The Red Tooth Hypothesis: Predator-prey relations and sexual reproduction

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This paper presents an extension of the Red Queen Hypothesis (hereafter, RQH) that we call the Red Tooth Hypothesis (RTH), after Tennyson’s characterization of the predatory nature of Nature as being “red in tooth and claw.” RTH highlights the role of predator-prey relations in the maintenance of sexual reproduction in higher animals. RTH is based on an interaction between learning on the part of predators and evolution on the part of prey. We present the results of a predator-prey simulation that illustrate the effects of this interaction.

RQH was originally proposed by Van Valen (1973) as a means of explaining log-linear taxonomic survivorship curves. Jaenike (1978), Hamilton (1980), Bell (1982), Howard & Lively (1994, 2003), and others subsequently suggested that RQH was responsible for the existence and maintenance of sexual reproduction in essentially all species of higher animals. Without recourse to (discredited) theories of species selection, RQH specifies the benefits provided by sexual reproduction that would offset its elevated genetic cost to individual organisms — namely, half of their genetic material, what Williams (1975) called the “cost of meiosis.” The most common current construal of RQH is in terms of host-parasite relations. The idea is that the reproductive rates of parasites are four to six orders of magnitude faster than that of their hosts and, as a result, for each generation of the host, the parasites have hundreds of thousands of generations of mutation-engendered opportunities to unlock the defense mechanisms of potential hosts. So, while a fortunate mutation might provide an individual with an effective defense against a given parasite, mutation alone would not be sufficient to protect that individual from a wide range of different parasites. RQH posits that only the exchange of genetic material via sexual reproduction would allow some individuals to acquire the full range of protective mechanisms required to fend off a wide range of parasites. So, while the cost of sexual reproduction is half of one’s genetic material, at least the half that survives into the next generation has a reasonable chance of surviving attacks by parasites. In other words, while asexual reproduction would ensure full transmission of an individual’s genes, these unchanging genes would eventually succumb to parasites.

The present article acknowledges the role of RQH in the emergence and maintenance of sexual reproduction, but, in addition, suggests that sexual reproduction would probably have evolved because of predator-prey relations, even in the absence of classic parasite/host relations characterized by highly different reproduction rates.

First, we begin with the observation that virtually all higher animals are in predator-prey relationships with other animals. Particularly when the predator is close at hand, prey when escaping rely on unlearned, reflexive escape patterns (Alexander, 2003). These patterns are presumably genetically engendered. A baby gazelle, for example, does
not have to be taught its escape pattern the first time it encounters a lion. Pongráz and
Altbäcker (2000) have recently shown that the predatory escape-patterns of rabbits
\textit{(Oryctolagus cuniculus)} do not require any previous experience with predators,
buttressing the claim of innate (i.e., genetically engendered) escape patterns.

Second, we assume that predators have sufficiently developed neural circuitry to
allow them to learn from their hunting experiences, both successes and failures. This
implies that if prey escape patterns did not vary, predators could learn them, or at least
parts of them, which would give them a significant adaptive advantage over their prey.

It would, therefore, be advantageous for prey to be able to have “unpredictable
elements” in their escape response to prevent predators from gaining this advantage. This
behavioral unpredictability has been called “protean behavior” (Driver & Humphries,
\textit{C. crangon}, comment that, “Unpredictable elements of the escape response have been
shown to be a prominent feature of \textit{C. crangon} escape swimming and are probably
important in preventing predators from learning a fixed pattern of response.” Miller
(1997) also makes a similar point about the advantage of the use of random escape
patterns. But this raises the crucial issue of exactly how these “unpredictable elements of
the escape response” can arise. Random behavior mechanisms in an organism are never
really random and, in any case, choosing among different possible flight responses would
be time-consuming and potentially life-threatening. This, however, is not necessary if the
unpredictability required to enhance escape arises not from the individual, but, rather,
from the population of individuals. In other words, an individual prey animal is best
served by having a fixed, reflexive, and therefore, maximally rapid escape sequence, but
that is unlearnable by predators because other similar animals have randomly different
escape sequences.

From the predator’s point of view, there is no difference between an individual prey
animal possessing a large set of random escape patterns itself and individual prey animals
each having fixed escape patterns, but with those patterns being randomly distributed
over the population. In both cases, for the predator the result is the same: predicting what
an individual prey animal will do becomes impossible. For prey, population-level
randomization of escape patterns is the optimal solution: the animal can escape in a
maximally reflexive (and thus rapid) manner, yet be protected as if it had made a decision
to choose one among many escape patterns to fool the predator.

This randomness of escape patterns is best generated through crossover at the level
of the genes responsible for producing escape patterns. We present a series of simulations
in which predators are modeled as simple recurrent neural networks (Elman, 1990)
designed to learn sequences. These networks gradually learn short segments of the escape
sequences of prey. Each instance of pursuit of prey constitutes a learning trial for the
predator. On the other hand, a prey’s failure to escape a predator is (obviously) not a
learning experience for the prey. Escape patterns of prey therefore evolve, not during the
lifetime of the animal, but over evolutionary time. We compare prey survivorship rates
when this evolution is based on mutation alone or on sexual reproduction (Figure 1). We
use a standard genetic algorithm (Holland, 1975; Goldberg, 1989, Mitchell, 1996) to
model sexual reproduction over generations of escape patterns of the prey. Fitness is
measured by how far the prey is from the predator after a fixed number of time steps after
initiation of the predator’s attack. Escape patterns for prey that are caught by the predator are assigned a fitness of zero.

The conundrum of mutation-driven evolution, as Williams (1975) pointed out, is that evolution, which relies on mutation-driven variability, has evolved myriad mechanisms to keep mutation rates as low as possible. This would imply that the innate, genetically engendered escape patterns of prey animals would evolve only slowly if mutation were the sole mechanism modifying them and this would increase the likelihood that predators could learn them. On the other hand, sexual reproduction would provide precisely the mechanism that would ensure escape-pattern randomness at the population level and also allow each individual prey animal to have its own reflexive — but, nonetheless, unlearnable — escape pattern. Figure 1 shows the different survival rates of prey under sexual reproduction versus mutation. Further, while Figure 1 demonstrates that high mutation rates alone can generate escape-pattern randomness at the population level, high mutation rates have other, almost invariably deleterious effects on individuals in the population. This, again, argues for the advantages of sexual reproduction as a strategy that produces highly random escape patterns at the population level, while allowing mutation rates to remain as low as possible.

![Figure 1](image.png)

Figure 1. The survival rates of prey where escape-trajectory genes are influenced only by mutation versus when sexual reproduction mixes the gene pool.

Our simulations demonstrate a manner in which learning can drive evolution that is not Lamarckian and does not rely on Baldwin-like effects (Baldwin, 1896; Morgan, 1896; Hinton & Nowlan, 1987; French & Messinger, 1994). We will discuss a number of predictions that derive from RTH, such as, the randomness in the population of prey escape patterns will be proportional to the intelligence of the predator, predictions about rates of parthenogenesis in animals raised in sterile, predator-free environments versus sterile environments in which predators remain, etc. Some of these predictions could be tested with heterogamous animals, as they have been for RQH (Lively, 1987). RTH would, for example, predict that heterogamous animals in asexual reproductive mode would tend to switch to sexual reproduction when the predator density in their
environment increased, which is known to be the case for the freshwater crustacean *Daphnia* which is known to reproduce by parthenogenesis then switches to sexual reproduction as competition and predation increase.

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**References**


