EVOLUTIONARY BIOLOGY

Microbes Hint at a Mechanism Behind Punctuated Evolution

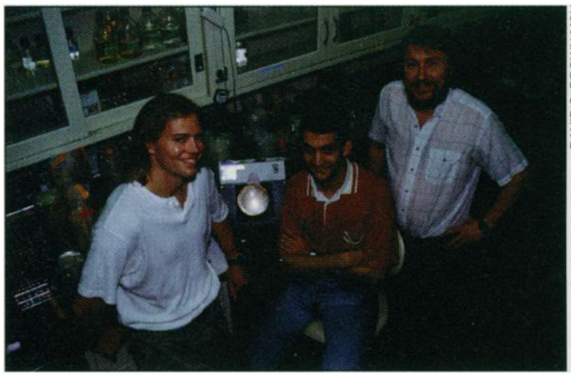
Back in 1988, evolutionary biologist Richard Lenski inoculated a flask of low-sugar broth with a dollop of bacteria and began a long-running experiment in evolutionary dynamics. Among the questions he hoped to address was one of the prominent evolutionary issues of the past 2 decades: whether evolution is best described as a smooth pattern of gradual change, or as the stop-and-start pattern known as punctuated equilibrium.

Every day, Lenski or a co-worker siphoned a bit of the bacterial broth into a fresh flask of food to keep the cells growing and dividing, and every 15 days they froze a sample for later analysis. Four years later, the team had amassed a freezer full of data on how the bacteria had evolved over an impressive 10,000 generations—long enough to see evolution in action. Now, on page 1802, Lenski, postdoc Santiago F. Elena, and graduate student Vaughn S. Cooper, all of Michigan State University (MSU), report a punctuated pattern in the evolution of bacterial cell size. They found that cells tended to persist at one average size for many generations, then suddenly go through growth spurts. "You can very clearly see dynamics that are punctuated, and that it's arising in this extremely simple system," says Lenski.

Evolutionary biologists say that this elegant experiment offers a rare window into change on an evolutionary time scale in living organisms—although paleontologists note that these results don't quite fit the classical idea of punctuated equilibrium and may not help explain patterns in the fossil record. But the experiment suggests that a simple genetic mechanism—natural selection of rare, beneficial mutations—may lead to complex punctuated patterns. "Showing that microbes go through long periods of hanging out followed by bursts of adaptation … is an important step" in understanding evolution, says biologist Margaret Riley of Yale University.

Lenski's group ran its experiment on the microbial workhorse, *Escherichia coli*. They started with a single cell of a strain that, unlike many bacteria, is unable to exchange DNA. Thus, spontaneous mutations were the only source of genetic change in the population. The team also built a selective force into the experiment by keeping food scarce. Over time, measurements showed that the cells grew larger, which researchers suspect is an advantage for life in the low-sugar lane. Large cells may have more energy reserves than smaller ones, says Lenski, although he notes that large size could also simply be a side effect of another trait that confers faster growth.

But there's no doubt that over time, the bacteria adapted to their low-sugar environment. In a paper published in the *Proceedings of the National Academy of Sciences* in 1994, Lenski and Michael Travisano, also of MSU, analyzed the fitness of different generations by pitting ancestral bacterial cells against their descendants in the same flask. They found that later (and larger) generations had higher fitness, producing more offspring than their ancestors.



DAVID S. BROWN/MSU

Cultural evolution. Cooper, Elena, and Lenski watched bacteria evolve for thousands of generations.

The change in fitness seemed to occur in a punctuated pattern. But Lenski and colleagues also wanted to examine a concrete morphological character—the kind of trait that may be preserved in the fossil record. So they scrutinized cell size in detail. Statistical analysis showed that the data were best represented not with a smooth curve, but with a stepped curve that took several jumps. That is just the sort of pattern—stasis followed by rapid change—that punctuated equilibrium theory suggests has often characterized the appearance of new species over millions of years.

What's more, the experiment provides a clear demonstration of how such patterns may arise, at least at the population level. Researchers infer that during periods of stasis, the bacteria are in a sense "waiting around" for beneficial mutations, explains population geneticist Montgomery Slatkin of the University of California, Berkeley. When such mutations—in this case those leading to large cell size—did appear, they swept through the population very rapidly. "It's a nice demonstration … showing that the availability of mutation is limiting the rate of evolution," says Slatkin. And Lenski's team thinks that this simple mechanism could be driving at least some of the punctuated patterns of change seen in the fossil record.

But Slatkin and others question how strongly this evidence supports punctuated equilibrium, a term coined in 1972 by paleontologists Niles Eldredge and Stephen Jay Gould to describe patterns of speciation over millions of years. Paleontologist Philip Gingerich of the University of Michigan, for example, finds it telling that the punctuation showed up only when the researchers looked at cell size every 100 generations, or 15 days. At a longer time scale of every 500 generations, the change looks like smooth, gradual evolution to a larger cell size. For Gingerich, a leading proponent of gradualism, this question of scale is crucial. "If you look closely enough at anything, you will eventually see the steps," he says. "It's a slippery fish."

Even Eldredge, now at the American Museum of Natural History in New York, is dubious about overextrapolating from this bacterial experiment. Sexual organisms have much more complex evolutionary patterns than do asexual ones, he notes, and what happens in a population may be different from what happens in an entire species. "There is an understandable but unfortunate tendency for evolutionary biologists to confound the biology of populations with specieswide phenomena," he says. As Gingerich puts it, "I don't think we can generalize from this to mammals." But Riley, who switched from studying mammals to *Drosophila* and is now experimenting with evolutionary processes in bacteria, thinks such extrapolation is valid. She argues that no matter what the organism or the scale, the same evolutionary forces are at work, albeit with different strengths.

Lenski and other evolutionary microbiologists agree, and point out that the simplified and manipulable system of *E. coli* allows them to watch evolutionary change as it happens. And there's no shortage of questions to study. Next on Lenski's list: genetic analysis of the bacterial generations, which will link the changes in morphological traits to changes in DNA. Says Lenski: "Evolution can be an experimental as well as an observational science."

–Christine Mlot

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