

Why do cicadas have prime life-spans?

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1 Periodic Cicadas

You have probably heard the cicadas sing a lazy summer afternoon in the countryside. You may not be aware though, that cicadas spend most of their life underground, coming out only for about two weeks, during which they sing, reproduce and die. Most surprising in this respect are two species of cicadas that live in the Eastern and Southern United States. These cicadas spend respectively seventeen and thirteen years underground. Then they emerge all at once, in areas hundreds of miles wide, within a couple of days. They lay eggs in trees; these eggs fall to the ground and, when new cicadas are born in the form of nymphs, the nymphs enter the ground and attach themselves to roots. There they slowly develop over the next thirteen or seventeen years (thirteen in the South, seventeen in the Eastern United States), until within a couple of days they are all out again to repeat the cycle. Thus there are “cicada years”, rare events that take place every so many years that they come each time as a surprise: suddenly there are myriads of holes in the ground, and cicadas all around singing and mating.

The strange behavior of these periodic cicadas requires an explanation. Why do they wait so long to come out? And why do they do it all at once? A plausible answer [1] involves a mechanism called *predator satiation*. The idea is the following: When the cicadas are out, predators –particularly birds– feed off them. If the cicadas emerged frequently, these birds would prosper; so much in fact that they could drive the cicadas to extinction. By emerging at very long intervals, the cicadas make sure that no birds will make a living off them; at most every third or fourth generation of birds will have a formidable banquet once in their life. Moreover, when the cicadas come out, they do it by the millions. Thus even if the birds manage to eat a few, there will always be very many left to perpetuate the species; hence the name predator satiation.

This mechanism also explains the need for such precise synchronization: if a cicada emerges too early or too late, it will make a sure prey for the waiting birds. By coming at the same time as everybody else, it reduces significantly the probability of ending up devoured.

For the lay person, this is probably the end of the mystery of the peculiar way

of life of the cicadas. But the mathematically aware person may still be worried: he or she has probably noticed that the life-spans of the cicadas, thirteen and seventeen years, are not just any large numbers: they are also *prime*. One may wonder: is this a coincidence? Or is there any reason why prime numbers should be evolutionary preferable to non-prime ones?

This is in fact a matter of debate for biologists: many think that 13 and 17 just came out of chance [3][4]. However, Stephen Jay Gould provides a beautiful explanation of why prime numbers may have been selected [1]. His argument goes as follows:

Many potential predators have 2–5–year life cycles. Such cycles are not set by the availability of cicadas (for they peak too often in years of nonemergence), but cicadas might be eagerly harvested when the cycles coincide. Consider a predator with a life-cycle of five years: if cicadas emerged every 15 years, each bloom would be hit by the predator. By cycling at a large prime number, cicadas minimize the number of coincidences (every 5×17 , or 85 years, in this case). Thirteen –and 17–year cycles cannot be tracked by any smaller number.

This argument, however enchanting, has its problems. In fact, we may use essentially the same argument to prove that the cicadas may be better off with anything but a prime number. For, if they live, say, 15 years, and their predators 5, they will not even see their predators at bloom if these blooming events do not coincide with their years of emergence! The clue to this counter-argument, as well as to its possible failure, is in the sentence “Such cycles are not set by the availability of cicadas”. We rightly feel that this is not necessarily so: the birds will adapt to the life-span of the cicadas and, after a while, will adjust their cycle so as to peak simultaneously with the cicadas’ emergences.

But cicadas events occur so rarely, that they affect very little the life of the birds: how can then these evolve to adapt to circumstances that take place only once, and for only two weeks, every other three generations? The answer is given by a mathematical concept: resonance; this is mechanism which permits small perturbations to accumulate over long times, thus producing significant effects.

2 Resonance

Perhaps the most familiar example of resonance takes place in playground swings. If we push a swing even so slightly at regular intervals, and these intervals are multiples of the period of the swing, the swing will reach higher and higher altitudes. Similarly, each cicadas’ emergence acts as a “push” on the population of their predators, the birds, which find themselves among an almost unlimited supply of food. If these pushes take place regularly at a multiple of the average life-span of one species of birds, this particular species will flourish,

which will eventually lead to the cicadas' extinction. Thus the cicadas most fit for survival are those which emerge at a prime number of years, since primes are not multiples of any predator's life-span.

How does the mathematics of resonance work? Let us consider the example of the swing first. We can model a swing with the following simple ordinary differential equation:

$$\frac{d^2x}{dt^2} + \frac{g}{L}x = 0, \quad (1)$$

where x represents the displacement of the swing from its equilibrium position, g is the acceleration of gravity (approximately $10m/s^2$), and L the length of the ropes holding the swing. Equation (1) has very simple solutions of the form

$$x(t) = x_h(t) = A \cos(\omega t - \alpha), \quad (2)$$

where ω , the *frequency* of the swing, is given by

$$\omega = \sqrt{\frac{g}{L}}, \quad (3)$$

and A and α are arbitrary constants, which can be determined from the initial conditions at $t = 0$. The name x_h stands for "homogeneous solution", meaning a solution for the unforced swing. The solutions in (2) represent periodic oscillations, with period $T = 2\pi/\omega$ and amplitude A . Since we are not including any friction in our model, the swing will continue to oscillate forever once set into motion.

How can we model a forced swing, i.e. a swing that is being pushed? The simplest equation describing such "forced oscillator" is the following variation of (1):

$$\frac{d^2x}{dt^2} + \frac{g}{L}x = f(t), \quad (4)$$

where $f(t)$ is the time-dependent forcing. Let us consider periodic forcing, intended to represent a person pushing the swing at regular intervals (just as the cicadas "push" the birds every 17 years). A simple example is $f(t) = B \cos(\lambda t)$, where λ is the frequency of the forcing. It so happens that, with this choice for the forcing, (4) has simple closed solutions of the form

$$x(t) = \frac{B}{\omega^2 - \lambda^2} \cos(\lambda t) + x_h(t). \quad (5)$$

We see that these solutions have two components: one homogeneous, $x_h(t)$, which oscillates just as in the unforced case, and one non-homogeneous, which oscillates at the frequency of the forcing. Notice that this latter part is very big when the frequency λ of the forcing is close to ω , the "natural" frequency of the swing. In fact, when the two are exactly equal, the solution (5) stops making sense. It is easy to check that, in this latter case, the real solution is

$$x(t) = \frac{B}{\omega} t \sin(\omega t) + x_h(t). \quad (6)$$

This solution oscillates at the frequency of the swing, but with an ever growing amplitude! After a while, these oscillations are so big that the model (4) stops making sense. This is a manifestation of the phenomenon of *resonance*.

Physically, what is going on is that we are pushing the swing once per oscillation, and this is adding more and more energy to the movement of swing. What would happen if we should push the swing every two oscillations? It appears at first sight that, with $\lambda = \omega/2$, nothing much would happen in the solution (5). Yet this does not sound physically right, and in fact it is not right at all. Our pushes on the swing are periodic functions, yes, but not quite sines and cosines. We know, however, that we can decompose any periodic function into a sum of sines and cosines, its Fourier series. If the basic frequency is $\omega/2$, then a term with frequency ω will take part of the series. Since the solution (6) corresponding to this term grows linearly in time, we shall see resonance again. The same reasoning clearly applies whenever the period of the pushing is any multiple of the period of the free swing.

Figure 1 displays numerical solutions to (4) for $g/L = 1$ (so $\omega = 1$, and the period is 2π) and a forcing of the form

$$f(t) = \begin{cases} 1 & \text{for } 0 < t < \frac{T}{8} \\ 0 & \text{for } \frac{T}{8} < t < T \\ f(t-T) & \text{for } t > T \end{cases} \quad (7)$$

corresponding to periodic pushes with period T . We see that, when T approaches a multiple of the natural period 2π , the oscillations of the swing get very big. At precise multiples, the magnitude of these oscillations grows linearly in time. The Matlab program used to perform these computations is described in the appendix. The reader is strongly recommended to try some runs of his/her own!

3 A Model for the Cicadas

In order to apply the concept of resonance to our cicadas and birds, we need to make a few adjustments to (4). First of all, neither cicadas nor birds can have just any natural frequency ω : their typical life-spans need come in integer number of years (By the way, the mechanisms by which living organisms adjust themselves to the cycle of the seasons may involve resonances as well!). This tells us that, rather than a model with a continuous time such as (4), we may be better off with a *discrete* model, in which we measure the populations of cicadas and birds once per year.

Following these lines, we shall develop here a computational model for cicadas and birds, adapting a previous model by Hoppensteadt and Keller [2] for cicadas alone, which did not include resonant effects. Our model will include various species of cicadas and birds, each with a different life-span. The idea is to test whether those species of cicadas with prime life-spans are more likely

to survive. In order to follow the evolution of each generation of cicadas over the years, we shall keep track of the age of each cicada (and bird). Thus we introduce the variables

nc	Number of species of cicadas
$x(j, k)$	Population of cicadas of species k and age j
$nx(k)$	Life-span of the cicadas of species k

for the cicadas and

np	Number of species of predators
$y(j, k)$	Population of predators of species k and age j
$ny(k)$	Life-span of the predators of species k

for the birds. We shall monitor the evolution of $x(j, k)$ and $y(j, k)$ over the years. To do this, we need to decide how to update these populations. For $1 < j \leq nx(k)$, $x^{n+1}(j, k)$, the number of cicadas of species k in year $n + 1$, will be given by $x^n(j - 1, k)$, i.e. the number of cicadas that were one year younger the year before, times a coefficient $ax(k)$ measuring the cicadas yearly rate of survival underground. In symbols,

$$x^{n+1}(j + 1, k) = ax(k) * x^n(j, k). \quad (8)$$

Clearly a similar equation applies to the birds. However, in their case, the yearly rate of survival depends, even though only slightly, on the number of adult cicadas that come out each year. Thus, for the birds, we have the equation

$$y^{n+1}(j + 1, k) = ay(k) * y^n(j, k), \quad (9)$$

where

$$ay(k) = ay0(k) + ay1(k) * xn,$$

where xn is the total number of emerging adult cicadas.

What about the new-born cicadas, i.e. the $x^{n+1}(1, k)$? The number of these depends on the number of adult cicadas coming out of the earth, $x^n(nx(k), k)$. However, it depends on other things as well. For starters, the birds may eat some cicadas before they have time to lay their eggs. Thus we need to multiply $x^n(nx(k), k)$ by the probability of a cicada of species k being eaten. This probability is proportional to the number of birds (maybe weighted by their age, since not all birds eat the same), and inversely proportional to the total number of cicadas of all species out there, from which the birds make their pick. Thus we have the equation

$$x^{n+1}(1, k) = (rx(k) * ax(k) - xy) * x(nx(k), k),$$

where $rx(k)$ is the number of offspring per cicada, xy , the proportion of cicadas of species k that are eaten, is given by

$$xy = dxy * yt / xn.$$

Here dxy is a constant, yt is the total number of birds, weighted by their age, xn is the total number of adult cicadas.

However, the amount of nutrients underground is not infinite, so maybe not all nymphs will have enough food to survive. In order to model this, we introduce a number K , the capacity of the soil to support nymphs. After counting all the nymphs already underground from previous years, say K_t , we can only add $K - K_t$ new nymphs. If more than these are born, the remaining nymphs will not have a chance to make it into adulthood. Thus the quantity $x^{n+1}(1, k)$ computed above is further reduced, so that no more nymphs will survive that those that fit underground.

We can place similar constraints on the number of newborn birds; we shall not, however, incorporate any of *their* predators, in order to keep the model simple.

Further details of this model are explained in the comments in the Matlab program itself. Most of the art goes into tuning the parameters right, so as to make sure that the conditions are not such that no species of cicadas can ever survive (as would be the case if the birds reproduced too rapidly), or that life is too comfortable, and cicadas can follow their own rhythm without even noticing the birds. We should also try not to bias our model toward any species of cicada or bird, since we would like to check the effects of long-time resonances between the two.

Figures 2 and 3 show two runs of the model, with random initial data. We have chosen three species of cicadas, with life-spans of 12, 13 and 15 years respectively, and three species of birds, with life-spans of 2, 3 and 5 years. We would like to see whether the 13-year cicada is more likely to survive. The plots represent the number of newborns of each species of cicadas and birds as a function of the year.

We see that, initially, mass extinctions take place, killing whole generations of cicadas. At the end, at most one or two generations of one or two species may survive. These surviving species are almost always the ones with prime life spans, thus confirming our theory of resonances. Moreover, when an individual generation of a particular species goes extinct, it is nearly always accompanied by a huge population growth in a species of bird whose life-span is an exact divisor of the life-span of the corresponding species of cicadas. After the latter go extinct, this overpopulation of birds rapidly decays to a more normal condition.

In the run represented in figure 2, only 13 year cicadas survive; and of these, only two generations. In the one in figure 3, only one generation of the 13 year cicadas survives, in agreement with the reality of the Southern United States. Figure 4 shows a detail of these latter results, with one generation of cicadas emerging every thirteen years. The reader is strongly encouraged to modify the matlab program provided, and do experiments of his/her own. What happens if we start with only one species of non-prime cicadas? Does it go extinct? What if we start with very many? And then, what is the effect of small changes in the parameters in the program? Also, can you do any of the underlying hypothesis

more realistic? There are lots of questions to answer, and a simple experimental set up to try them all!

References

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