Red Queen Runs into Trouble?

An important evolutionary model—the Red Queen hypothesis—has been reformulated, potentially to give a different view of the world

It is not often that theorists in evolutionary biology appeal to paleontologists for help in resolving evolutionary models. But this happened recently over the contrasting claims of the similarly derived mathematical models known as the Red Queen and Stationary hypotheses, which address the likely evolutionary state of communities at equilibrium.

The Red Queen model predicts continued evolutionary change under conditions of constancy in the physical environment. Its competitor indicates that in an undeviating environment evolution would grind to a halt, to be kicked into gear again only when external conditions alter. In essense, the question is whether a major engine of evolutionary change comes from biotic sources (changes in other species in the community), as in the first model, or from abiotic sources (changes in the physical environment), as in the second.

Theory alone cannot make a choice between the two models because the values of certain variables in the mathematical formulations are simply not known; these values relate to aspects of interactions between species within a given ecosystem. Therefore, say Nils Stenseth of the University of Oslo, Norway, and John Maynard Smith of the University of Sussex, England, "the choice between Red Queen and Stationary models will have to depend primarily on paleontological evidence" (*1*).

So far two teams of paleontologists have independently taken up the challenge, the result of which is that, perhaps unsurprisingly, each model has been awarded one vote (*2, 3*). This split decision is a measure of two things: first, the legendary "imperfection" of the fossil record; second, and more important, the great complexity of the evolutionary dynamics of ecological communities over periods of evolutionary time, during which *nothing* is truly constant, least of all the physical environment.

Although they conflict in their results, these two paleontological excursions into the territory of evolutionary theory represent a major achievement in a difficult subject and offer specific suggestions for further improvement.

The Red Queen hypothesis was independently conceived in 1973 by Leigh Van Valen of the University of Chicago and Michael Rosenzweig of the University of Arizona at Tucson. At its core is the idea that the most important component of a species' environment is other species; an evolutionary advance achieved by any one species will, through a close network of interactions, represent a deterioration in the environment of all other species; as a result, these other species are under selective pressure to achieve evolutionary advances of their own, simply to catch up. Rosenzweig called it the "Rat Race," partly because he was interested in predator/prey relationships, but Van Valen's suggestion of the Red Queen hypothesis—running in order to remain in the same place—prevailed.

In the Red Queen model there is an assumption that for each species there is an optimum adaptive peak to which the species is evolving. The problem is that the peak continually recedes because the environment—specifically the biotic environment—is constantly deteriorating. So, even if climatic and other physical factors remain unchanged, evolution will tick over at a steady rate, some species gradually changing, some going extinct, and new ones originating. The model is less precise about what is to be expected at times of shifting environmental conditions, but the rate of evolutionary change is likely to be enhanced in one direction or another.

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In reformulating the Red Queen hypothesis Stenseth and Maynard Smith adopt the assumptions that species are an important aspect of each other's environment and that for each species there is a local adaptive peak towards which selection is pushing it. They introduce the idea of evolutionary lag, or "lag load", which is a measure of how far from the adaptive peak a species finds itself and therefore of the rate of evolution it is likely to be undergoing.

A key departure from Van Valen's formulation, however, is in the matter of the "zero sum" assumption. This aspect of the Red Queen model suggests that the beneficial effect enjoyed by a species in evolutionary advance is precisely matched by the sum of the negative effects experienced by all the other species, which is a component of the argument that the rate of evolution will be constant. The zero sum assumption is based in part on the notion that the total resources available in the system are constant which Stenseth and Maynard Smith dismiss as invalid.

Following through with their reformulation of the Red Queen model, the two theorists conclude that of a series of predictions that emerge from the mathematics, there are just two plausible alternatives: the Red Queen hypothesis is one and the Stationary hypothesis the other. Which way the model's equations would go depend on values that reflect the degree of ecological connectedness among communities.

Maynard Smith explains it this way: "If the world were strongly connected, so that every time one species changed then all others are forced to change too, then the Red Queen model would hold. But if it were only weakly connected, so that evolution in one species only little affects other species, then you'd have the Stationary model. Where along that spectrum the real world lies, I do not know."

The Stationary model predicts no evolutionary activity during periods of absolutely no perturbations in the physical environment; but as soon as the physical environment alters, lag loads are likely to increase, thus driving evolution. Periods of stasis would thus be punctuated by periods of change, including speciation and extinction, the balance between which would determine the overall shift in species diversity. As the Red Queen hypothesis is most precise about what is to be expected during intervals of environmental change, the proper test to discriminate between the two in the fossil record is to look at physically quiescent periods.

Antoni Hoffman of the Lamont-Doherty Geological Observatory and Jennifer Kitchell of the University of Wisconsin sought an answer in evolutionary patterns among pelagic plankton over the past 40 million years as revealed in 111 Deep Sea Drilling Project sites from the low- to mid-latitude Pacific Ocean (*2*). Their conclusion was positive but modest support for the Red Queen. But, as it is virtually impossible to determine whether a steady level of evolutionary activity observed in the fossil record is the result of the highly connected world of the Red Queen or a small, not readily detectable, but real oscillation in physical environmental conditions, the test cannot be unequivocal.

The second test, by Kuo-Yen Wei and James Kennett of the University of Rhode Island, also utilizes the planktonic record, this time collected globally and representing the past 22 million years (*3*). These researchers recognize three distinct periods in this slice of evolutionary history: an initial stage of diversification, between 22 and 16 million years ago; a period of relative equilibrium, lasting from 16 to 5 million years ago; and a declining stage from 5 million years on.

Important in the current context is the observation that the boundaries between the stages are marked by drastic environmental changes, such as major cooling events. Such changes inevitably increased evolutionary lag load, which therefore triggered evolutionary activity. Overall species diversity increased when the current diversity level was below the equilibrium level, decreased when it was above, and remained stable when they were roughly equal. Some climatic changes apparently reset equilibrium diversity levels.

Wei and Kennett judge these observations to be consistent with the predictions of the Stationary model. They can see no way of finding with any great confidence periods of environmental constancy during the oceanic fossil record of the past 22 million years, and therefore concede that, as currently formulated, "The Red Queen hypothesis can be neither corroborated nor rejected." Wei and Kennett, like Hoffman and Kitchell, would prefer to compare specific predictions for periods of environmental change.

When Van Valen's Red Queen hypothesis was first proffered it was greeted as a "major step toward . . . interpreting the evolutionary record in terms of general rules and processes." Its further development and marriage with some high-quality paleontological and paleoenvironmental data promise further valuable insights.—ROGER LEWIN

References

1. N. C. Stenseth and J. Maynard Smith, *Evolution* **38**, 870 (1984).
2. A. Hoffman and J. A. Kitchell, *Paleobiology* **10**, 9 (1984).
3. K.-Y. Wei and J. P. Kennett, *ibid.*, in press.

Eastern Quakes Pinned Down?

Two groups of researchers have found convincing evidence in a drainage ditch near Charleston, South Carolina, that the large, damaging earthquake that occurred there in 1886 had at least two prehistoric predecessors. The discovery is the first step in testing the increasingly popular idea that, in contrast to the West, large earthquakes can strike almost anywhere along the eastern seaboard. If only a few, presumably identifiable geological structures along the East Coast can produce large earthquakes, engineers designing nuclear power plants and other critical facilities could be far more certain of the level of safety needed in their design.

Dead horses usually do not figure in a field geologist's or seismologist's work, but one certainly helped researchers pick up the trail of prehistoric Charleston earthquakes. During the search for geological evidence, a farmer informed inquirers that his granddad had told how a jet of wet sand shot out of the ground in 1886. Many reports of such sand blows survive, but lingering evidence of them on the surface had not been found. The farmer knew the spot, however, because a pesky horse had been shot and dumped on the sand-blow crater, the skeleton remaining as a marker. After cutting trenches through the spot, John Cox and Pradeep Talwani of the University of South Carolina had a good idea of what traces remain after the shaking of a large earthquake liquefies shallow, water-saturated sand so that it shoots to the surface through a crater or fissure.

It was Stephen Obermeier and his colleagues at the U.S. Geological Survey (USGS) in Reston, Virginia, who first hit the sand-blow bonanza at the ditch near Hollywood, South Carolina, on which they report in this issue of *Science* (p. 408). Cut to drain the wet, low-lying land, the 2- to 3-meter-deep ditch revealed dozens of filled sand-blow craters along its walls. Some look fresh enough to have been created in 1886, but many others have enough slow-growing organic soils developed in them to show that they predate 1886. Carbon-14 dating of the soils from one crater constrains its age to lie between 1400 and 4700 years. And at least one prehistoric crater cuts through all parts of another, demonstrating that one large (greater than magnitude 5.5) prehistoric earthquake followed another.

Cox and Talwani later independently studied sand-blow craters in the Hollywood ditch and have confirmed the existence of at least two prehistoric Charleston earthquakes. They also have about a dozen carbon-14 dates from soil and roots that limit the two prehistoric events to the period between 1200 and 3000 years ago.

Evidence of recurring Charleston earthquakes is important because no one has ever been able to find the deeply buried fault that slipped and caused the 1886 damage and loss of life. Some researchers have argued that there is not simply the one fault in the Southeast capable of generating large earthquakes. Charleston may not be a special case; instead, there could be many sites—unrecognized and perhaps unrecognizable—where large earthquakes could strike. According to one model, much of the eastern seaboard is underlain by a horizontal fault or detachment that could, for instance, slip beneath North Carolina as readily as it did in 1886 near Charleston. Another model has numerous threatening faults along the coast.

Such uncertainty led the USGS to advise the Nuclear Regulatory Commission in late 1982 that a historical record of only one large earthquake was not sufficient reason to presume—as had been done—that such earthquakes could not strike elsewhere east of the Appalachians. The siting of a nuclear power plant a great distance from Charleston, the USGS suggested, might not provide it with sufficient protection.

The new fieldwork in the Charleston area supports the view that there is something geologically special about Charleston—some structure in the crust leads to repeated large earthquakes there. The next step will be to search for paleoseismological evidence of large earthquakes on the eastern seaboard where there is no historical record of them, such as near the central Virginia zone of low-level seismicity or near the Ramapo fault outside New York City. Only then can anyone say how widespread large earthquakes can be on the East Coast.—RICHARD A. KERR