NATIONAL CENTER FOR CASE STUDY TEACHING IN SCIENCE

The Riddle of the Red Queen

Exploring Evolution and Extinction

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Now, here, you see, it takes all the running you can do, to keep in the same place.
— Lewis Carroll's *Through the Looking-Glass*

Everything changes, as Lyell (1832) knew from the fossil record, but everything is the same. — Leigh Van Valen, 1977

Introduction

Extinction is an ever-present threat for species. In order to remain competitive, populations must adapt not only to the changing environment but also to other species. Two ecologically competitive species, engaged in competition for similar resources or in a host-parasite symbiotic relationship, are known as antagonists (Riley, 2003). For example, if a particular bacterial population evolves resistance to its host's defenses, the host population must also evolve to combat the bacterial assault. Antagonistic species will continue to compete in this tit-for-tat manner until they reach a given level of equilibrium. This equilibrium may be static or dynamic; the former is met as species achieve an optimal state of coevolution and the latter when fully engaged in an evolutionary arms race. The latter scenario describes two at-odds populations locked in a perpetual duel to adapt reciprocally—where if one side falters, it loses its niche or adaptive advantage and faces extinction. This is the essence of the Red Queen Hypothesis (Rédei, 2008). First described by Van Valen (1973), the Red Queen Hypothesis commands that "any gain in fitness by one unit of evolution is balanced by losses in fitness by others," where improved fitness endows the successful species with greater control within the food chain (Van Valen, 1977). Over time, the "losing" species faces extinction.

Early evidence supporting this theory came from Van Valen's (1973) work examining patterns demonstrating logarithmic linearity in survivorship curves between genera/families within the fossil record (Figure 1). He noted in his work that the log of the slope at a given age is proportional to the probability of extinction at the same age. Therefore, he hypothesized that species evolve without a net increase in their overall fitness since they are continually countered by their competitors' adaptations. Thus improvement progresses at a constant rate that is (also) relative to one another. According to Brockhurst (2011), "He [Van Valen] suggested that this coevolutionary mechanism could explain why rates of extinction within animal groups remain near constant through geological time." As species incorporate more adaptations, the environment deteriorates, fostering a constant rate at which the species is expected to go extinct (Riley, 2003).

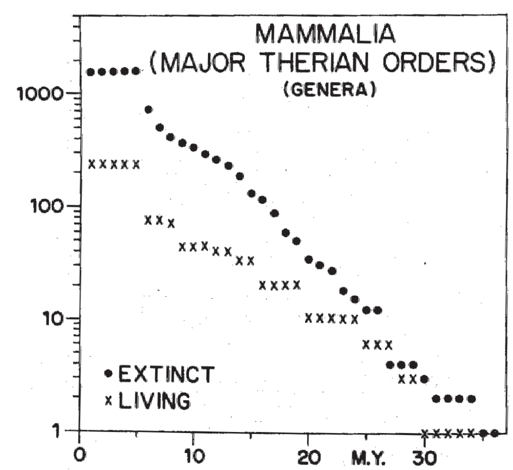

Figure 1. Survivorship curve. X-axis: number of species surviving. Y-axis: time in millions of years. *Credit:* Van Valen, L. 1973. A new evolutionary law. *Evolutionary Theory* 1: 1–30. Used with permission.

 Illustration of the Red Queen and Alice as they run in quest of promotion from Lewis Carroll's *Through the Looking Glass*, drawn by John Tenniel.

The Red Queen Hypothesis has remained relevant in evolutionary theory due to the benefits sexual reproduction affords organisms in the posited ability to rapidly develop new defenses, in particular for hosts against fast evolving parasites (Decaestecker et al., 2007). Sexual reproduction, within the Red Queen mode, is a means to respond to evolutionary challenges; yet sex as an adaptive strategy is not exclusive to antagonistic coevolution (Otto & Nuismer, 2004).

Studying the Red Queen dynamic is problematic. Changes in fitness are difficult to observe given they are not readily visible and occur over vast periods of (often geologic) time. Changes between antagonists may be minor, often occurring with slight modifications of genotypes over numerous generations, promoting little to no noticeable change in the phenotypes (Decaestecker et al., 2007). Additionally, outside ecological relationships such as predation and selection factors may influence alleles; therefore few naturalistic examples have been observed. However, in 19 mammalian clades developed from well-preserved fossils from 66 million years ago, it was determined that losses in species diversity was due to a Red Queen modality: a high rate of extinction compared to a lower rate of speciation (Red Queen Forces Extinctions, 2013). There is also evidence of the Red Queen's race taking place below the species level. The human immune system is hypothesized to be under the Red Queen effect, considering the rapid selective speed T-lymphocytes undergo to quickly respond to a multitude of innumerable antigens (Freitas & Rocha, 1997).

Objectives for this Case Study

By the end of this activity, you should be able to:

- Evaluate the research literature supporting the Red Queen Hypothesis.
- Interpret data to describe the Red Queen Hypothesis in a naturalistic experiment.
- Compare the Red Queen Hypothesis to other modalities of evolutionary theory, historical and present.

Part I – Explain, Describe, and Understand

Read the story below from Carroll's novel where Alice (of Wonderland fame) meets the Red Queen in Chapter 2 of *Through the Looking Glass.* If you are unfamiliar with the game of chess, see the brief explanation of key points in the box to the right. After reading the excerpt below, answer the questions that follow.

Notes on the Game of Chess

- Each player begins the game with sixteen pieces that are moved individually (per turn) to capture the opponent's pieces according to movement rules. The rule or ability of a piece to move is dictated by its type (or piece).
- The chess board is the surface in which the game is played between 2 players or opponents with 32 total pieces.
- A queen (only 1 per player) is considered the strongest piece of a set of pieces, able to move in any number of squares and in any direction per turn.
- A pawn (eight per player) is considered the weakest, only able to move 1 space in 1 direction per turn.
- Promotion is a rule in chess which a pawn may become any advanced piece (like a queen) by reaching the opposite side of the board without being taken by the opponent's pieces.
  - This is a difficult maneuver therefore very few pawns ever become queens.

For some minutes Alice stood without speaking, looking out in all directions over the country — and a most curious country it was. There were a number of tiny little brooks running straight across it from side to side, and the ground between was divided up into squares by a number of little green hedges, that reached from brook to brook.

"I declare it's marked out just like a large chessboard!" Alice said at last. "There ought to be some men moving about somewhere — and so there are!" She added in a tone of delight, and her heart began to beat quick with excitement as she went on. "It's a great huge game of chess that's being played — all over the world — if this Is *the world at all, you know. Oh, what fun it is! How I* wish *I was one of them! I wouldn't mind being a Pawn, if only I might join — though of course I should* like *to be a Queen, best."*

She glanced rather shyly at the real Queen as she said this, but her companion only smiled pleasantly, and said, "That's easily managed. You can be the White Queen's Pawn, if you like, as Lily's too young to play; and you're in the Second Square to began with: when you get to the Eighth Square you'll be a Queen —" Just at this moment, somehow or other, they began to run.

Alice never could quite make out, in thinking it over afterwards, how it was that they began: all she remembers is, that they were running hand in hand, and the Queen went so fast that it was all she could do to keep up with her: and still the Queen kept crying "Faster! Faster!" but Alice felt she could not *go faster, though she had not breath left to say so.*

The most curious part of the thing was, that the trees and the other things round them never changed their places at all: however fast they went, they never seemed to pass anything. "I wonder if all the things move along with us?" thought poor puzzled Alice. And the Queen seemed to guess her thoughts, for she cried, "Faster! Don't try to talk!"

Not that Alice had any idea of doing that. *She felt as if she would never be able to talk again, she was getting so much out of breath: and still the Queen cried "Faster! Faster!" and dragged her along. "Are we nearly there?" Alice managed to pant out at last.*

"Nearly there!" the Queen repeated. "Why, we passed it ten minutes ago! Faster!" And they ran on for a time in silence, with the wind whistling in Alice's ears, and almost blowing her hair off her head, she fancied.

"Now! Now!" cried the Queen. "Faster! Faster!" And they went so fast that at last they seemed to skim through the air, hardly touching the ground with their feet, till suddenly, just as Alice was getting quite exhausted, they stopped, and she found herself sitting on the ground, breathless and giddy.

The Queen propped her up against a tree, and said kindly, "You may rest a little now."

Alice looked round her in great surprise. "Why, I do believe we've been under this tree the whole time! Everything's just as it was!"

"Of course it is," said the Queen, "what would you have it?"

"Well, in our *country," said Alice, still panting a little, "you'd generally get to somewhere else — if you ran very fast for a long time, as we've been doing."*

"A slow sort of country!" said the Queen. "Now,* here, *you see, it takes all the running* you *can do, to keep in the same place. If you want to get somewhere else, you must run at least twice as fast as that!"

Questions

1. What would each item—the chessboard, Red Queen and the pawn—represent in the Red Queen Hypothesis?

2. Promotion is a rule in chess which a pawn may become any advanced piece (like a queen) by reaching the opposite side of the board without being taken by the other player's pieces. This is a difficult maneuver; very few pawns ever become queens. Compare and contrast promotion in the story with evolution by adaptation.

3. The last paragraph within the excerpt contains the phrase that inspired the name of Van Valen's theory. Using the entire quote (in bold), describe how the Red Queen's words represent the ideas of antagonistic coevolution.

Part II – Examine, Interpret, and Compare

Now we will examine the coevolutionary relationships between host and parasite in a naturalistic setting. Look at the graphs in Figure 2 of *Daphnia* (water fleas) and *Pasteuria* (bacterial microparasite), two symbiotic species preserved in pond sediment over time. Use these graphs to answer the following questions.

Questions

4. Describing the data:
   a. In Figure 2a and 2d, what can you determine about the ability of the parasite to infect its host?

   b. Figure 2b and 2e as compared to Figure 2c and 2f, how did spore production correlate with the *Daphnia's* ability to reproduce? (Note the y-axis indicates a decrease in *Daphnia* fecundity.)

5. Using this data, how has *Pasteuria* adapted (i.e., spore production, virulence and/or infectivity) as a parasite to its host over time?

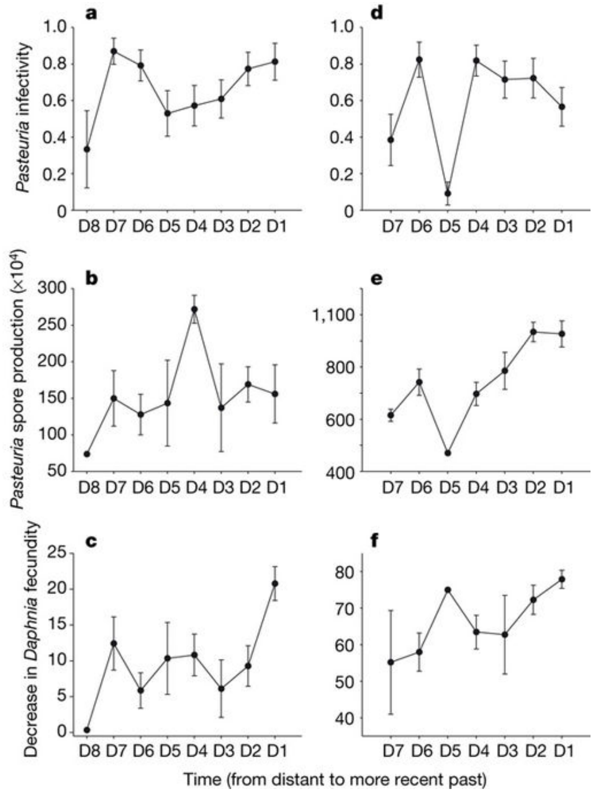

Figure 2. Pastura infectivity and virulence over time. **a–c**, Experiment 1; **d–f**, experiment 2. **a**, **d**, *Pasteuria* infectivity; b,e, *Pasteuria* spore production; **c**, **f**, decrease in *Daphnia* fecundity (clonal average of control individuals minus clonal average of infected individuals). Results are means ± s.e.m. and include only "contemporary" combinations. Time reflects parasite isolate depth, with D8 referring to the oldest sediment layer. The effects of parasite isolate depth as continuous covariable in a general linnear model (including significant effects of experiment; parasite isolate depth was nested in experiment) are as follows: on *Pasteuria* infectivity, $F_{2,108}$ – 0.52, P = 0.59; on *Pasteuria* spore production, $F_{2,80}$ = 9.6, P = 0.0002; on decrease in *Daphnia* fecundity, $F_{2,81}$ = 5.03, P = 0.009.

Source: Decaestecker et al., 2007. Reprinted by permission from Macmillan Publishers Ltd: *Nature*, © 2007.

6. In this experiment, lake sediments preserved stable samples of the parasite and host. What is one potential difficulty in studying antagonistic evolution in real-time or extant populations?

Part III – Apply and Analyze

Newly studied parasite-host relationships have demonstrated the influence of and preference for sexual reproduction in antagonistic coevolving species. Evaluate the following study to answer the questions further below.

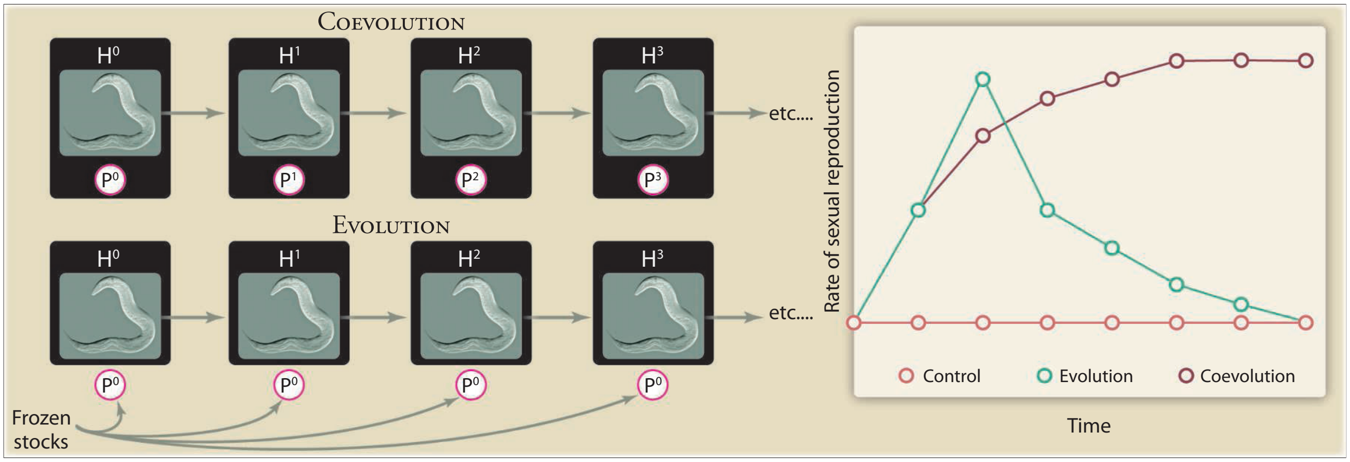

Figure 3. Parasite–host interaction in nematodes. *Credit:* From Brockhurst, M.A. 2011. Sex, death and the Red Queen. *Science* 333(6039): 166–167. Reprinted with permission from AAAS.

Brockhurst (2011), in a commentary on a study by Morran *et al.* (2011), discussed experimental evidence that coevolving parasites may select for sexual reproduction in their host species; specifically, how sexual reproduction may accelerate adaptation by examining a host, capable of both asexual and sexual reproduction, adapting to a parasite over a period of time. Using a Nematode worm host (H) and its corresponding parasite (p), they devised two tests. First, they allowed the two species to co-evolve over numerous generations of both host (H^0, H^1, H^2, H^3) and parasite (P^0, P^1, P^2, P^3). Then, using frozen stocks of parasite (P^0, P^0, P^0, P^0), they infected a new generation of the host (H^0, H^1, H^2, H^3) to examine the one-sided evolutionary progression of the host only. The rate of sexual reproduction of the host was graphed for both scenarios and compared to a control.

Questions

7. Compare the rate of sexual reproduction for the coevolving scenario as compared to the evolution scenario. What was the preferred adaptive strategy of the host species for coevolution? For evolution? Why?

8. What was occurring at the spike and quick decline in the evolution graph? Base your response in the context of the Red Queen Hypothesis (i.e., host adaptation, parasite adaptation, fitness loss, and deteriorating environment).

9. Sexual reproduction is not an adaptive advantage solely for species in antagonistic coevolving interactions. Explain how another symbiotic relationship (i.e., mutualism) supports sex as an adaptive strategy using two distinct species in a mutualistic symbiosis. Make sure to cite your sources.

Part IV – Evaluate and Create

The passage below is from Darwin's first edition of his landmark work, *On the Origin of Species*. In later editions, he removed the last statement regarding "wedges" due to a lack of experimental evidence at that time. Read the passage and then answer the question.

> *In looking at Nature, it is most necessary to keep the foregoing considerations always in mind—never to forget that every single organic being around us may be said to be striving to the utmost to increase in numbers; that each struggles at some period of its life; that heavy destruction inevitably falls either on the young or the old, during each generation or at recurrent intervals. Lighten any check, mitigate the destruction ever so little, and the number of species will almost instantaneously increase to any amount.* ***The face of Nature may be compared to a yielding surface, with ten thousand sharp wedges packed close together and driven inwards with incessant blows, sometimes one wedge being struck, and then another with greater force.***

Figure 4. Portrait of Charles Darwin, late 1830s, by G. Richmond, public domain.

Question

10. Compose a letter to Darwin comparing his early ideas to modern evolutionary theory. In your correspondence, address the arguments (underlined) regarding the struggle for existence, threat of extinction, and how his "wedges" idea is supported by current evidence and the ideas of the Red Queen Hypothesis. Cite any sources.