Plague or Prediction?

by Meredith Greer

In the summer of 2007, for the first time, the MAA will hold MathFest in coordination with the annual meeting of the Society for Mathematical Biology (SMB). This will be an outstanding opportunity for members of each group to learn more about the other. Looking ahead to that event, I hope to pique your interest with a description of just one of many fascinating biomathematical models.

Is a swarm of locusts a biblical plague, or a natural and mathematically predictable occurrence? Consider the observations made by P. Collinson [1] in 1764.

> In Pennsylvania the Cicada is seen annually, but not in such numbers as to be remarkable; but at certain periods, of 14 or 15 years distance, they come forth in such great swarms, that the people have given them the name of *Locusts*. About the latter end of April these Cicadae come near the surface: this is known, by the hogs routing after them. They creep out of the ground, near the roots of trees, in such numbers, that in some places, the earth is so full of holes, it is like an honey-comb.

Biologists and mathematicians alike have studied, and continue to study, the *Magicicada* phenomenon. Several species of this type of cicada emerge periodically, every 13 or 17 years. The cicadas synchronize their emergence: they all appear at the same time, within a few busy and very loud weeks, and they do not show themselves during the intervening years. Let's take a math modeling look at cicada behavior.

To put together appropriate equations, we need to first understand the basic life cycle of the cicada. An adult cicada lives a few weeks, during which time it lays eggs. The eggs hatch, producing nymphs, the young form of the cicada. These nymphs burrow underground and live around tree roots for most of their lifespan - typically 3, 4, 7, 13, or 17 years, depending on their species. When they near the end of their lifespan, they emerge as adults, lay eggs, and the cycle begins anew.

Now we can describe the four functions that are relevant in our model.

We refer to the current year as year t. Then the number of new nymphs that became established underground k years ago is $n(t-k)$. The number of predators in year t is $p(t)$. There may already be some nymphs living underground, and there are limited resources and space to go around, so each year there is a limited number of new nymphs that can be supported. We call this the carrying capacity in year t, and denote it $c(t)$. We also need to refer to the number of new nymphs actually produced in year t, $N(t)$. Due to carrying capacity constraints, the number becoming established underground, $n(t)$, may be less than the total number produced, $N(t)$, so we will have equations for each.

Here are the parameters we will consider in our discussion of cicadas. Nymphs live underground for most of their lifespan. Not all of them survive from each year to the next. We will assume that, as each year passes, the same percentage of living nymphs survives to the next year. We call this percentage s.

Predators can't live forever either. They also, of course, produce young. We combine their death and birth rates, setting aside any effects due to cicadas, into the parameter r.

When adult cicadas emerge, predators have more food than usual, and they produce more young. A rate a relates the number of adult cicadas to the number of extra predators produced.

The ground itself has an intrinsic carrying capacity, starting with no nymphs present. This number is related to but distinct from $c(t)$, which can vary each year depending on already-established nymphs. We call the total intrinsic carrying capacity D.

The lifespan of the cicadas is denoted by k. Remember that k can take values from 3 to 17 years. We will vary this parameter to try to see which cicada species exhibit synchronized emergence.

The number of eggs laid and hatched depends on the number of adult cicadas that emerge. We will use a constant of fecundity, f, to represent this.

There is one added wrinkle: we know that many functions have negative outputs. Since our functions represent things like the number of cicadas or the number of predators, negative results do not make sense. We simply will not let them happen! To prevent negatives, use the function

$$[x]_+ = \begin{cases} x & \text{if} \quad x \geq 0 \\ 0 & \text{if} \quad x < 0 \end{cases}.$$

In words, this function takes any negative quantities and replaces them with zeroes.

Now we are ready to write equations.

Predators: $p(t) = rp(t-1) + as^k n(t-k-1)$. Notice that the number of predators depends on two things. First, $rp(t-1)$ is the normal number of predators expected this year, based on last year's number of predators. Second, there may be extra predators if any adult cicadas emerged last year. Since the cicada lifespan is k, any cicadas that emerge in year $t-1$ are those that were new k years before that, in year $t-k-1$. Only the proportion s survived as each of those k years passed to the next, and we multiply $n(t-k-1)$ by s^k to represent that. The parameter a connects this number of emerging cicadas to the number of extra predators produced. Available carrying capacity:

$$c(t) = \left[D - \sum_{j-1}^{k-1} s^j n(t-j) \right]_+ .$$

Each year, the carrying capacity is the total possible carrying capacity minus the sum of all the nymphs already underground. We do not allow this number to be less than zero.

New nymphs produced: $N(t) = [S^k n(t-k) - p(t)]_+ \cdot f$. All living adults emerge k years after they were produced. Predators eat some of them. If a positive number remain, they produce some multiple f of eggs.

New nymphs established underground: $n(t) = \min(N(t), c(t))$. This is the minimum of the new nymphs produced and the available carrying capacity.

All these equations and parameters are similar to those used by Hoppensteadt and Keller [2], who modeled cicadas thirty years ago. We share the parameters they chose: $s = r = 0.95$, $a = 0.042$, $D = 10000$, and $f = 10$. We start by establishing 100 new nymphs underground for each of k years, then allow all four equations to interact. The results, displayed as graphs, show us that indeed the cicada populations with lifespans of 13 or 17 years move — rather quickly! — toward synchronized emergence. Those with shorter lifespans move the other way: a fraction of the population emerges each year.

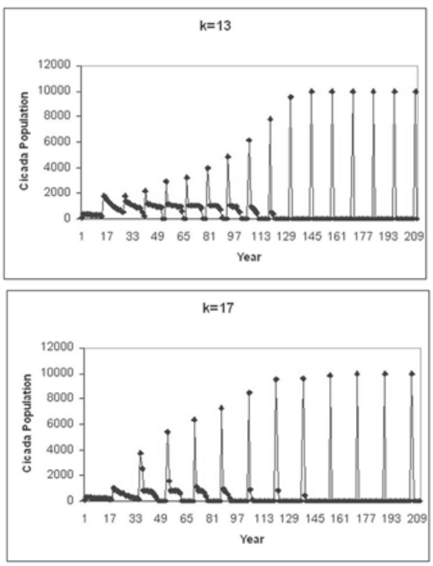
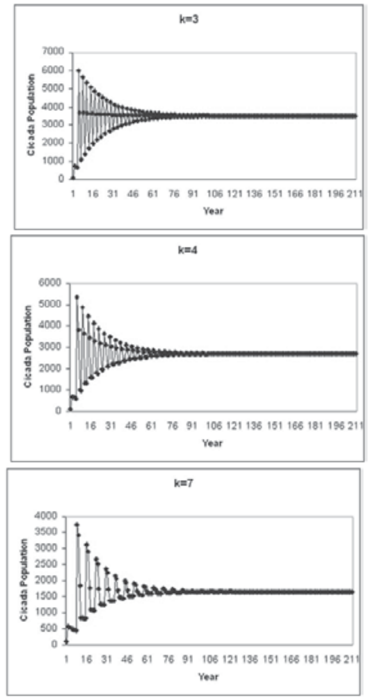


Figure 1: When cicadas have lifespans of 13 or 17 years, their populations move quickly toward synchronized emergence.



Cicada species with shorter lifespans of 3, 4, or 7 years do not synchronize their emergence. Instead, similar numbers of adult cicadas emerge each year.

We can conclude that the length k of the cicada lifespan definitely affects the emergence pattern. The graphs here look only at lifespans we know to exist, but with the model we used, lifespans of 10 or greater show synchronized emergence, and shorter lifespans do not.

Many math folks have noticed that actual cicada species with synchronized emergence have lifespans that are prime numbers. Might this be significant? Most predators of cicadas have short lifespans, only two to five years. Perhaps longer, prime-number cicada lifespans prevent these predators from having unusually large populations in the years when adult cicadas emerge. Then more cicadas live long enough to lay eggs. Models exist in both camps: some support this hypothesis, and some do not. This is one of many further directions we can take in trying to understand and explain cicada emergence patterns.

References

[1] P. Collinson, Some Observations on the Cicada of North America, Collected by Mr. P. Collinson, F. R. S., *Philosophical Transactions* **54** (1764) 65–68.
[2] Frank C. Hoppensteadt and Joseph B. Keller, Synchronization of Periodical Cicada Emergences, *Science* **194** (1976) 335–337.

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