Competition and Stragglers as Mediators of Developmental Synchrony in Periodical Cicadas

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ABSTRACT: Periodical cicadas are enigmatic organisms: broods spanning large spatial ranges consist of developmentally synchronized populations of 3–4 sympatric species that emerge as adults every 13 or 17 years. Only one brood typically occupies any single location, with well-defined boundaries separating distinct broods. The cause of such synchronous development remains uncertain, but it is known that synchronous emergence of large numbers of adults in a single year satiates predators, allowing a substantial fraction of emerging adults to survive long enough to reproduce. Competition among nymphs feeding on tree roots almost certainly plays a role in limiting populations. However, due to the difficulty of working with such long-lived subterranean life stages, the mechanisms governing competition in periodical cicadas have not been identified. A second process that may affect synchrony among periodical cicadas is their ability to delay or accelerate their emergence as adults by 1 year and accelerate it by 4 years (stragglers). We develop a nonlinear Leslie matrix–type model that describes cicada dynamics accounting for predation, competition, and stragglers. Using numerical simulations, we identify conditions that generate dynamics in which a single brood occupies a given geographical location. Our results show that while stragglers have the potential for introducing multiple sympatric broods, the interaction of interbrood competition with predation-driven Allee effects creates a system resistant to such invasions, and populations maintain developmental synchrony.

Keywords: synchrony, Allee effect, Leslie matrix, competitive exclusion.

Introduction

A fundamental problem in ecology is understanding the processes that determine the distribution and abundance of species. The concept that competition plays a central role in displacement of co-occurring species was recognized early by Darwin (1859) and, subsequently, has comprised a central theme in ecological theory (Armstrong and McGehee 1980; McPeek 2014). While the theory of competitive exclusion is considered a fundamental truism, the concept has also been criticized for being tautological or untestable (Levin 1970). Nevertheless, interspecific competition is considered to play an important role in shaping species ranges in many types of organisms (Araújo and Rozenfeld 2014).

A critical problem in evaluating the role of interspecific competition as a driver of the geographical range of species is the difficulty of measuring the strength of competition in actual interspecific interactions. While competition clearly plays a dominant role in the demography of many plants, its role is much less clear for other organisms, such as insect herbivores. Lawton and Strong Jr. (1981) concluded that competition among folivorous insects is generally weak or nonexistent. In contrast, Denno et al. (1995) identified more subtle competitive interactions that play important roles in herbivore communities, particularly within and among species of sap-feeding insects. However, the evidence is inconsistent for the importance of competition in delimiting the geographical overlap among species in general and herbivorous insects in particular.

Periodical cicadas (*Magicicada* spp.) are model organisms for probing the role of various processes (including competition) in preventing geographic overlap, whereas, in this case, it is different broods—not species—that do not overlap in their spatial distribution. In this system, cicada species exhibit life cycles of either 13 or 17 years in length, and individuals exist in broods distributed across large geographical areas (ranging from 50,000 to 500,000 km^2) over which all individuals are developmentally synchronized, emerging as adults in the same year. Each brood is comprised of the same 3–4 sympatric species, and even though

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they are comprised of individuals that are phenotypically identical, broods generally do not overlap. Instead, sharp boundaries exist between broods that are apparently stable over several generations (Williams and Simon 1995).

The phenomenon of nonoverlap of different broods of cicadas leads to the central questions we investigate here. Given that there are extensive boundaries separating different broods that are in close proximity, individuals of one brood could potentially be able to move to areas occupied by other broods that emerge at different times. Even though range exclusion is a spatial phenomenon, the role that competition plays in setting geographic boundaries and preventing overlap can be approached from a perspective that does not include space. Specifically, if a brood is rare, can it invade an existing brood? Or, phrased differently, what synchronizes the emergence of periodical cicadas?

The dramatic characteristics of synchronized emergence in periodical cicadas have been the subject of numerous theoretical studies (e.g., Yoshimura 1997; Webb 2001) since this behavior may shed light on a range of ecological processes and interactions. Yet considerable uncertainty remains about one of the most basic characteristics of these insects: Why are they periodical (i.e., developmentally synchronized)? It is clear that the synchronous emergence of large numbers of adults in a single year satiates predators and allows a substantial fraction of emerging adults to survive long enough to reproduce (Karban 1982). Cicada emergences trigger multiannual numerical responses in avian predators (Koenig and Liebhold 2013), but the absence of large numbers of adult cicadas in successive years prevents long-term increases in predator populations and allows cicada populations to escape from the effects of this numerical response. Yet it still remains somewhat of a mystery as to why broods remain geographically distinct with nonoverlapping brood boundaries. Dramatically, there is a virtual absence of locations where two or more broods exist sympatrically (Cooley et al. 2009). Explaining this observation is our primary goal here.

Understanding these extreme allopatric distributions of periodical cicada broods may yield insight into the drivers of allopatric distributions among different species. In the case of periodical cicadas, however, the various broods are essentially phenotypically identical so their allopatric distributions might be considered as an extreme case of competitive displacement. Competition among sympatric broods might play a crucial role in driving the existence of only a single brood at any location. Unfortunately, relatively little is known about either intra- or interbrood competition in periodical cicadas. Limited field studies by Karban (1984, 1997) document that competition among root-feeding nymphs of the same brood may be substantial, but the functional form of this competition is not clear, and essentially, nothing is known about competition among individuals at different stages of development (i.e., interbrood competition).

Here, we develop a biologically realistic model of periodical cicada population dynamics to explore the role of competition in exclusion versus coexistence of multiple sympatric broods. Our model is a nonlinear Leslie matrix–type model that describes cicada development and accounts for predation of adults and competition among nymphs of the same and different broods (Leslie 1945). While other theoretical investigations have also considered the role of competition and predation in driving the spatial distribution of periodical insects (e.g., Hoppensteadt and Keller 1976; Bulmer 1977; Behncke 2000), our study expands this framework in two primary ways. First, in the absence of better empirical evidence for the mechanisms driving competition, we consider multiple forms that make varying assumptions about the role of intra- and interbrood competition. Second, cicadas are capable of leaking to join other broods via delayed or accelerated development. An especially peculiar property of this phenomenon is that these stragglers have only been observed to emerge 1 year late, 1 year early, or 4 years early. Furthermore, the magnitude and rate of these leakage events also remain poorly understood (e.g., Heath 1968; Lloyd and White 1976; White and Lloyd 1979; White et al. 1979; Williams and Simon 1995; J. Machta, J. C. Blackwood, A. Noble, A. M. Liebhold, and A. Hastings, unpublished data). We therefore explicitly account for stragglers in our model and separately consider the dynamics in the presence of small leakage events that occur each year in addition to large leakage events that occur less frequently.

Using numerical simulations, we identify interactions that lead to a steady state in which only a single brood occupies a given geographical location. Further, we identify conditions under which a single brood resists invasion from another brood via delayed or accelerated development.

Model Formulation

We develop a nonlinear Leslie matrix–type model to capture the population dynamics of periodical cicadas. Two key features of our model are the inclusion of competition and leakage, or the ability of individuals to delay or accelerate their emergence. Given the associated dynamics, our primary goal is to determine the conditions required for the stable existence of only a single brood that synchronously emerges, as typically observed in natural populations.

Periodical cicadas are semelparous (only adults reproduce, and they die immediately afterward), and they are subject to competition as well as predation-driven Allee effects. We define the population density (per square meter) of each age i (where $i = 0, \ldots, 16$) at time t by $\tilde{x}_{i,t}$ and the survivorship (both density independent and competition driven) of individuals from age i to $i + 1$ as $s_i(\tilde{\mathbf{x}}_t)$. The surviving adult population that successfully emerges following competition (which, for now, we denote as $\tilde{x}_e := s_{16}(\tilde{\mathbf{x}}_t)\tilde{x}_{16,t}$)

has an overall fecundity of $\mathcal{R}(\tilde{x}_e)$. Under this construction, we are assuming that the vector of cicada densities captures population sizes at the beginning of each respective age class. Our model is defined by

$$\begin{bmatrix} \tilde{x}_{0,t+1} \\ \tilde{x}_{1,t+1} \\ \tilde{x}_{2,t+1} \\ \vdots \\ \tilde{x}_{16,t+1} \end{bmatrix} = \begin{bmatrix} 0 & 0 & \dots & 0 & \mathcal{R}(\tilde{x}_e)s_{16}(\tilde{x}_t) \\ s_0(\tilde{x}_t) & 0 & \dots & 0 & 0 \\ 0 & s_1(\tilde{x}_t) & \dots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \dots & s_{15}(\tilde{\mathbf{x}}_t) & 0 \end{bmatrix} \begin{bmatrix} \tilde{x}_{0,t} \\ \tilde{x}_{1,t} \\ \tilde{x}_{2,t} \\ \vdots \\ \tilde{x}_{16,t} \end{bmatrix}, \tag{1}$$

where $\tilde{\mathbf{x}}_t$ is a vector of the population density for each age class at time t. Hereafter, we refer to the Leslie matrix in our model as $\mathbf{L}_t$. More succinctly, this can be written as

$$\tilde{x}_{0,t+1} = \mathcal{R}(\tilde{x}_e)\tilde{x}_e, \tag{2}$$

$$\tilde{x}_{i,t+1} = s_{i-1}(\tilde{\mathbf{x}}_t)\tilde{x}_{i-1,t}, \tag{3}$$

where $i = 1, \dots, 16$, or in vector form as

$$\tilde{\mathbf{x}}_{t+1} = \mathbf{L}_t\tilde{\mathbf{x}}_t. \tag{4}$$

To construct $\mathcal{R}$, we assume that emerging adults first undergo competition and have density-independent survival (e.g., due to background mortality) and that they then emerge, face predation-driven Allee effects, and finally reproduce. (A schematic representation of how our model captures the order of events in the cicada life cycle is provided in fig. 1*A*.) A more detailed treatment of the survivorship (competition) function is provided in the following section.

We assume that predation follows a standard Holling type II functional response, which accounts for predator satiation at high densities of cicadas (Karban 1982, 1984). We define $P_{\max}$ as the maximum number of cicadas per square meter that can be killed in a given year by predation, and we define A_{half} as the adult population density at which exactly $P_{\max}/2$ cicadas are killed per square meter. Assuming that the per capita fecundity for individuals that escape predation is m, the total expected reproductive output per adult is given by

$$\mathcal{R}(\tilde{x}_e) = \max\left[0, m\left(1 - \frac{P_{\max}}{A_{\text{half}} + \tilde{x}_e}\right)\right], \tag{5}$$

where the term in parentheses is the proportion of cicadas escaping predation. This creates a strong Allee effect because if the avian population is capable of consuming more adult cicadas than are present, the cicada population is set to zero. We used data from Karban (1984) to estimate the parameter values for m, $P_{\max}$, and A_{half} (app. A; apps. A–D are available online).

It is convenient to nondimensionalize the population density so that

$$x_{i,t} = \frac{\tilde{x}_{i,t}}{A_{\text{half}}}$$

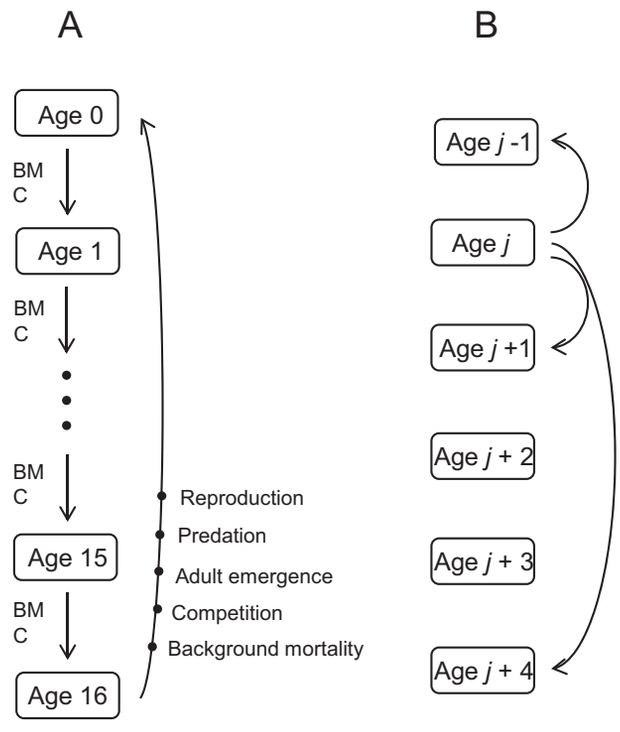

Figure 1: Schematic representation of the cicada life cycle as captured in our model. *A*, Events captured in the nonlinear Leslie matrix–type $\mathbf{L}_t$: background mortality (or density-independent survivorship), competition, adult emergence, predation, and reproduction. Background mortality and competition are abbreviated as BM and C, respectively, for juvenile age classes. *B*, The three possible types of leakage events can occur for individuals in the jth age class: 1-year accelerations and delays and 4-year accelerations.

for all i. Under this nondimensionalization, population density is scaled so that if $x_e = 1$, then $P_{\max}/2$ adult cicadas are killed per square meter by predation. Now, the reproduction term simplifies to

$$\mathcal{R}(x_e) = \max\left[0, m\left(1 - \frac{P}{1 + x_e}\right)\right], \tag{6}$$

where $P = P_{\max}/A_{\text{half}}$. A summary of all parameters and their values is provided in table 1.

Forms of Competition

In this section, we define the survivorship terms, $s_i(\tilde{\mathbf{x}}_t)$, which capture both density-independent survival and competition. For simplicity, we assume there is a fixed proportion, s, of survival between generations that accounts for any density-independent background mortality (parameterized using Karban 1997; see app. A). In contrast to reproduction, little is known about the mechanisms driving competition among nymphs in periodical cicadas. There-

Table 1: Summary of known and estimated parameters

Parameter	Definition	Default value
P_{max}	Maximum adult cicadas annually killed by predation	3.929[a]
A_{half}	Adult population density at which $P_{max}/2$ cicadas killed	3.285[a]
P	Dimensionless quantity P_{max}/A_{half}	1.196
m	Offspring per surviving adult cicada	56.18[a]
ϕ	Proportion of cicadas that leak for each form of leakage	Varies
s	Density-independent survivorship	.915[b]
α_{ij}	Competition coefficient	Varies

[a] Source: Karban 1984.
[b] Source: Karban 1997.

fore, we introduce and analyze four different functional forms for competition: (1) all-to-all competition, (2) early instar competition only, (3) body-size-dependent competition, and (4) intrabrood competition only.

We make the most parsimonious assumption for all-to-all competition: all cicadas compete, and both inter- and intrabrood competition are constant among all broods. We assume that competition is captured by an inverse exponential of a weighted sum of the densities of each juvenile age class so that greater densities result in lower survivorship. Given that competition occurs among all cicadas, the proportion of cicadas of age $i - 1$ surviving to age i is given by

$$s_{i-1}(\tilde{x}_t) = s \exp\left(-\sum_{j=0}^{16} \tilde{\alpha}_{ij}\tilde{x}_{j,t}\right) \tag{7}$$

for $i = 1, \ldots, 17$, where $\tilde{\alpha}_{ij} \geq 0$ is the competition coefficient capturing the effect of individuals of age j on those of age i.

We rewrite these equations in terms of the nondimensional variable $x_{i,t}$, as defined in the previous section, and to simplify further, we let $\alpha_{ij} = \tilde{\alpha}_{ij}A_{half}$. Because there are limited data available to parameterize the competition coefficient, we also assume it is a single constant for all i and j; consequently, we define $\alpha = \alpha_{ij}$. Now, equation (7) can be written as

$$s_{i-1}(\mathbf{x}_t) = s \exp\left(-\sum_{j=0}^{16} \alpha x_{j,t}\right). \tag{8}$$

We adopt this notation for the remainder of this article.

Now that we have a general structure for competition, we can consider alternative forms that may also be biologically plausible. For example, there is some evidence suggesting that the bulk of underground competition and related nymphal mortality occurs in the earliest years of the cicada life cycle, during the first two instars (first 3 years of a cicada's life cycle; White and Lloyd 1979; Karban 1984; Williams and Simon 1995). Under the assumption that competition occurs only during the first two instars, we can simplify the competition term to

$$s_{i-1}(\mathbf{x}_t) = s \exp\left(-\sum_{j=0}^{2} \alpha x_{j,t}\right) \tag{9}$$

for $i = 1, 2, 3$, and it is simply equal to s otherwise.

Thus far, we have assumed that the competition coefficients are equal for all competitive interactions. However, the body size of cicadas increases dramatically between the first and final instar, and it is possible that larger insects are better competitors. Therefore, we assume that the competitive ability of nymphs increases with body size. For simplicity, we assume that body size increases linearly between years and that competitive advantage is proportional to body size. A simple way to capture this effect is to let

$$s_{i-1}(\mathbf{x}_t) = s \exp\left(-\sum_{j=0}^{16} \alpha\left(1 + \frac{j-i}{16}\right)x_{j-1,t}\right). \tag{10}$$

We additionally considered a nonlinear form of body-size-dependent competition (app. C). The results are qualitatively similar to those associated with the linear form.

Finally, we considered the case of only intrabrood competition so that

$$s_{i-1}(\mathbf{x}_t) = s \exp(-\alpha x_{i-1,t}). \tag{11}$$

Note that we have used the symbol α to denote the competition coefficient for each functional form, but the mathematical interpretation of α varies between forms of competition.

Tracking the Emergence of Stragglers

A unique aspect of periodical cicadas is that individuals do not always stay in their original broods, with studies reporting small to large numbers of 17-year periodical cicadas emerging 4 years early, 1 year early, or 1 year late. For cicadas of ages 2–13, we assume that a proportion of each age class may either accelerate emergence by 1 year, delay emergence by 1 year, or accelerate emergence by 4 years. In the absence

of data to estimate these proportions as well as to simplify our parameterization, we assume that leakage occurs with a fixed proportion ϕ among all three forms of leakage.

We implement leakage under the assumption that it is not cyclic. For example, a 14-year-old cicada cannot accelerate its emergence by 4 years to return to the 1-year-old age class and skip emergence altogether. Moreover, a 14-year-old cicada cannot enter a hypothetical 18th age class; therefore, a cicada in its 14th year can only accelerate or delay by 1 year. The same properties apply to 15- and 16-year-old cicadas. Using a similar justification, 17-year-old cicadas are additionally prohibited from accelerating emergence by 1 year. Finally, 1-year-old cicadas are barred from delaying emergence by 1 year, which would place them either back into the 17th age class or into a hypothetical 0th age class.

To capture this mathematically, we define a leakage matrix, **D**, such that

$$\mathbf{x}_{t+1} = \mathbf{D}\mathbf{L}_t\mathbf{x}_t. \tag{12}$$

Here **D** is a sparse matrix. The ith entry along the main diagonal captures the proportion of cicadas that do not leak out of the ith age class between years t and $t + 1$. Then, the diagonals one above, one below, and four above the main diagonal capture the proportions of cicadas in the ith age class that move into age classes $i + 1$, $i - 1$, and $i + 4$, respectively, between years t and $t + 1$. We define the nonzero entries of **D** as

$$\begin{aligned} d_{1,1} &= 1 - 2\phi, \\ d_{i,i} &= 1 - 3\phi, \text{ for } 2 \le i \le 13, \\ d_{i,i} &= 1 - 2\phi, \text{ for } 14 \le i \le 16, \\ d_{17,17} &= 1 - \phi, \\ d_{i+4,i} &= \phi, \text{ for } 1 \le i \le 13, \\ d_{i+1,i} &= \phi, \text{ for } 1 \le i \le 16, \\ d_{i-1,i} &= \phi, \text{ for } 2 \le i \le 17. \end{aligned} \tag{13}$$

Notice that when $\phi = 0$ (i.e., there is no leakage), **D** reduces to the 17×17 identity matrix (see fig. 1*B* for a schematic representation of leakage).

The biological underpinnings of leakage remain largely unknown, and most hypotheses regarding the timing and mechanisms of leakage are purely theoretical or speculative. For example, it is not known whether there are small amounts of all types of leakage each year or if large leakage events occur but more sporadically in time. Therefore, we implement leakage in two ways: (1) leakage of all types occurs each year at low levels and (2) a single large leakage event of only one type occurs.

Simulations

Due to the uncertainty surrounding the magnitude and frequency of leakage, we first analyze the general properties of the dynamics when there is a small amount of leakage during each year. We use this as a means of determining the conditions under which there is a stable state in which a single brood exists (i.e., the state that is most consistent with natural populations). We then consider the dynamics when there is a single large leakage event and determine when the new leakage brood can competitively eliminate the original brood.

In all simulations, the initial conditions are fixed so that there is a single brood populated with 10 individuals. We also performed the simulations with 100 individuals initially in one brood, and the results were nearly identical. For all results, unless otherwise stated, we ran the model for 12,002 years so that it is both divisible by 17 (and therefore simulates an integer number of complete generations) and representative of the time span in which periodical cicadas have existed in their North American range (current broods are believed to have originated just after the last glaciation; Lloyd and Dybas 1966). This also provides a long time period for transients to decay.

All of our figures and conclusions are based on the final 204 years of each simulation, a number that was chosen to again be divisible by 17. Moreover, when our objective is to determine conditions necessary for a single-brood steady state, we treat this 204-year period as both a representative snapshot of recent history—capturing the years in which cicada emergences have been empirically documented—and as a quasi equilibrium. When considering a single large leakage event, we assume that the leakage pulse occurs at the beginning of the final 204 years of simulation. We then analyze how that pulse propagates in the immediate 12 cicada generations (or 204 years) that follow, which is again a time frame that is representative of recent history. Finally, we note that in simulations that require computing the number of broods present (i.e., figs. 2*A*, 3, 4), we count only broods that are large enough to overcome the predation-driven Allee effect.

Results

The results are broken into two main sections. In the first, we analyze the dynamics under the assumption of steady leakage and determine a phase diagram in the leakage versus competition plane. We find regions that correspond to population extinction, single brood persistence, and the persistence of multiple broods. In the subsequent section, we use our phase diagram to identify competition and leakage parameter values that lead to a single-brood stable state (i.e., parameters that are most likely to be consistent with natural populations) and then assess the dynamics when leakage events are rare. That is, we analyze the population dynamics following a single large leakage event. In this scenario, we also determine the magnitude of a leakage event

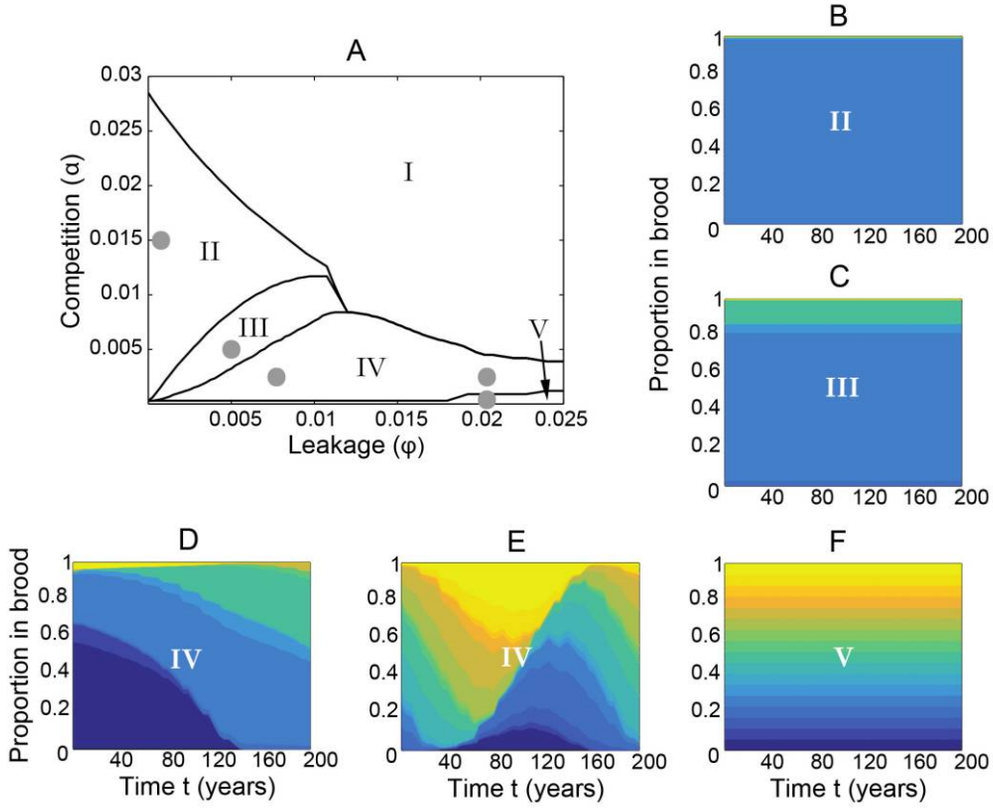

Figure 2: *A*, Phase diagram of the qualitatively different regions of parameter space as the magnitude of competition (α) and leakage (ϕ) are varied. This figure displays the results for all-to-all competition, and the other functional forms of competition are provided in appendix B. Region I corresponds to population extinction, region II is single-brood persistence, region III is steady coexistence of multiple broods, region IV is successional multiple-brood coexistence, and region V is steady all-brood persistence. *B–F*, Time series of the proportion of the total population for each brood (distinct colors are different broods) in each of the qualitatively distinct regions from *A*. The gray circles in *A* represent the parameter combinations used in *B–F*. *B*, Time series for region II. *C*, Region III. *D*, Leftmost circle in region IV. *E*, Rightmost circle in region IV. *F*, Time series for region V. Multiple time series are shown for region IV to demonstrate that within this region, larger leakage values lead to faster changes in brood dominance. In all simulations, a single brood is assumed to initially be populated with a density of 10 cicadas per square meter, and all other broods initially have no individuals. All time series shown are for the final 204 years (12 generations) of the simulations and are displayed using a moving average of 17 years to eliminate spikes in population sizes following reproduction.

required to change the stability so that the leakage brood displaces the original brood. This final analysis may provide insight into the conditions necessary for a brood to expand its spatial range and therefore is most relevant at the spatial boundaries between broods.

Interactions between Competition and Steady Leakage

We investigate how the dominance of a single brood is affected by the relative strength of leakage (ϕ) and competition (α) for each form of competition. In particular, we identify the number of broods present in the final 12 generations of each simulation for a range of α and ϕ values.

We create a phase diagram by dividing $\alpha - \phi$ parameter space into five qualitatively distinct regions: (I) population extinction, (II) single-brood steady state, (III) steady multiple-brood coexistence, (IV) successional multiple-brood coexistence, and (V) steady all-brood coexistence.

The first region is self-explanatory. Region II corresponds to a single brood persisting with a fixed population size when averaged over a complete generation. Region III is similar to II, with the exception that multiple broods coexist, with one of the broods dominating the majority of the total population size. In this region, at most four broods coexist; that is, some combination of the original brood and broods created from leakage from the original brood are able to overcome Allee effects and persist. In region IV, broods created by leakage are able to grow over time and eventually outcompete other broods, leading to periodic changes in the most prevalent brood over time. In region V, all broods are

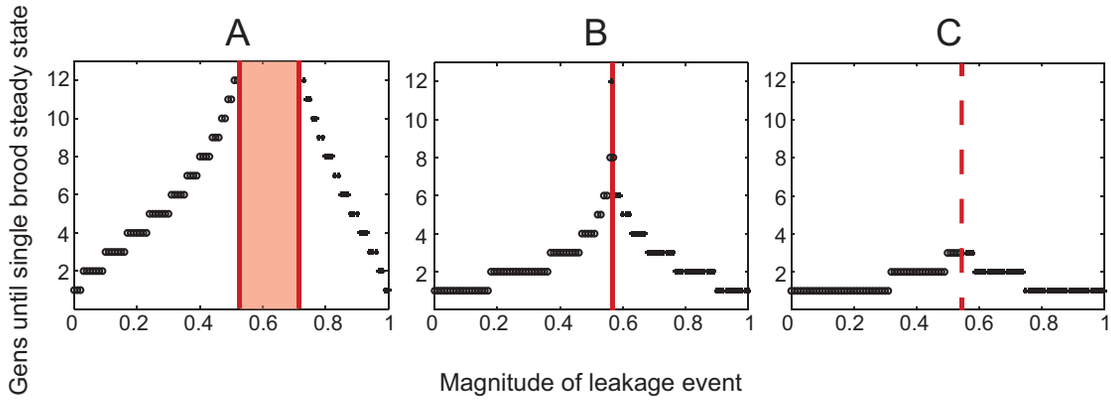

Figure 3: Dynamics following a leakage event. The leakage brood has a 1-year delay, and competition is all to all. The populations are followed for 12 generations following the leakage event. For each subplot, the fraction of the population emerging late is shown on the horizontal axis, and the number of generations until only a single brood is present is shown on the vertical axis. In each figure, the circles (to the left of the vertical red line) correspond to dynamics in which the original (or parent) brood takes over, and the height of the circle corresponds to the number of generations until the leakage brood disappears. Crosses represent dynamics in which the new (leakage or daughter) brood takes over, and the height of the cross is the number of generations until the parent brood disappears. The three subplots correspond to three values of competition: $\alpha = 0.001$ (*A*), $\alpha = 0.01$ (*B*), and $\alpha = 0.022$ (*C*). In *A*, competition is weak enough so that two broods can coexist for more than 12 generations over a range of leakage magnitudes indicated by the red shaded region. In *B*, two-brood coexistence persists for more than 12 generations only in a narrow range indicated by the vertical red line. In *C*, there is no unstable two-brood equilibrium and two-brood coexistence decays in three or fewer generations. These plots also demonstrate how the results shown in figure 4 are obtained.

present with equal average population. Figure 2 shows the resulting phase diagram for all-to-all competition, and the other phase diagrams are provided in appendix B. To numerically separate region IV from regions V and III, we find the magnitude of the variance for each of the broods following reproduction across the final 12 generations of the simulations. We then average across the resulting variances found for each brood. Region IV is assumed to contain all parameter values in which the mean variance was greater than the mean population size. While this threshold is chosen somewhat arbitrarily, the difference in variance between regions is quite large (as can be observed in fig. 2*C*–2*F*), and many other thresholds would work as well.

Each of the six forms of competition exhibit population extinction for sufficiently high competition (region I) and the existence of the single-brood steady state for relatively low levels of leakage over a range of competition values (region II). Machta et al. (unpublished data) approximated a Leslie matrix–type model of periodical cicadas using a continuum model. In that analysis, a similar threshold was identified for competition that divides the single-brood steady state from population extinction. In region II, leakage is low enough so that predation-driven Allee effects and competition successfully eliminate stragglers (fig. 2*B*). As leakage increases, the range of competition values that lead to a single-brood steady state shrinks. In particular, competition needs to be at an intermediate level: if competition is too high, then population extinction will occur, and if competition is too low, then leakage broods can stably coexist (e.g., as in region III; fig. 2*C*).

With the exception of the case with intrabrood competition only, multiple broods coexist and the dominant brood (s) change over time when there are relatively low levels of competition and substantial leakage (region IV; fig. 2*D*, 2*E*). These successional dynamics are seeded by leakage and within-generation changes in brood size (through, e.g., reproduction) that lead to competitive advantages. Within this region, the timescale in which one brood succeeds another decreases as leakage increases. In this case, high levels of leakage are able to seed within-generation changes in brood size at a faster rate. For very low levels of competition, the dynamics leading to coexistence are dominated by leakage with minimal effects from competition. Here, all 17 broods coexist with little variation in population size (fig. 2*F*).

The phase diagram for intrabrood-only competition differs slightly from the other forms of competition in that only three of the regions described above are present: extinction, the single-brood state, and coexistence of all broods (see app. B for phase diagram). This follows from the assumption that there is no interbrood competition; as long as competition is sufficiently weak and leakage sufficiently high, then all broods eventually become populated and their population size is not impacted by any other broods.

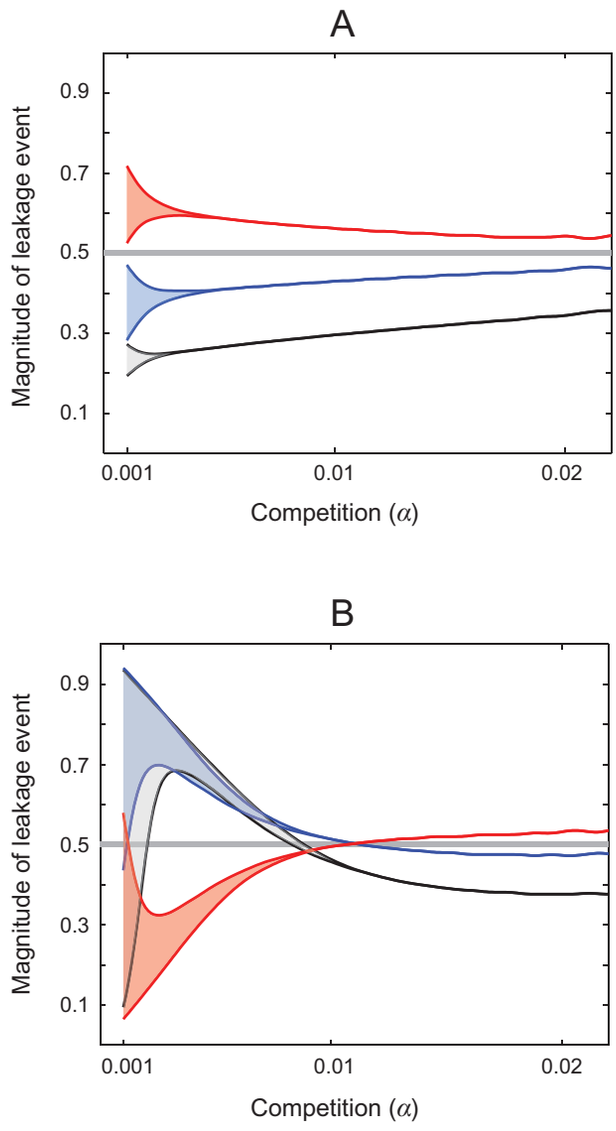

Figure 4: Magnitude of leakage event required to replace the parent brood with the leakage brood. In each subplot and for each color, the region above a line (or region) of a given color corresponds to dominance by the leakage brood and elimination of the parent brood within 12 generations. The region below the line (or region) corresponds to dominance of the parent brood and elimination of the leakage brood within 12 generations. Blue represents leakage events with a 1-year acceleration, red represents a 1-year delay, and black represents a 4-year acceleration. In the shaded regions, the parent and leakage broods coexist for more than 12 generations following the leakage event. *A*, Results for all-to-all competition. *B*, Linear body size dependence.

Dynamic Impacts of Isolated Large Leakage Events

We now assume that leakage does not occur each year (app. D provides a sensitivity analysis that assumes there is a small amount of annual leakage); instead, we assume that there is a single large leakage event and examine the dynamics that follow. Here, our goals are fourfold: (1) identify the magnitude of the leakage event required for the leakage brood to dominate and drive the original brood to extinction, (2) determine how the findings for goal 1 change as the magnitude of competition increases, (3) characterize the differences between each type of leakage (1-year acceleration or delay and 4-year acceleration), and (4) determine how goals 1–3 differ between forms of competition.

For each relevant value of α—as determined by the values in the phase diagrams that correspond to a single-brood steady state in the absence of annual leakage—we vary the magnitude of the leakage event as measured by the proportion of the original brood that emerges as stragglers. In other words, a magnitude of zero implies that there was no leakage, and a value of one implies that the entire original brood emerged together but either early or late. We then determine the number of complete generations required for either the original brood to outcompete the leakage brood and drive it to extinction, or vice versa. We again consider the first 12 generations (or 204 years) following the leakage event; therefore, while it is possible that competitive exclusion takes more than 12 generations, we end all simulations after the 12th generation.

Figure 3 summarizes the dynamics following a large leakage event where the stragglers appear 1 year late. Each subplot shows, for a given competition strength, the number of generations until only a single brood is present as a function of the magnitude of the leakage event. If the leakage magnitude is sufficiently small (indicated by circles in the figure), the surviving brood is the original parent brood, while if the magnitude exceeds a threshold, the leakage brood takes over. For sufficiently weak competition, we have shown elsewhere that there is an unstable two-brood equilibrium (Machta et al., unpublished data). The long coexistence times visible for weak competition in figure 3*A*, 3*B* reflect this unstable equilibrium. The shaded region in figure 3*A* corresponds to coexistence times exceeding 12 generations. The coexistence time diverges exactly at the unstable equilibrium, as indicated by the vertical red line in figure 3*B*. However, the addition of stochasticity to the model will remove this divergence. On the other hand, if the competition exceeds a critical value, the unstable two-brood equilibrium ceases to exist and the coexistence time remains small for all leakage fractions, as seen in figure 3*C*. The dashed red line in this subplot indicates the magnitude of leakage for which the leakage brood first takes over.

The location of these peaks (associated with the shaded red regions and vertical red lines) is summarized for each competition and leakage type as α is varied (fig. 4). While an initial hypothesis might be that the dominant brood switches from the original to the leakage brood when there is a leakage event great than magnitude 0.5—that is, more

than half of the brood leaks—the dynamics are more subtle due to interactions between competition, leakage, and reproduction. For all-to-all competition, the magnitude of the leakage event required for the leakage brood to dominate for a 1-year delay is greater than 0.5, and it is less than 0.5 for a 1-year acceleration (fig. 4*A*). This arises because the brood that is closer to reproduction eventually has a competitive advantage: the more advanced brood reproduces first and has a corresponding spike in population size. In the all-to-all scenario, first-instar nymphs are equally as competitive as fifth-instar nymphs, allowing the brood that emerges first to ultimately dominate. Four-year accelerations behave similarly to 1-year accelerations in that a leakage event of less then 0.5 can allow the leakage brood to outcompete the original brood. However, these individuals emerge even earlier than the original brood and therefore require even less of a leakage event compared to that required for a 1-year acceleration. For all three types of leakage, these effects are dampened as the role of competition increases. This result follows because increasing levels of competition weaken the effects of a large leakage event, bringing the magnitude required to cause a change in dominance closer to 0.5.

When competitive ability depends linearly on body size (and, therefore, age), the magnitude of the leakage event required for the leakage brood to outcompete the original brood substantially depends on the magnitude of competition. When competition is low, for example, the size of a 1-year acceleration has to be much greater than 0.5 for a switch in dominance to occur. In contrast to the all-to-all case, the competitive advantage of the accelerated brood is dwarfed by body size dependence. In this case, the accelerated brood will reproduce first and have an advantage because of the increase in population size. However, during that same year, the original population is in their 16th year and has a major competitive advantage over the 1-year nymphs. This competitive advantage of larger-bodied insects weakens as the magnitude of competition increases; when α is sufficiently high, the smaller individuals can compete well enough to eventually dominate. For large values of α, body size dependence mirrors that of all-to-all competition (fig. 3*B*). The results corresponding to 4-year accelerations are similar to that of 1-year accelerations, with more dramatic changes in the magnitude of the leakage event required to cause a change in brood dominance. A similar argument can be made for 1-year delays, which exhibit the opposite pattern as compared to 1-year accelerations. Nonlinear body size dependence in competition yields nearly identical results to linear body size dependence (see app. C).

The magnitude of a leakage event required to cause a change in brood dominance directly depends on the form of leakage when there is only early instar competition. For example, the leakage brood corresponding to a 1-year acceleration will almost always go extinct. This result follows from the assumption that individuals in their first two instars cannot compete with other instars. In this scenario, when the leakage brood reproduces (and therefore has a competitive advantage over the original brood due to a spike in population size), it cannot compete with the original brood. In contrast, the original brood reproduces and competes with the leakage brood after the leakage brood has already undergone 1 year of competition. From this same argument, the leakage brood arising from a 1-year delay almost always eventually outcompetes the original brood. The only time this argument fails is when competition is very low ($\alpha < 0.002$), and the two broods coexist for more than 12 generations. Four-year accelerations, on the other hand, always lead to coexistence of the original and leakage brood. In this case, the two broods are far enough apart in age that they never compete.

Finally, the results for intrabrood competition only are straightforward and a direct consequence of the form of competition implemented. In particular, all leakage events lead to stable coexistence of both broods as long as their population sizes are large enough to overcome the Allee effects (results not shown). This result follows because the leakage brood and the original brood never compete with each other.

Discussion

Understanding the processes that determine the distribution of species across space remains a fundamental goal in ecology. The question of what leads to nonoverlapping spatial distributions of different species is one particular problem in this area. Periodical cicadas, with broods that emerge at different times, are analogous to different species and provide a useful window into the processes that lead to disjoint spatial distributions.

Additionally, the synchronized emergence of different cicada broods can be viewed as one of the most dramatic examples of large-scale spatial synchrony in ecology. Both views of the unique behavior of cicada populations suggest that a clear understanding of the processes that produce observed dynamics of cicadas may shed light on fundamental ecological questions. There are both many examples of spatial synchrony of ecological populations, though perhaps not quite so dramatic, and examples of organisms that reproduce just once and therefore may have synchronized reproduction over space. Given the ubiquity of these phenomena, models that explain the presence of synchronized emergence in cicadas should provide insights into general ecological questions by highlighting the processes that lead to synchrony and exclusion.

The term "semelparous" is used to refer to organisms such as periodical cicadas, salmon, and many plants in which re-

production is limited to a brief period at the end of the life cycle. This phenomenon is relatively common among several taxa of insects. In most species, populations are composed of a mixture of cohorts developing together, but in a small fraction of semelparous insects, development is completely synchronous with adults appearing at the same time. These insects are referred to as periodic, and the causes of this synchrony are poorly understood (Heliövaara et al. 1994). Using matrix models similar to those used here, previous studies have explored how different forms of competition may lead to stability among developmental cohorts or even to exclusion of all but a single cohort (developmental synchrony, i.e., periodic behavior), such as exists for periodical cicadas (Davydova et al. 2005; Mjølhus et al. 2005). However none of these studies has considered how such stability is affected by leakage between cohorts. The analyses presented here on either recurrent or pulsed leakage events that characterize periodical cicada populations thus are quite unique.

While multiple populations comprise broods of a given life span (13 or 17 years), the allopatric distribution of these broods provides a model system for probing how competition may facilitate exclusion. We developed and analyzed nonlinear Leslie matrix–type models that describe the dynamics of cicadas in an attempt to better understand the mechanisms driving synchronous emergence—that is, exclusion of other developmental cohorts by a single brood. While our results provide insight into the complex processes governing cicada dynamics, considerable uncertainty remains. Here, we focus on the two main processes that are central to cicada population dynamics: competition and leakage.

The analysis here demonstrates the close interplay between competition and Allee effects that maintains the periodical (synchronized) life history observed in periodical cicadas. However, Lloyd and Dybas (1966) proposed that the array of periodical cicada broods that currently exist in eastern North America descended from a single ancestral brood, splitting off as straggler populations, and this theory remains widely accepted. If this theory is correct, then one of the challenges that remains for understanding this system is elucidation of how leakage occasionally might result in a portion of a brood synchronizing their emergence on a different year, overcoming the processes documented here that prevent such a switch.

Results presented here demonstrate that though periodic population behavior can emerge under a variety of types of competition, such competition must be sufficiently strong to maintain the existence of only a single brood at any location. Unfortunately, very little mechanistic information exists about competitive interactions among periodical cicada nymphs (Karban 1984, 1997). Thus, future studies of both intra- and interbrood competition would help clarify mechanisms responsible for developmental synchrony in this system.

Among the most similar previous studies are those on salmon species in which almost all females return to spawn the same year, a behavior called obligate semelparous. The focus of these studies has been on the role of both stochastic events and competition in these semelparous species, but in most salmon populations, more than one year class coexists at a given location, and the goal is to explain why one class is much more common (Worden et al. 2010; White et al. 2014). As in the cicada case, individuals may return to spawn at different ages; so why does one age class often dominate? Further investigations contrasting these two cases as well as similar dynamics of some flowering plants should prove interesting.

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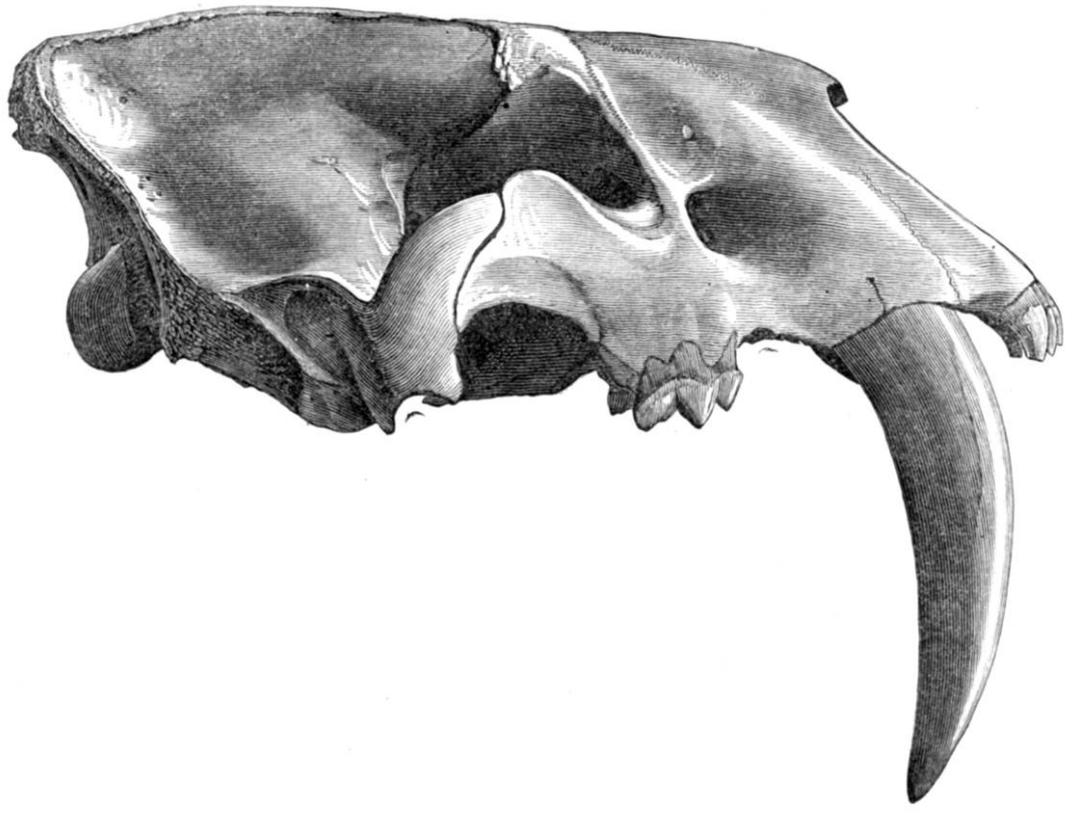

"The known species belong to the Pliocene period, and were the cotemporaries of the gigantic sloths and *Glyptodons*, which at that time ranged over the entire American continent. Their powerful limbs terminated by immense claws, bespeak for them exceptional force in striking and tearing their prey, and the long compressed canine teeth are well adapted for penetrating the tough hides and muscles of the large Edentata, which were doubtless their food." Figured: *Smilodon necator* Gervais. From "On the Extinct Cats of America" by E. D. Cope (*The American Naturalist*, 1880, 12:833–858).