Magicicadas: Life cycle Modeling

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Periodical cicadas (*Magicicada* spp.) have been studied since as early as the 18th century, initially because of the mass emergence occurrences that were associated with it and because of the apparently prime-number-long periodic life cycles thereafter. There has been a moderate amount of research on the cause of such periodic life cycles, with some of the leading theories defending a predator avoidance strategy or a hybridization avoidance strategy as the origin of such behavior. With this study we aimed at testing both these theories for consistency with reality. To achieve this we employed NetLogo as our primary simulation and development tool. We designed a program which aimed to test both theories and run a series of simulation with varying parameters. As a result we were able to partially confirm the hybridization theory while we obtained no positive results for the testing of the predator avoidance theory.

Introduction

Magicicadas (also known as periodical cicadas) are a genus of insects found in North America which are known for their interesting life cycles: species belonging to this genus live most of their lives underground and emerge synchronously, and in huge numbers, only after 13 or 17 years, depending on the species or brood, during 2 to 6 weeks[1]. During that time, they mate and lay eggs to start a new 13 or 17 years life cycle. One of the most interesting thing is that both 13 and 17 are prime numbers. Just a reminder: citing directly from Wikipedia, "(…) prime number (or a prime) is a natural number greater than 1 that has no positive divisors other than 1 and itself".

We find that there are two main lines of thought that try to explain the emergence of these life cycles – one which says that it evolved in order to avoid hybridization between different varieties of this genus[2][3], and other that says it is the result of the interaction with predators/parasites[4][5].

The two most seemingly influential Hybridization Avoidance theories postulate that prime-number-long life cycles (**LC** from now on) evolved as a way to avoid hybridization between broods with different LC durations. According to the theories, hybridization between different broods would disrupt the genetic basis of the duration of the LC, which would be a disadvantage considering the importance of synchrony.

As for the other line of thought, the Predator Avoidance theory hypothesizes that these prime-number-long LC came to be as a product of the interaction between predators and cicadas. For the cicadas, emerging at the same time a predator was present in the wild would cause that particular brood (and therefore, a particular LC) to suffer a loss in number of individuals, which would limit its reproductive potential, while the predator would receive a boost in fitness. To avoid this scenario, cicadas which develop a LC that could allow for them to encounter predators less frequently would have an advantage over other LC. These optimum LC are prime-number-long, as they synchronize less frequently with other LC.

In this project we tested versions of both of these hypothesis, using the NetLogo environment. Although we never used it before, it seemed like a good environment to model these insects.

Results & Discussion

Using our NetLogo model we performed a battery of simulations, with the help of BehaviorSpace (a NetLogo's tool), for every set of parameters we deemed important, aiming to test both theories. For every experiment we ran 40 simulations which would run for a predetermined amount of ticks
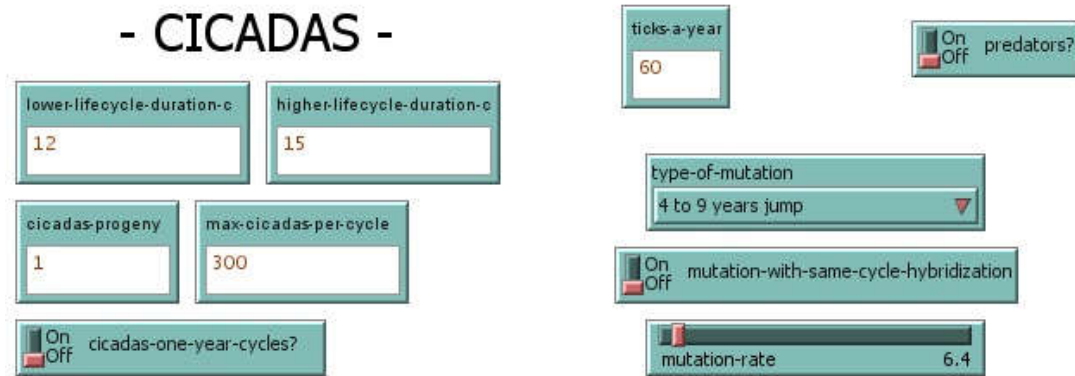
Figure 1 – Conditions of simulation, Hybridization Avoidance Theory

(NetLogo's time step), 30000 for the hybridization avoidance related simulations and 50000 for the predator avoidance related simulations. Such a high number of ticks was used to allow enough time for a stabilized LC to appear. Also, the differences in the number of ticks exists because cicadas tend to stabilize much faster if there is no predator present. Also, different stop conditions were used on the simulations regarding each theory: simulations regarding hybridization avoidance would stop if every cicada had the same cycle, and simulations regarding predator avoidance would stop if either the predators or cicadas wound up extinct.

After every simulation was finished, a couple of custom python scripts were used, along with Matplotlib library, to obtain histograms corresponding to the number of times each LC was fixed.

Hybridization Avoidance Theory

We based our model on Yoshimura's theory[3], which postulates roughly the following:

- LC duration of magicicadas's ancestors was elongated (to 12 – 18 years depending on the geographic zone) due to environmental reasons;
- Adult populations decreased because of increased duration of development and high juvenile mortality;
- Low adult densities led to high emergence synchrony;
- Hybridization between broods with different LC led to progeny with LC out of sync with the other broods;
- Groups of cicadas emerging out of sync with other broods would not be successful at reproduction because of low adult densities;
- Broods with a prime-number-long LC hybridized less with other broods;

- This broods had an evolutionary advantage in relation to the other broods, which went extinct.

Being based on Yoshimura's theory we, therefore, wanted to test if the model was able to correctly output prime-number-long LC. Concretely, we wanted to test if the following assumptions, in addition to the assumptions intrinsic to the model, were enough to fixate populations of cicadas with prime-number-long LC:

- Existence of many broods of cicadas, each with a different LC duration, this duration being long (between 12 and 18);
- Low cicada's density;
- Mating between cicadas of different broods has a probability of leading to progeny with different LC;

We tested the values of the lower bound LC duration and higher bound LC duration as suggested by the theory of Yoshimura:

"(…) I postulate that the 7-9-yr life cycle of the ancestors was elongated to 14-18 yr in northern parts of their range and 12-15 in southern parts."

From what we know, he gives no explanation of why he postulates these intervals. The theory postulates that the 17 year LC would get fixed in the 14-18 year case and the 13 year LC in the 12-15 year case.

We ran a simulation corresponding to each case, as indicated before, with the parameters shown in Figure 1 (lower-lifecycle-duration-c and higher-lifecycle-duration-c values varied). These parameters were chosen because they were the most stable (from the ones we tested). Of all the types of mutation we implemented, "4 to 9 years jump" is the most disadvantageous in cases of hybridization so we used it to be more in accord with Yoshimura's theory. At the end of the
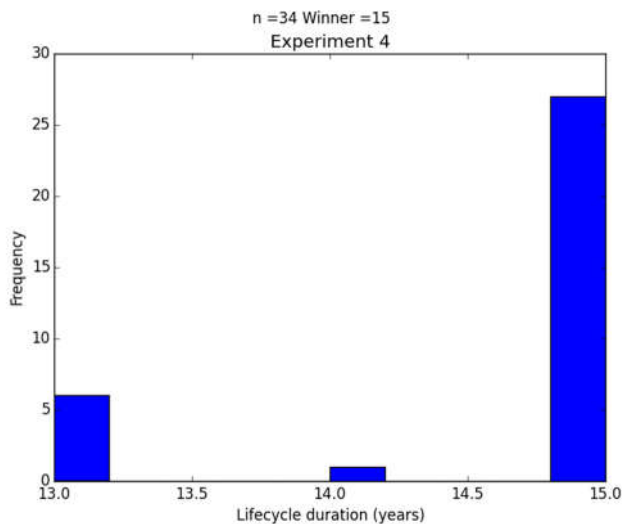
Figure 2 - Histogram illustrating the number of times each LC was fixed at the end of all the runs. 12-15 year case. n is the number of simulations included in the results. Winner is the LC duration that was fixed a higher number of times
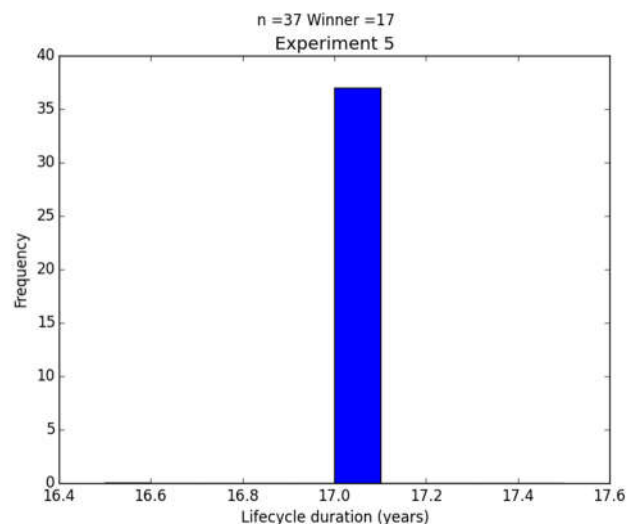

Figure 3 - Histogram illustrating the number of times each LC was fixed at the end of all the runs. 14-18 year case

simulations, those that finished with no cicadas, or with more than one brood, were excluded from the final results, which are shown in Figure 2 and Figure 3. As predicted by Yoshimura, the 17-year LC is the one with the higher probability of getting fixed in the 14-18 case. However, the 15-year LC is the one with the highest probability of getting fixed in the 12-15 case and not 13, as predicted. Therefore, our model, with the parameters used here, supports Yoshimura's theory only partially.

We also tested other cases, similar to the ones postulated by Yoshimura, using different values of lower-lifecycle-duration-c and higher-lifecycle-duration-c. These simulations were done in analogy to the previous ones. In Table 1, we show the

results of these simulations along with the results of the two previous ones, for the sake of comparison. The "Expected" column corresponds to the LC duration we would expected to have a higher probability of getting fixed. When there was only one brood with a prime-number-long LC, we expected that brood to have a higher probability of getting fixed. When there was more than one brood with a prime-number-long LC, we expected that the brood with the LC duration corresponding to the highest prime-number would have a higher probability of getting fixed, because it would encounter other broods less often.

These results support the main idea of Yoshimura's hypothesis considered here – cicadas with prime-number long LC will tend to survive more because

lower-lifecycle-duration-c	higher-lifecycle-duration-c	Most frequent fixed lf	Expected	n
9	13	13	13	27
10	13	13	13	37
10	14	14	13	35
11	14	13	13	29
12	15	15	13	34
13	16	16	13	17
13	17	17	17	34
14	18	17	17	37
15	18	17	17	35
15	19	19	19	26
16	20	19	19	13
17	20	19	19	5
9	20	19	19	13

Table 1 - Results of simulations when different values of lower-lifecycle-duration-c and higher-lifecycle-duration-c were used. In the column "n" is the number of simulations included in the result. In orange, the cases where the predictions were different from the results. In grey, the cases where less than half of the simulations were included in the results.

- CICADAS -   ## - PREDATORS -

Figure 4 - Conditions of simulation, Predator Avoidance Theory

they hybridize less with other broods of cicadas. We only got unexpected results in 3 out of 13 cases (including the 12 – 15 case proposed by Yoshimura).

Predator Avoidance Theory

Early in development we began testing this theory as though a predator was always present in nature, ie representing the fact that these cicadas are targeted by multiple opportunistic predators, and so we could assume a constant predator presence. Campos et al. concluded that it was possible[4] to obtain prime numbers in these conditions, but assumed predators could live for several years without feeding. Despite this article's claims, we pushed through and, although the idea was solid, we quickly found out that it represented the same scenario as a hybridization avoidance theory simulation, only with fewer cicadas surviving each cycle. Then we switched strategies, and began implementing cyclic predators that would, hopefully, try to synchronize with the cicadas.

Our main goal was to infer whether there was a tendency for cicadas to evolve a prime-number-duration LC assuming cicadas emerge en masse in the presence of a cyclic predator. Goles et al. concluded that this is indeed the case[5], however, and quoting the authors:

"(…) there is as yet no evidence for relevant periodic predators of cicadas."

But still it was a theory worth testing as, again, the authors point out:

"(…) the predator hypothesis can be maintained by assuming parasitoids that attack eggs or adults, which may have become extinct."

Based partially on the theories of Goles et al., we postulated the following:

- Both predators and cicadas, emerge during the same period of the year
- Both start with just one and the same LC
- 1 year long LC were not allowed (because it would be equivalent to cicadas/predators not being cyclic).

We ran 19 experiments, ranging in LC from 2 years to 20 years, all with the same parameters specified in Figure 4 (lower-lifecycle-duration and higher-lifecycle-duration values for both predators and cicadas varied). Once again, these were the most stable parameters we obtained from trial and error. "Exponential range of years jump" was the type of mutation that allowed for an exponential less abundancy of individuals further away from its predecessors, which would result in a higher concentration of close LC, giving room for more interaction between predators and cicadas. At the end of the simulations, we were not able to obtain theory supporting data. In every single experiment, most simulations ended with the great majority of cicadas restricted to the cycle they started the experiment with, as can be seen, as an example, in Figure 5. Therefore, with our model, we were not able to verify the authenticity of the predator avoidance theory.

Model Explanation

We developed our model using NetLogo, which is an environment suited for the kind of simulations we ran. Although we were previously inexperienced with it, we quickly learned how to use it with ease, mostly because we both have some kind of background in programming. Our model has the
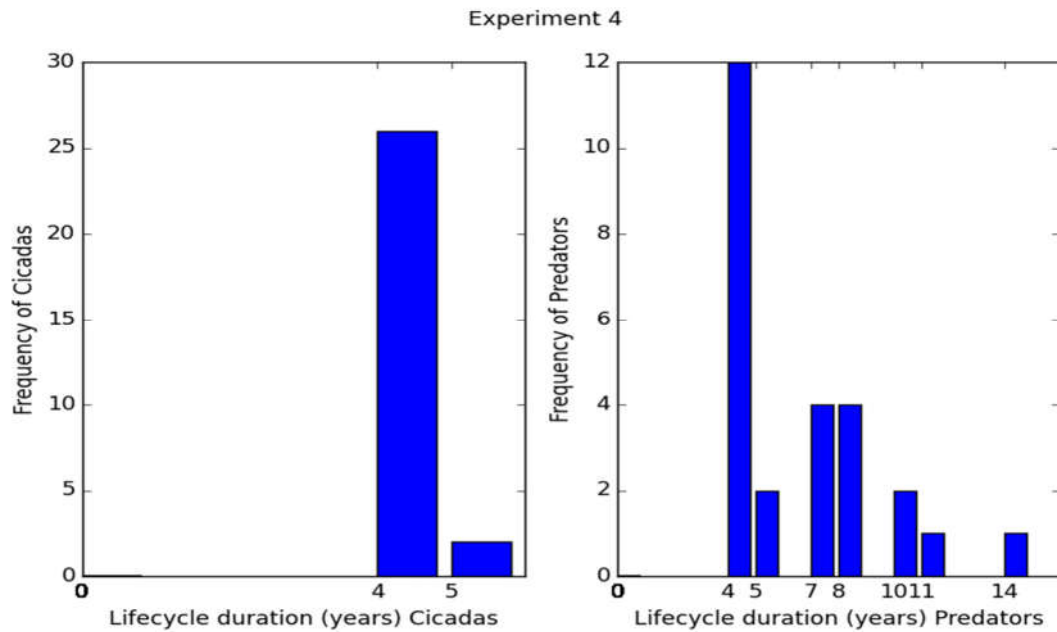
Experiment 4

Figure 5 - Histograms illustrating the number of times each LC was the most populated at the end of all the simulations of one experiment. 4 years initial LC case. For both predators and cicadas, if there were no individuals ate the end of a run, that data would not count towards total number of simulations.

cicada LC as its backbone. A simulation starts with one or more broods of cicadas, each brood with a different LC duration and the same number of cicadas. The duration of the LC and the number of broods is defined by the variables *lower-lifecycle-duration-c* and *higher-lifecycle-duration-c*. For example, if *lower-lifecycle-duration-c* is set to 12 and *higher-lifecycle-duration-c* to 15, there will be 4 broods of cicadas, with LC duration ranging from 12 years to 15 years. To initialize just one brood, both variables have to be set to the same number. The initial number of cicadas in each brood is defined by the variable *max-cicadas-per-cycle*. The variable *ticks-a-year* corresponds to the in-model duration of a year, represented in ticks. This influences how much time the cicadas have to mate. We have also added the possibility to limit the number of cicadas

of each brood, again by the variable *max-cicadas-per-cycle*. If a cicada has a LC duration of 2 years, it emerges during a certain period, every 2 years. "Emerge" means that it can interact with other agents of the simulation. In this model, the year 0 is the same for all cicadas. In Figure 6 this is illustrated with the blue and red lines. Cases like the ones illustrated by the yellow line (which corresponds to a 2-year LC, like the blue line, but has a deviation of 1 year) don't happen in our model.

During periods of emergence, which happens during a small part of the year, cicadas move randomly in the virtual world. Each cicada has a certain number of offspring each time it encounters other cicadas with which it can mate. This number is set by the variable *cicadas-progeny*. If the mates are of the same brood, the offspring will have the
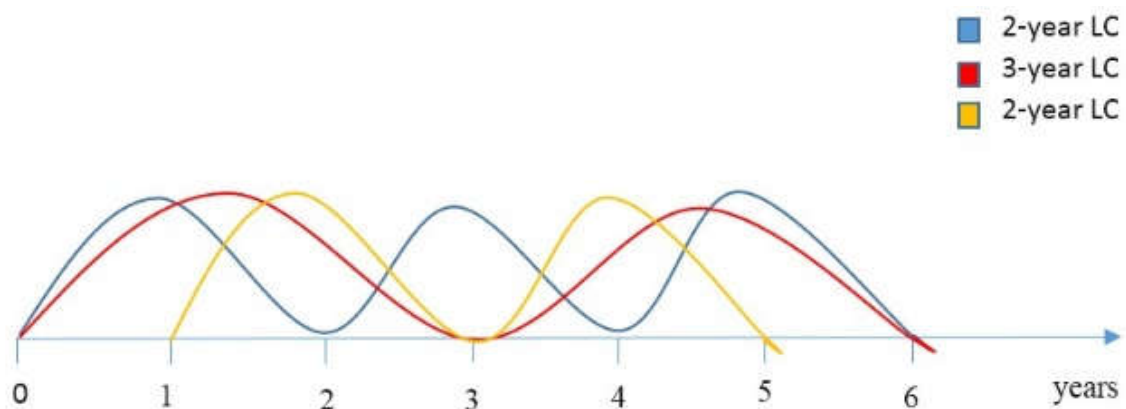

Figure 6 - Illustration of LC

same LC duration as one of the parents if the switch *mutation-with-same-cycle-hybridization* is set to Off. If this switch is set to On, the LC duration of the offspring will differ by a certain amount from that of one of the parents with a probability *mutation-rate* %. How much it will differ depends of the variable *type-of-mutation*. If the mates are of different broods the LC duration of the offspring will be different from one of the parents. Again, this difference depends on the variable *type-of-mutation*. In all cases of mutation there is a 50% chance that the duration of the LC will increase and 50% that it will decrease in relation to one of the parents. If the switch *cicadas-one-year-cycles?* is set to Off, a LC duration can't be decreased to 1 year.

In the end of the emergence period, all the cicadas that emerged in that period die (the offspring remain alive).

If the *predators?* switch is set to On, there will also be predators in the simulation. The functionality of each predator is almost identical to the cicadas, with this few exceptions: each time a predator meets a cicada, this cicada is eaten by the predator; the number of offspring each predator has when he meets another predator is equal to *predators-progeny* plus the number of cicadas eaten by that predator until that moment. The number of cicadas each predator can eat is set by the variable *max-cicadas-eaten-per-predator*.

At the bottom of the model are a couple of *predetermined-scenarios* which output the most favorable results. These are used as examples of the model's functionality. To use them, simply select one scenario, hit the predetermined button and run the simulation.

Additional Comments

This model, as any other, has its own limitations.

One of the biggest is the fact that we did not implement a way for LC of the same length to exist by a certain offset. That is, there cannot be different broods with the same life cycle. In our model, those are technically the same brood.

Another limitation is with the way we implemented a year. The way it works, for the interaction between cicadas and predators to be changed, the waiting time between emergences also increases by the same factor, but, as we assume cicadas only emerge during a month, the waiting time will always be 12 times higher. For higher interaction times, higher waiting times where "nothing"

happens. We had some ideas during development to circumvent this, but we eventually dropped them as we had other more important tasks on our hands.

The number of variables made available by the model also presents a problem. With so many variables we had to select a few of them that worked in certain conditions, and as a consequence we ended up not testing everything. Some combinations of variables could even possibly allow for the predator avoidance theory to work on our model.

We are aware that our model has a lot of other probably unrealistic assumptions, but we will not enumerate them here for the sake of brevity.

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