or the other photomultiplier tube detected a photon, and the number of coincidence events per second, N_c, in which both photomultiplier tubes detected photons.

From these data, it is not possible to deduce the second-order correlation function as a function of time delay, but a related quantity has the same behavior. This quantity, called α by Grangier, is the probability of coincidence events divided by the product of the probabilities for singles events, where the probability for each type of event is given by the number of events per second divided by the number of triggers per second. For classical radiation, including laser light, α is greater than or equal to 1.

At low trigger rates, the measured α had a value far below 1, whereas it increased toward 1 as the trigger rate grew. The experimental data closely followed the theoretical curve. In particular, at a low trigger rate of 8800 per second, after 5 hours of counting, the value of α was 0.18 ± 0.06, 13 standard deviations below the minimum classical value of 1. This corresponds to 9 coincidences per second, as compared to the classical value of 50.

Having established that the source met the single-photon criteria, the investigators turned toward verification of the wave nature of single photons. One photon at a time was allowed to pass through a Mach-Zehnder interferometer similar to that in part B of the figure. Once again, while the interference is a property of single photons, it is necessary to repeat the experiment a large number of times to generate an interference pattern. The experiment was to measure the number of counts in the outputs MZ_1 and MZ_2 as the difference in the path length through the two arms of the interferometer was varied by means of a piezoelectrically driven mechanical system. As the condition for constructive and destructive interference changed with the path length, the expected effect was a sinusoidal oscillation in the counts recorded by the two photomultipliers, with one detector being 90 degrees out of phase with the other. These intensity variations represent the interference fringes.

The path length could be controlled to about 1/50 of the wavelength of the light from the single-photon source, which was 4227 angstroms. The quality of the fringes, visibility in the jargon, is given by the ratio of the difference between the maximum and the minimum photomultiplier counts to the sum of the maximum and minimum. The experimental value of the visibility consistently was 98.7 ± 0.5 percent for a wide range of trigger rates, thereby verifying the wave nature of single photons. ■

Arthur L. Robinson

Punctuated Equilibrium Is Now Old Hat

The rapid changes seen in the fossil record can be accounted for by traditional explanations from population genetics, according to two recent mathematical models

THERE is an old saying about the reception of a new idea, which goes as follows. At first it is dismissed as being wrong; then it is characterized as being against religion; and finally it is said to be something everyone knew all along. So it is with the notion of punctuated equilibrium, which has been the subject of much lively debate among evolutionary biologists for a decade and a half. This hypothesis, once rejected as being wrong or at least anti-Darwin, now appears to have entered the last of these three stages.

Using similar mathematical models of population genetics theory, two research groups independently report that the evolutionary pattern that is the basis of punctuated equilibrium—to wit, long periods of stasis of individual species in the fossil record, punctuated by bursts of rapid change—can, after all, be explained by classical Neo-Darwinian mechanisms, including selection. There is, therefore, no need to suggest that other mechanisms—such as developmental constraints—are important in influencing the pattern of change in the fossil record, they say.

Now, there are three principal aspects of these arguments. The first involves the pattern of change through time that can be inferred from the fossil record. Specifically, does change typically occur in gradual trajectories, or is it more often concentrated in rapid bursts? The second focuses on the mechanisms that shape the overall pattern of change. For instance, does selection operate to the virtual exclusion of other influences, such as developmental constraints? And the third sets the context of pattern: sometimes the environment will be changing, sometimes it will be constant.

Classical Neo-Darwinism viewed organisms as being closely adapted to their environments. It therefore followed that, when environmental conditions shifted, so too did a species' adaptations, sometimes to the point of generating a distinctly new species. There was no reason to expect—and Darwin and the Neo-Darwinians were explicit about this—that change would for the most part be other than a steady accumulation of small modifications. In other words, the pattern of change would be gradual. The fact that the fossil record does not show this—instead, it typically reveals long periods of stasis and bursts of change—has long been explained as the result of the record's woeful incompleteness. Capturing just brief glimpses of the past, it has been argued, the smooth, gradual transitions are mostly invisible in the record.

When, in 1972, Niles Eldredge, of the American Museum of Natural History, New York, and Stephen Jay Gould, of Harvard University, proposed the hypothesis of punctuated equilibrium, they were proferring two main messages.

First, that the pattern of stasis and abrupt change apparent in the fossil record is real, and not an artifact of its incompleteness. In other words, once a species has arisen it remains essentially unchanged for most of its history, but when change occurs it does so swiftly.

And second, that the long periods of stasis in individual species through periods of environmental change were not predicted by classical Neo-Darwinian theory and required another explanation. Eldredge and Gould suggested that the very conservative mechanisms of embryological development imposed constraints on the evolutionary change of a species, even in the face of some shift in environmental conditions.

The hypothesis was unpopular among classical evolutionary biologists, and was dismissed as being wrong. However, there ensued an enthusiastic search through the fossil record, focusing on organisms as small as microscopic marine species and ones as large as terrestrial vertebrates. The upshot of it all was that a complete spectrum of patterns of change could be identified, from gradual to essentially instantaneous change. It also became clear that stasis was a real phenomenon, which required explanation.

So, faced with the need to accept the reality of the pattern of punctuated equilibrium, particularly the aspect of stasis, debate began to emphasize the process by which it is produced. Just as selection can produce change, it was argued, so too can it maintain stasis, if the selection profile also remains stable. In fact, as Gould and Eldredge point out in a recent paper, this argument misses the point of the punctuated equilibrium proposal: namely, that stasis often persists in the face of environmental change. The critics' reply to this has frequently been that under such circumstances you do indeed see change in a species, if you look hard enough at the record.

The two recent papers, one by Russell Lande of the University of Chicago, and the other by Charles Newman of the University of Arizona, Tucson, Joel Cohen of Rockefeller University, New York, and C. Kipnis of Ecole Polytechnique, Palaiseau, France, take the issue a step further. Using essentially the same mathematical approach, which involves equations that describe the dynamics of diffusion, both suggest that the pattern of punctuated equilibrium—stasis and rapid change—is predictable from Neo-Darwinian theory. The context of the pattern is the absence of environmental change.

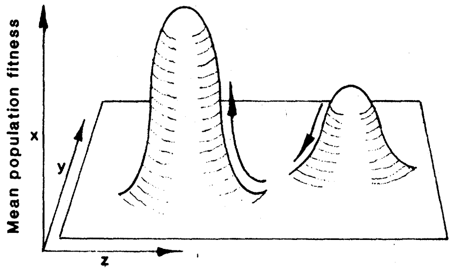
The mathematical models draw on the now classic population genetics representation of a species' fitness that Sewall Wright, of the University of Chicago, developed in the 1930's. One must imagine a three-dimensional "adaptive landscape" in which the two horizontal axes represent measures of certain characters, as shown in the diagram. In a particular set of environmental conditions, any combination of characters *y* and *z* will have a certain fitness, *x*, in the vertical axis. By measuring the fitness of all combinations of *y* and *z*, one produces discrete adaptive peaks, where fitness is higher than in neighboring locations: hence the notion of an adaptive landscape. Natural selection will tend to push populations to the tips of the peaks, which represent fitness optima.

If environmental conditions were to change, however, different combinations of *y* and *z* would be favored, changing the value of *x* for points (*y*, *z*). In this way the position and form of the peaks may alter: the shape of the adaptive landscape depends entirely on the nature of selection imposed by the prevailing environment.

This mathematical abstraction can be put into more concrete—but strictly hypothetical—terms, if one imagines the two peaks to represent two possible types of birds that could exist in that prevailing environment. One could be a large bird with a big bill, which eats nuts; and the other is a small bird with a smaller bill, which is a seed-eater. (In this case *y* and *z* would represent body size and bill size, or at least the genetic determinants of those characters.) A change in environment, which would include a shift in the nature and availability of food, might favor the existence of birds of different body and bill sizes.

The question that Lande and Newman and his colleagues asked was, how, under constant environmental conditions, might a population that occupies the summit of one peak move to the summit of the next. In other words, what would be the dynamics of an evolutionary change from, say, a large, big-billed nut-eater to a smaller, small-billed seed-eater, in a stable environment? Would the change be gradual, or would it be rapid?

As mentioned earlier, natural selection will tend to push the mean fitness of any given population toward the summit of the adaptive peak. Working against this (at least some of the time) is the random genetic "noise" of mutation, recombination and so on: sometimes this random factor will take a population up a peak, sometimes down. The balance between selection and random genetic change is known as drift. The Lande/Newman question therefore becomes, how can genetic drift take a population down one peak and up the other?



Wright's adaptive landscape

Under a given set of environmental conditions, each combination of characters y *and* z *has a certain fitness* (x)*, some of which will be greater than others. The result is an adaptive landscape, with one or more fitness optima representing possible morphologies. Transition from one optimum to another by genetic drift always occurs rapidly.*

Now, there is no problem in explaining what would happen to a population once it found itself at the foothills of the second peak: most probably it would advance rapidly toward the peak, propelled by natural selection. But what of the journey down the first slope? Would this be fast or slow? Intuitively, one might expect it to be slow and laborious, stuggling against the forces of natural selection. In fact, as the mathematics show, it too is rapid.

Newman and his colleagues explain this surprising result this way. A successful downward drift is inherently improbable, but if it is to occur it will do so in the most likely way possible, which is rapidly. In other words, if the downward drift were slow, the chances of its being reversed by natural selection would be high. By contrast, a fast excursion down the slope—which involves becoming less fit for the prevailing environment only very briefly—has a better chance of evading selection.

The upshot of these mathematical models is that transitions between peaks are always rapid, and this applies to large populations as well as small. There is a slight slowing effect with increase in the size of a population, but it is not dramatic. By contrast, population size does have a marked effect on the length of time between transitions. With small populations such transitions might occur quite frequently (in geological time, that is). But with large populations the chance of a shift can become vanishingly small. In other words, say Newman and his colleagues, their model "predicts stasis and punctuation for a small to moderate population but only stasis for a large population."

Lande takes the calculations a little further and proffers some numbers. For instance, under one set of conditions the expected time between transitions for a breeding population of 100 individuals would be on the order of 10^6 generations. That figure rises to as much as 10^{11} for a breeding population of 200.

What do the new results mean for the evolutionary biologists' debate? In terms of substance, it is clear that all concerned are now much more comfortable with the existence of the pattern of punctuated equilibrium, from both an empirical and theoretical point of view. The models of Lande and of Newman and his colleagues predict this pattern—evolution by jerks, as it has been called—during environmental constancy. But the debate began with the challenge of explaining the punctuated equilibrium pattern—and specifically stasis—in the face of a changing environment. This remains to be explained to the satisfaction of all sides. Specifically, what, if anything, is the contribution of developmental constraints to the phenomenon of stasis? An answer to this is likely to come, not from the fossil record, but from experimental observations on living organisms, an approach that is already beginning to yield encouraging results.

In terms of the tenor of the debate, which at times has been strident, the new results will bring the various parties closer together. Cohen readily concedes that population geneticists very probably would not have applied their mathematical tools to the issue in this way had there not been such a big fuss stirred up by the paleontologists' claims. "They deserve credit for that," he says. ■

ROGER LEWIN

ADDITIONAL READING

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