Kakishima, J. R. Cooley, C. Simon, J. Yoshimura, and T. Sota. 2018. Triplicate parallel life cycle divergence despite gene flow in periodical cicadas. Communications Biology 1:26.

Hanski, I., L. Hansson, and H. Henttonen. 1991. Specialist predators, generalist predators, and the microtine rodent cycle. Journal of Animal Ecology 60:353–367.

Karban, R. 1981. Effects of local density on fecundity and mating speed for periodical cicadas. Oecologia 51:260–264.

———. 1982. Increased reproductive success at high densities and predator satiation for periodical cicadas. Ecology 63:321–328.

———. 1984. Opposite density effects of nymphal and adult mortality for periodical cicadas. Ecology 65:1656–1661.

———. 1997. Evolution of prolonged development: a life table analysis for periodical cicadas. American Naturalist 150:446–461.

Koenig, W. D., and A. M. Liebhold. 2005. Effects of periodical cicada emergences on abundance and synchrony of avian populations. Ecology 86:1873–1882.

———. 2013. Avian predation pressure as a potential driver of periodical cicada cycle length. American Naturalist 181:145–149.

Kritsky, G. 1987. An historical analysis of periodical cicadas in Indiana (Homoptera: Cicadidae). Pages 295–322 *in* Proceedings of the Indiana Academy of Science. Vol. 97.

Kye, G., J. Machta, K. C. Abbott, A. Hastings, W. Huffmyer, F. Ji, A. M. Liebhold, and J. C. Blackwood. 2021. Sharp boundary formation and invasion between spatially adjacent periodical cicada broods. Journal of Theoretical Biology 515:110600.

Liebhold, A. M., M. J. Bohne, and R. L. Lilja. 2013. Active periodical cicada broods of the United States. USDA Forest Service.

Lloyd, M., and H. S. Dybas. 1966. The periodical cicada problem. II. Evolution. Evolution 20:466–505.

Machta, J., J. C. Blackwood, A. Noble, A. M. Liebhold, and A. Hastings. 2019. A hybrid model for the population dynamics of periodical cicadas. Bulletin of Mathematical Biology 81:1122–1142.

Manter, J. A. 1974. Brood XI of the periodical cicada seems doomed. Memoirs of the Connecticut Entomological Society 1974:100–101.

Marshall, D. C. 2001. Periodical cicada (Homoptera: Cicadidae) life-cycle variations, the historical emergence record, and the geographic stability of brood distributions. Annals of the Entomological Society of America 94:386–399.

Nagel, R., C. Stainfield, C. Fox-Clarke, C. Toscani, J. Forcada, and J. I. Hoffman. 2021. Evidence for an Allee effect in a declining fur seal population. Proceedings of the Royal Society B 288:20202882.

Nelson, W. A., O. N. Bjørnstad, and T. Yamanaka. 2013. Recurrent insect outbreaks caused by temperature-driven changes in system stability. Science 341:796–799.

Simon, C., J. R. Cooley, R. Karban, and T. Sota. 2022. Advances in the evolution and ecology of 13- and 17-year periodical cicadas. Annual Review of Entomology 67:457–482.

Sota, T., S. Yamamoto, J. R. Cooley, K. B. R. Hill, C. Simon, and J. Yoshimura. 2013. Independent divergence of 13- and 17-y life cycles among three periodical cicada lineages. Proceedings of the National Academy of Sciences of the USA 110:6919–6924.

Speare, A. T. 1921. *Massospora cicadina* Peck: a fungous parasite of the periodical cicada. Mycologia 13:72–82.

von Ende, C. N. 1979. Fish predation, interspecific predation, and the distribution of two *Chaoborus* species. Ecology 60:119–128.

Williams, K. S., and C. Simon. 1995. The ecology, behavior, and evolution of periodical cicadas. Annual Review of Entomology 40:269–295.

Williams, K. S., K. G. Smith, and F. M. Stephen. 1993. Emergence of 13-yr periodical cicadas (Cicadidae: *Magicicada*): phenology, mortality, and predators satiation. Ecology 74:1143–1152.

Associate Editor: Benjamin M. Bolker
Editor: Jennifer A. Lau