Coevolution of Predators and Prey in a Spatial Model

An Exploration of the Red Queen Effect

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ABSTRACT

The term "Red Queen effect" is used to describe the relationship which sometimes occurs between two competing species, such as a predator and a prey. In a typical evolutionary predator-prey interaction, three outcomes are possible: (i) the prey population evolves a strong defense and the predator population dies off, (ii) the predator population evolves a strong offense and the prey population dies off, or (iii) both sides (predator and prey) constantly evolve the same relative levels of offense and devense, allowing both populations to survive (the Red Queen effect). A Red Queen effect occurs when both species maintain the same relative values of a phenotypic trait, like strength of a toxin, even though the absolute value changes dramatically. We present an agent-based model which examines mobile predators and prey on a landscape, interacting in competitions, and evolving offensive and defensive capabilites. We carry out a series of experiments where we vary the relative strength of each species. Finally, we show that this model which incorporates both space and time can reproduce similar results to those found from using non-spatial, non-temporal models, while at the same time providing a base ontology more similar to real world coevolutionary systems.

Keywords: Red Queen Effect, Coevolution, Parasite-Prey, Spatial Modeling, Individual-based Modeling, Agent-based Modeling

1. INTRODUCTION

"Now here you see it takes all the running you can do, to keep in the same place. If you want to get somewhere, you have to run at least twice as fast as that." Or so says the Red Queen in Lewis Carroll's *Through the Looking Glass*. In Carroll's world Alice and the Red Queen run as fast as possible and yet never move away from the tree they started under. As Van valen first discussed, evolution can take the same course at times [6]. For instance, the rough-skinned newt (taricha granulosa) has evolved a potent neurotoxin.

However, the common garter snake (thamnophis sirtalis) has evolved a resistance to this neurotoxin [1]. With each succeeding generation the toxin of the newt grows stronger, which means fewer and fewer snakes can resist this toxin. However those few snakes that do resist the toxin, are more likely to give rise to new snakes that can resist the toxin. In turn, these new snakes are able to consume more newts, and so only the newts with the highest levels of toxin are able to survive to reproduce. Despite the fact that both species are evolving as quickly as they can, they remain in the same place with respect to each other. This has been termed the "Red Queen Effect [6]."

The Red Queen (RQ) effect refers to the relation between two competing species, such as a predator-prey or parasite-host relations. In these situations both sides of the competition enter, what is sometimes referred to as an "arms race" in which certain traits escalate to seemingly unnatural proportions. In the idealized version of the effect, regardless of the actual values that the species will evolve to obtain, they will have not moved in relation to each other. Much like the Red Queen and Alice they will be stuck beneath the same tree. The possible outcomes of the any competitive coevolution are described by Dieckman, Marrow and Law (1995): (i) the prey population evolves a defense so strong that no predator in the current population can overcome it, as a result the predator population dies out and the prey survive and prosper, (ii) the predator population evolves an offensive strategy so strong that no prey in the current population can resist it and thus the prey population dies out and the predators survive and prosper, or (iii) both speciess the predator and the prey evolve in step with each other, and thus both are able to survive (the Red Queen effect) [3].

In this paper we begin by discussing the Red Queen and previous work on examining this phenomenom. We then present a model of the Red Queen effect in which both predators and prey are modelled as mobile agents moving around on a landscape. Over time the predators evolve offensive capabilities to consume the prey, and the prey evolve defensive capabilities to resist the predators. We run this model for a variety of initial settings and discuss the results. Finally we conclude and discuss future work.

2. DESCRIPTION OF THE RED QUEEN EFFECT

The RQ effect begins when one species gains a selective advantage and its evolutionary fitness increases. At the same

time, however, because of coevolution the competitors who are one step away in the entropic pyramid, are also gaining selective advantage. This produces an arms race as one species develops a better defense forcing the predator to become a better hunter.

There have been many attempts at building models of the Red Queen effect to examine this relationship in more depth. For instance, Dieckmann, Marrow, and Law who created a dynamical system equation-based model that shows that there are three possible outcomes of competitive co-evolution and that evolutionary cycling is clearly a possible outcome [3]. van der Laan and Hogeweg also investigated the evolutionary dynamics of a Red Queen model using a Lotka-Voltera type system [5] but focussed their analysis on the interactions across time. Furthermore, Savill and Hogeweg presented an individual-based model of Red Queen dynamics with a stationary prey and were able to achieve similar results to the van der Laan and Hogeweg analysis [4]. Finally de Back, de Jong, and Wiering replicated the Savill and Hogeweg results and compared them to the van der Laan and Hogeweg analysis [2].

This papers differs from the previous work in that it uses an agent-based model, as opposed to an equation-based model, where both predators and prey are mobile not requiring one of them to be stationary, which means that it is applicable to a larger group of real species. Moreover, this model contains an individual-level reproduction mechanism and does not have individuals reproduce on the basis of either population or prey-density. This individual-level reproduction mechanism is closer to a real-world reproduction event, than a density-based reproduction mechanism is. Finally, we show that this model is still capable of producing all three outcomes described by Dieckmann, Marrow, and Law: (i) predator extinction, (ii) prey extinction, and (iii) Red Queen persistence of both predator and prey [3].

3. THE MODEL

The model in this paper was designed to simulate an imaginary situation with two bacterium species, an autotroph and a heterotroph. The autotroph produces a toxin that prevents it from being ingested by most predators. The heterotroph produces a powerful anti-toxin to counteract the autotroph's defenses. As time passes both aim to strengthen their defenses against each other.

The model has several parameters:

1. Initial Number of Predators and Prey (n_{prey} and n_{pred}): The initial number of predators and prey, which determines how many of each creature are initially created in the model.

2. Initial Mean Value of Resistance and Poison (μ_r and μ_p): The initial mean value of resistance and poison. The initial values of resistance and poison for each individual are drawn from a normal distribution with these means and a standard deviation of 1.

3. Carrying Capacity (C): The maximum population of both predators and prey that can exist in the system. This means that the predators and prey are competing for the same scarce resource.

These parameters and their initial settings for the experiments described below are detailed in Table 1.

The model begins by creating n_{pred} predator agents, and n_{prey} prey agents. All predator agents have a location x, y and a resistance level r associated with them. All prey agents have a location x, y and a poison level p associated with them. The world on which the agents are located is a toroidal real-valued 35 by 35 grid. The initial x and y values for each agent are drawn uniformly from the ranges $x \epsilon [-17.5, 17.5)$ and $y \epsilon [-17.5, 17.5)$ The resistance value for each predator is drawn from a normal distribution with mean μ_r and standard deviation of 1. The poison value for each prey is drawn from a normal distribution with mean μ_p and standard deviation of 1.

After these initial agents are created the model is typically run for a number of timesteps or "ticks" (5000 in all examples below), and during each timestep a number of events occur. Every agent is iterated through and each one is given a chance to act. At the beginning of each creatures "turn" when the total number of prey and predators is less than the maximum population each one will reproduce with a 50% probability. The new agent's initial poison / resistance will be drawn from a distribution with the parent's poison / resistance as the mean value and a standard deviation of 1. This reproduction mechanism is based on simply a probability of each agent reproducing and not in any way dependent on the total population of either the predator or the prey. Of course, the more predators in existence the more likely they are to reproduce and vice versa for the prey.

After having the chance to reproduce, agents (predator and prey) move around on the toroid lattice. They "wiggle" by moving to the left a uniform random amount from $[0, 50)$ degrees and to the right a uniform random amount from $[0, 50)$ degrees, and then taking one step forward. If at the end of its step a predator is within 1 unit of a prey, then it will challenge the prey. If there is more than one prey the predator will choose one at random. The predator will compare its resistance value to the prey's poison value and which ever agent has the larger value will win the challenge and the other agent will be killed. If both agents have exactly the same value then nothing will happen. There is no death in this model except by predation or by a predator succumbing to the poison of a prey. Thus each tick of the model for each agent can be summarized as: (1) probabilistically reproduce, (2) move randomly, and (3) engage in a challenge if the appropriate are conditions are met. The model is typically run for a pre-set number of ticks and the results are examined.

Unlike previous models such as the van der Laan and Hogeweg model [5] and the Dieckmann, Marrow and Law model [3] this model incorporates time, space and mobile species in the model. This is a closer approximation of actual biological systems and allows for an easier understanding of the system for both students of biology and researchers. In addition, this reconceptualization of the model makes it easier to understand how to manipulate various parameters of the world to reflect empirical evidence on actual conditions, and to observe those conditions changing over time.

This model was built in the NetLogo agent-based modeling language, a freely available, widely used ABM platform [7], and is illustrated in Figure 1.

4. EXPERIMENTS

To examine this model we conducted a series of experiments to see if we could reproduce the results observed by
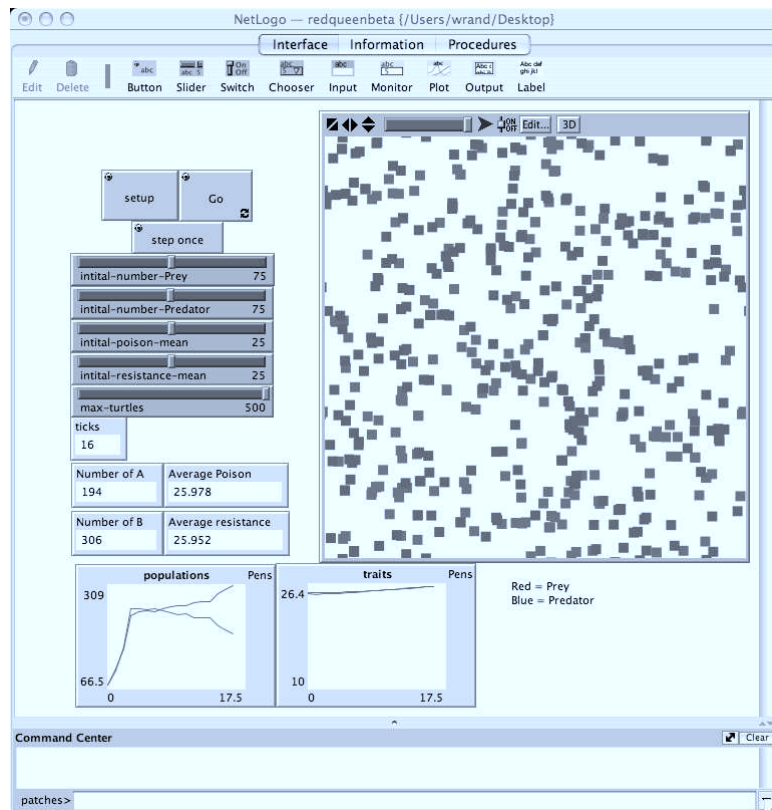
Figure 1: The Red Queen Model in NetLogo.

Dieckmann, Marrow, and Law [3]. To do this we initialized the model as described in Table 1. Our parameter of interest was μ_p; we held μ_r constant at 25 and varied μ_p from 0 to 50 at increments of 5. For each of the values of μ_p we would run the model for 5000 timesteps and observe the results. We repeated this process 10 times for each value of μ_p and averaged the results to create Figures 2 and 3.

Figure 2 illustrates the final population counts of both the predators and the prey for the various values of μ_p. As can be seen from this figure, under most initial conditions one species will wipe out the other, because of the size of their initial advantage in poison/resistance. However there are a few cases in which neither side can gain an advantage, and thus neither species is completely destroyed. These cases are where μ_p is similar to μ_r. In the case where $\mu_p = \mu_r$ both populations persist throughout all 5000 ticks in all 10 runs. Moreover, due to the stochastic nature of the model there are a few runs when μ_p is slightly less than μ_r and yet still both populations persist throughout all 5000 ticks. Figure 2 shows that only a few values produce the result that both species live. These values are when both sides start off near equal values for poison and resistance, if there is any significant difference between the two species respective values then one of them usually dies off immediately.

Figure 3 illustrates the final average trait values of both the resistance and the poison for the various values of μ_p. These values are calculated by simply averaging the value of every individual at the end of the run for both the predator and prey populations. If there are no predators or prey left then a value of 0 is plotted for the average resistance or poison, respectively. As can be seen from this figure, the values of both poison and resistance are kept very low in most cases, and remain near the initial values μ_p and μ_r. However, the exceptions are again when μ_p is roughly the same as μ_r. The biggest peak is when $\mu_p = \mu_r$, when this is the case then we clearly see the eventual state of the Red Queen effect where both the poison and resistance of the agents has elevated to much higher proportions than what it was originally set at. The final values on average are around 450 which is more than 1.5 orders of magnitude larger than the initial average values of 25. Given that all mutations are drawn from a normal distribution with standard deviation of 1 and mean centered around the parent's value this means that the population as a whole has to accumulate thousands of mutations to drive the trait values so high.

Since we are utilizing an individual-based model which creates data every time step rather than just producing final results, we were able to go back and investigate this phenomenom more fully. We examined several runs in-depth with $\mu_p = \mu_r = 25$. One of these runs is illustrated in Figure 4 from the $3000th$ tick to the $4000th$ tick. The result for the whole run looks similar but we have zoomed to this section so that some difference in the two trait values is observable.

As can be seen, the poison and resistance values constantly grow over time with neither value differing that much from the other value. Though in this run the resistance value tends to stay ahead of the poison vlaue slightly, this is not the case in all runs. Moreover, the values are very close and virtually indistinguishable at times. In the 1000 ticks presented here, the values of both traits increase from roughly 290 to roughly 375. Thus each population is roughly gaining an increase of .085 in their respective trait value every tick.

5. CONCLUSION AND FUTURE WORK

The results reproduce previous results that in order for the Red Queen effect to occur the poison and resistance values must be within a specific range of one another. In particular, we have shown that this agent-based model exhibits the same three phases of behavior that have previously been explored in other equation-based models [3].

From our experiments our experiments, we have gained insight into and been able to illustrate the cyclical nature of the internal mechanisms of the Red Queen effect. As the predator kills off the easy prey, only the prey with high poison values will remain allowing them to reproduce to the next generation. These new stronger prey will then kill of the predators and the cycle will conitnue.

The model presented here serves to exemplify the basic nature of the dynamics that occurs when there is adaptation on both sides of a predator/prey competition. This current model is in many ways the simplest possible form of competitive coevolution that can exist in any biological system. The model can be extended in a variety of ways. We plan to extend this model further by creating a version that works for sexually reproducing species not just asexual ones. It would also be warranted to investigate the addition of more species. We should also investigate whether there is any spatial patterning to this model. Are there pockets of high resistance and high poison located in different areas? Or are these values normally distributed across the grid? Finally, since this is an agent-based model and has parameters that can easily be compared to real-world data, it would be interesting to use real-world data on a competitive coevolutionary system, like a bacterial system.

It would be great to investigate a coevolutionary system like the garter snake and rough skinned newt [1]. Due to the average lifespans of these creatures, evolution occurs very slowly and thus it can be difficult to obtain enough data. However, if we can show that our model is properly validated, then we can use it to explore systems like the snake and newt at a much quicker pace since virtual evolution occurs much faster.

We have shown that we can reproduce classical equation-based models of the Red Queen effect, with a new model that has two different mobile species interacting on a spatial grid over time. The agent-based model allows us to draw a closer representation of reality than standard equation-based modeling does. Moreover, agent-based models provide an excellent teaching and experimental tool because their basic assumptions can easily be manipulated and explored. Finally, agent-based models generate such a wealth of information and data that they can easily be analyzed and thus facilitate an understanding of their emergent processes. This model is but one example of how to explore evolutionary processes using agent-based modeling.

6. REFERENCES

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Initial Model Settings	
Variable	*Setting*
Initial Number of Predators (n_{pred})	150
Initial Number of Prey (n_{prey})	150
Initial Mean Value of Resistance (μ_r)	25
Initial Mean Value of Poison (μ_p)	0, 5, 10, 15, 20, 25, 30, 35, 40, 45, 50
Carrying Capacity (C)	500
Experiment Settings	
Variable	*Setting*
Length of Each Run (in ticks)	5000
Number of Runs	10

Table 1: Model and Experiment Settings.
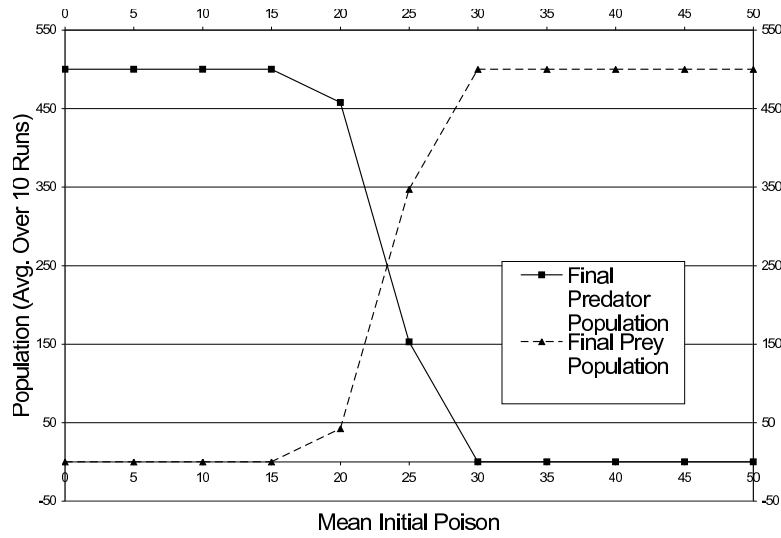
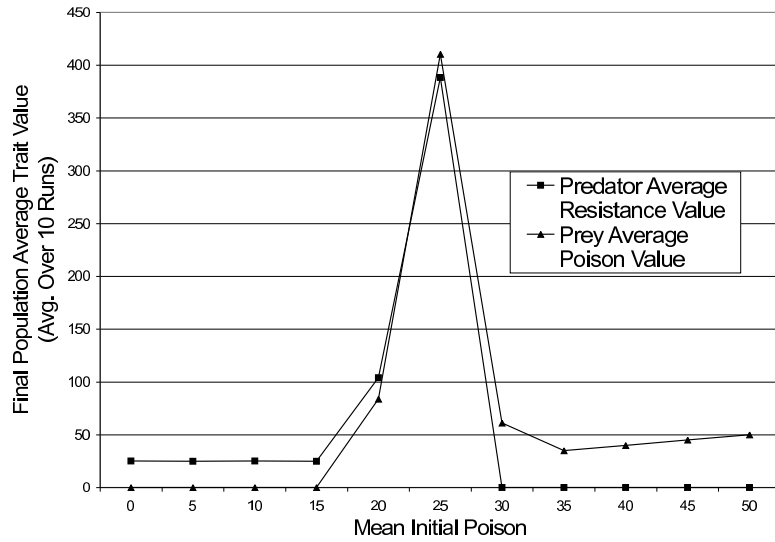Figure 2: Final population counts.
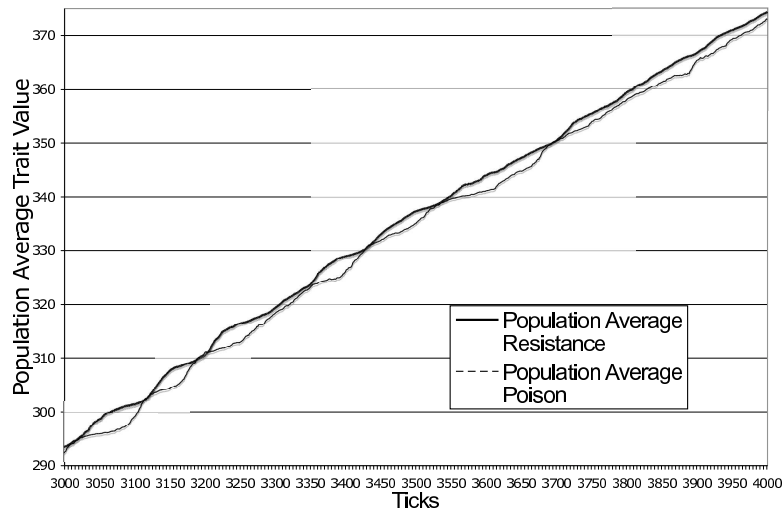

Figure 3: Final trait values.

Figure 4: Resistance and Poison values with Initial values, $\mu_p = \mu_r = 25$.

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