Red Queen hypothesis

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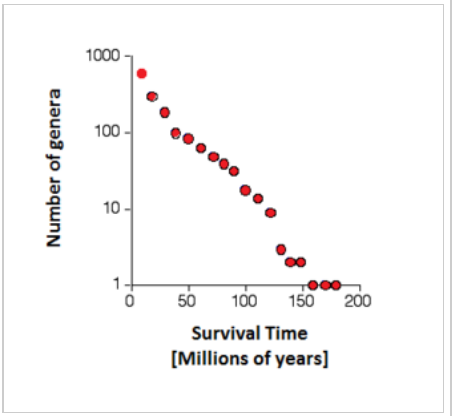
The **Red Queen hypothesis**, also referred to as **Red Queen's**, **Red Queen's race** or **The Red Queen Effect**, is an evolutionary hypothesis which proposes that organisms must constantly adapt, evolve, and proliferate not merely to gain reproductive advantage, but also simply to survive while pitted against ever-evolving opposing organisms in an ever-changing environment. The Red Queen hypothesis intends to explain two different phenomena: the constant extinction rates as observed in the paleontological record caused by co-evolution between competing species[1] and the advantage of sexual reproduction (as opposed to asexual reproduction) at the level of individuals.[2]

The original idea of the Red Queen hypothesis was given by Leigh Van Valen in order to explain the "Law of Extinction".[1] Leigh Van Valen showed that in many populations the probability of extinction does not depend on the lifetime of this population. In addition, the probability of extinction is constant over millions of years for a given population. This could be explained by the coevolution of species. Indeed, an adaptation in a population of one species (e.g. predators, parasites ...) may change the selection pressure on a population of another species (e.g., prey, hosts), giving rise to an antagonistic coevolution. If this occurs reciprocally, a potential dynamic coevolution may result.[3]

In another idea, the Red Queen hypothesis is used independently by Hartung [4] and Bell to explain the evolution of sex,[2] by John Jaenike to explain the maintenance of sex[5] and W. D. Hamilton to explain the role of sex in response to parasites.[6][7] In all cases, sexual reproduction confers species variability and a faster generational response to selection by making offspring genetically unique. Sexual species are able to improve their genotype in changing conditions. Consequently co-evolutionary interactions, between host and parasite for example, may select for sexual reproduction in hosts in order to reduce the risk of infection. Oscillations in genotype frequencies are observed between parasites and hosts in an antagonistic coevolutionary way[8] without necessitating changes to the phenotype.



The Red Queen at the genus level. The linear relationship between number of genera and the logarithm of survival times suggests that the probability of extinction is constant over time. Redrawn from Leigh Van Valen (1973).

Contents

Etymology

The phenomenon's name is derived from a statement that the Red Queen made to Alice in Lewis Carroll's *Through the Looking-Glass* in her explanation of the nature of Looking-Glass Land:

> Now, *here*, you see, it takes all the running you can do, to keep in the same place.[9]

Van Valen coined the hypothesis "Red Queen" because under this interpretation where species have to "run" or evolve in order to stay in the same place or remain extant.

Arms race

Biological definition

Parasites are in a constant arms race with their host: harvestman suffering from mite pest.

Leigh Van Valen (1973) proposed the metaphor of an evolutionary arms race which was appropriate for the description of biological processes with dynamics similar to arms races. In this processes, an adaptation in a population of one species (e.g., predators, parasites) may change the selection pressure on a population of another species (e.g., prey, host), giving rise to an antagonistic coevolution.[3]

Interspecies arms race :

- A number of predator/prey couple where the weapon involved is the running speed.

"The rabbit runs faster than the fox, because the rabbit is running for his life while the fox is only running for his dinner." Aesop[10]

- The interactions between parasitoid wasps and insect larvae, necessary for the parasitic wasp's life cycle, are also a good illustration of arms race. Indeed, some evolutionary strategy was found by both partners to respond to the pressure generated by the mutual association of lineages. For example, the parasitoid wasp group, *Campoletis sonorensis*, are able to fight against the immune system of their hosts, *Heliothis virescens* (Lepidopteran) with the association of a polydnavirus (PDV) (*Campoletis sonorensis* PDV). During oviposition process, the parasitoid transmits the virus (*Cs*PDV) to the insect larva. The *Cs*PDV will alter the physiology, growth and development of the infected insect larvae to the benefit of the parasitoid.[11]

Court jester hypothesis

A competing evolutionary hypothesis is the court jester hypothesis which indicates that an arms race is not the driving force of evolution on a large scale, but rather it is abiotic factors.[12][13]

The emergence of concept and illustrations

Van Valen proposed the Red Queen hypothesis as an explanatory tangent to his proposed "Law of Extinction" (also 1973), which he derived from observation of constant probabilities of extinction within families of organisms across geological time. Put differently, Van Valen found that the ability of a family of organisms to survive does not improve over time, and that the lack of correlation between age and extinction is suggestive of a random process.[1] The Red Queen hypothesis as formulated by Van Valen provides a conceptual underpinning to discussions of evolutionary arms races, even though a direct test of the hypothesis remains elusive, particularly at the macroevolutionary level. This concept remains similar to that

of a system obeying a self-organized criticality.[14]

For example, because every improvement in one species will lead to a selective advantage for that species, variation will normally continuously lead to increases in fitness in one species or another. However, since different species tend to co-evolve, improvement in one species implies that it will get a competitive advantage over the other species, and thus be able to capture a larger share of the resources available to all. This means that fitness increase in one evolutionary system will tend to lead to fitness decrease in another system. The only way that a species involved in a competition for resources can maintain its fitness relative to other competing species is by improving its specific fitness. (From Heylighen, 2000)

The most obvious example of this effect are the "arms races" between predators and prey (e.g., Vermeij, 1987), where the only way predators can compensate for a better defense by the prey (e.g., rabbits running faster than their parents) is by developing a better offense (e.g.. foxes running faster than their parents). In this case we might consider the relative improvements (rabbits running faster than foxes or vice versa) to be also absolute improvements in fitness. (From Heylighen, 2000)

Such examples of arms races can also be applied to human conflict and can be seen as a prominent cause of conflict. According to Azar Gat, the Red Queen effect is established when two competing groups find themselves in a security dilemma. The security dilemma, resulting from defensive measures taken to improve one's security which possess inherent offensive capabilities, triggers a military arms race. This arms race, much like the example previously referenced, causes each side to consume ever increasing amounts of resources in order to outpace the other and gain an advantage. If an advantage is gained, the arms race is over and the group with more resources has won. However, typically both sides continue to match each other stride for stride, thus triggering the Red Queen effect as no matter how many resources each side invests, neither is able to gain an advantage. The situation is somewhat similar to the prisoner's dilemma. Each side cannot stop the arms race because of mutual suspicion and fears that the other group will gain a significant tactical advantage. Because of this, the Red Queen effect is a common outcome of inter-human competition and conflict.[15]

Discussions of sex and reproduction were not part of Van Valen's Red Queen hypothesis, which addressed evolution at scales above the species level. The microevolutionary version of the Red Queen hypothesis was proposed by Bell (1982), also citing Lewis Carroll, but not citing Van Valen. See below.

The paradox of sex: The "cost" of males

Science writer Matt Ridley popularized the term "the red queen" in connection with sexual selection in his 1993 book *The Red Queen*. In the book, Ridley discussed the debate in theoretical biology over the adaptive benefit of sexual reproduction to those species in which it appears. The connection of the Red Queen to this debate arises from the fact that the traditionally accepted theory (*Vicar of Bray*) only showed adaptive benefit at the level of the species or group, not at the level of the gene (although, it must be added here that the protean "Vicar of Bray" adaptation is very useful to some species that belong to the lower levels of the food chain). By contrast, a Red-Queen-type theory that organisms are running *cyclic* arms races with their parasites can explain the utility of sexual reproduction at the level of the gene by positing that the role of sex is to preserve genes that are currently disadvantageous, but that will become advantageous against the background of a likely future population of parasites.

Further evidence was observed of the Red Queen to see allelic affects under sexual selection. The Red Queen Hypothesis leads to the understanding that allelic recombination is advantageous for populations that engage in aggressive biotic interactions, such as predator-host interactions. In cases of predator-host relations, sexual reproduction can quicken the production of new multi-locus genotypes allowing the host to escape invasion by parasites that have adapted to the prior generations of typical parasites.[16] Mutational effects can be represented by mutational models to describe how recombination through sexual reproduction can be advantageous. According to the mutational deterministic hypothesis if the deleterious mutation rate is

high, and if the deleterious mutations interact to cause a general decline in organismal fitness, then sexual reproduction provides an advantage over asexually reproducing organisms by allowing populations to eliminate the deleterious mutations not only more rapidly, but also most effectively.[16] Recombination is one of the fundamental means that explain the reason many organisms have evolved to reproduce sexually.

Sexual organisms must spend resources to find mates. In the case of sexual dimorphism, usually only one of the sexes contributes to the survival of their offspring. In such cases the only adaptive benefit of having another sex is the capability of sexual selection, by which organisms can improve their genotype. In this way, sexual reproduction can be highly inefficient.

Observational evidence

Evidence for this explanation for the evolution of sex is provided by comparison of the rate of molecular evolution of genes for kinases and immunoglobulins in the immune system with genes coding other proteins. The genes coding for immune system proteins evolve considerably faster.[17][18]

Further evidence for the Red Queen hypothesis were provided by observing long-term dynamics and parasite coevolution in a "mixed" (sexual and asexual) population of snails (*Potamopyrgus antipodarum*). The number of sexuals, the number of asexuals, and the rates of parasite infection for both were monitored. It was found that clones that were plentiful at the beginning of the study became more susceptible to parasites over time. As parasite infections increased, the once plentiful clones dwindled dramatically in number. Some clonal types disappeared entirely. Meanwhile, sexual snail populations remained much more stable over time.[19][20]

In 2011 researchers used the microscopic roundworm *Caenorhabditis elegans* as a host and the pathogenic bacteria *Serratia marcescens* to generate a host-parasite coevolutionary system in a controlled environment, allowing them to conduct more than 70 evolution experiments testing the Red Queen hypothesis. They genetically manipulated the mating system of *C. elegans*, causing populations to mate either sexually, by self-fertilization, or a mixture of both within the same population. Then they exposed those populations to the *S. marcescens* parasite. It was found that the self-fertilizing populations of *C. elegans* were rapidly driven extinct by the coevolving parasites while sex allowed populations to keep pace with their parasites, a result consistent with the Red Queen hypothesis.[21][22]

Historical studies

The influence of heterogeneity in species genomes has been recognized and studied since the time of Darwin (1876) in the areas of heterosis (hybrid vigor), inbreeding and genetic deterioration, operating on the theory that lessening of the choice of gene variants and of potential cooperation among different gene types limits the capabilities of the restricted organism.[23]

A study published in 2013 in *Science* which examined the history of groups of extinct mammals illustrates failure to adapt and evolve new species when confronted by a deteriorating environment.[24][25] An interesting insight can be obtained from physical research.[26]

See also

- Evolutionary arms race
- Chaos theory
- Punctuated equilibrium
- Heterosis
- Self-organized criticality
- Leigh Van Valen

- W. D. Hamilton

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Categories: Evolutionary biology
