

Article #1

Debating the Fastest Evolution on Record

More than 500 species of brightly colored fish called cichlids live in east Africa's Lake Victoria. Most of these fish cannot be found in any other lakes in the world. They have evolved a dizzying variety of roles: insect eaters, leaf choppers, snail crushers and scale scrapers, to name a few.



In 1996, geologist Tom Johnson from the University of Minnesota, Duluth, and colleagues reported in *Science* that Lake Victoria and nearby lakes dried out completely about 12,400 years ago. They concluded that the vast array of cichlids must have evolved from a few ancestors in the time since then -- making cichlid evolution the fastest on record for any vertebrate.

A paper in the April 11 *Science* puts the brakes on this rate of evolution. Evidence locked in the DNA of Lake Victoria's cichlids indicates that the first burst of speciation began 100,000 years ago, and that the fish have been evolving since. And, the authors say, the original set of founding species may have itself been diverse, kick-starting the evolutionary radiation that followed.

"If you start out 10 times longer ago, with fish that were already diversified, the [cichlid radiation] is easier to imagine," says lead author Erik Verheyen, an evolutionary biologist.



According to the April *Science* study, cichlids from Lake Kivu (marked LK) colonized Lake Victoria (LV), setting the stage for the rapid evolution of over 500 endemic cichlid species. No waterways currently connect the two lakes, although the authors suspect that ancient rivers did. Photo courtesy of NASA.

The study presents a new example of how geology and evolutionary biology can lead to different conclusions. "The contrast between geophysical and molecular evidence is absolutely fascinating," Johnson says.

The geologic perspective

Lake Victoria sits between two branches of the major rift that runs through east Africa. Approximately 400,000 years ago, the eastern flank of the western branch lifted up, causing rivers that had been flowing east to west to reverse direction. Water ponded, forming the lake.

In 1995, Johnson's team surveyed Lake Victoria's sediments in the hopes of finding a continuous record of changes in regional climate since the lake formed. They used seismic profiling to look for sediments with fairly uniform reflectivity down many tens of meters. Such a profile would indicate that the sediments accumulated gradually at the bottom of the lake, without any interruption. But the actual profiles revealed a jump in reflectivity about seven meters beneath the sediment surface. The team's seismic tracks crisscrossed the lake, always with the same result.

Piston cores that grabbed segments of this highly reflective layer allowed for a closer look. The segments crumbled easily, were much thicker than the sediments above, and were filled with vertical roots and pollen grains from cattails -- all signs that the sediment formed beneath air, not water, and that the lake was at one time not a lake, but a vast marsh, Johnson says. Carbon dating pinned the age of the ancient marsh to approximately 12,400 years old.

While the seismic surveys and piston cores did not extensively sample the whole lake, the basin bottom is so flat that the entire lake must have dried out when the water level dropped, the authors argued in the 1996 Science paper. They concluded that cichlids would not have been able to find any large or deep refuge in which to wait out the dry spell; few would have survived.

Previous phylogenetic studies had indicated that all of Lake Victoria's cichlids evolved from a single ancestor. Only one possibility remained, Johnson says: most of the 500 species found in the lake today evolved in the past 12,400 years.

The molecular perspective

In 2000, Sandra Nagl, a molecular biologist from the Max-Planck Institute for Biology in Germany, presented a different view, based on DNA sequences from Lake Victoria cichlids. Fish that belong to the same species tend to have similar DNA, especially in stretches sitting in the mitochondria. When one species evolves into two, random mutations in the DNA slowly cause the mitochondria of the two new species to diverge from one another. The greater the differences, the longer ago the two species split. From such molecular data, Nagl concluded that the Lake Victoria cichlids began to evolve 100,000 to 200,000 years ago, not 12,400.

At the heart of these calculations is what is known as a molecular clock: an estimate of the amount of time that elapses before a single difference in the DNA code between two species emerges. Nagl's group assumed a ticking rate of about a 5.6 percent divergence in DNA sequence every million years.

The authors of the April Science article made their own molecular clock calculations, coming to the same conclusion that the Lake Victoria cichlids began evolving about 100,000 years ago.

The study also finds another factor that slows the rate of evolution, Verheyen says: the species that began the Lake Victoria radiation were themselves quite diverse, limiting the degree of speciation needed to happen afterward to explain today's diversity. From the DNA data, the authors constructed lineages showing the relationships between the cichlids in Lake Victoria and surrounding lakes. They discovered that two genetically distinct classes of fish from nearby Lake Kivu colonized Lake Victoria. Until now, many evolutionary biologists believed that Lake Victoria's cichlids evolved from a single species. It is not clear how much diversity -- in terms of size, shape, color and behavior -- the initial two classes of cichlids encompassed, although it may have been great, Verheyen says. Today, just one of those genetic classes includes cichlids that graze on algae, others that eat insects, and still others that eat fish.

Bridging the two?

The two perspectives may have common ground. Even a few lingering ponds in a mostly desiccated lake could have provided strongholds for cichlids that hunkered down until the rains came, Verheyen says. That scenario is possible, Johnson acknowledges: "There was no big deep water lake there. At best there could have been a cattails swamp with a few ponds."

On the flip side, the DNA-based lineages indicate that several genetically distinct groups of fish that appear not to live in the lake now must have, at one point, existed. Perhaps the drying lakes eliminated these species, the authors say.

Johnson, however, argues that the molecular clock used to date the cichlid evolution could be flawed. Robert Schelly, a graduate student at Columbia University who is studying cichlid evolution for his dissertation, agrees. "You have variation in the rates of molecular evolution among different loci and different species," he says. The molecular clock applied to Lake Victoria, he notes, was calibrated using a different set of cichlid species living in nearby lakes.

Even if the new Science study turns out to be correct, the rate of cichlid evolution is still astonishing, says co-author Axel Meyer, an evolutionary biologist at the University of Konstanz, Germany. Whether it is 12,400 years or 100,000 years, cichlids will still hold the record for the fastest known evolution of vertebrates.

Greg Peterson
Web Extra Friday, April 25

Article #2

Lizard Experiment Suggests Rapid Evolution-Jeff Poling

An experiment with lizards in the Caribbean has demonstrated that evolution moves in predictable ways and can occur so rapidly that changes emerge in as little as a decade.

The experiment bears on two theories of evolution, that of punctuated equilibrium and that of gradualism. Gradualism states that evolution is a relatively slow, constant process, producing changes over millions of years. Punctuated equilibrium states that environmental constraints hold species remain unchanged for millions of years, which then undergo rapid evolution when environmental changes demand it. The results of the experiment suggest that there are no constraints, and no difference between gradual and rapid evolution.

The experiment involved the introduction of one species of lizard to fourteen small, lizard-free Caribbean island near the Exumas in the Bahamas. The lizards were left for fourteen years. The original intent of the experiment was to study extinction. The experiment, started by Thomas Schoener of the University of California at Davis, would have provided scientists with important information as they observed the extinction of the introduced lizards. Unfortunately, the lizards adapted to their new environments, and the focus of the experiment changed to study this rapid evolution.

Lizards on Caribbean islands have been carefully studied by biologists for their adaptation to different conditions on different islands with corresponding changes in body shape. Birds, most notably the Finches of the Galapagos islands, also show such specializations when favoring a certain island. One of the specializations of lizards noted by scientists over the years has been that lizards that inhabit large trees tend to have long legs, whereas those lizards that live on twig-like plants have short legs.

Jonathon Losos of Washington University in St. Louis stated that such adaptations allowed scientists to predict what would happen to the lizards placed on the islands, some of which are smaller than a football field. The more the vegetation differed from that of their original home, Staniel Cay, the more the lizards should evolve. The scientists predicted that evolutionary pressure would cause the long-legged lizards to produce short-legged forms as the Caribbean islands are almost treeless.

Losos and his colleagues report in the journal Nature that the lizards evolved in the direction as predicted. Those with the shortest legs are found on islands with the scrubbiest vegetation.

Douglas Futuyama of the State University of New York at Stony Brook, states that while there are many known instances of rapid evolution in biochemistry, such as evolving resistance to pesticide, there are fewer examples of bodily changes.

A long-standing issue in biology is whether small evolutionary changes are the same as the large evolutionary changes seen over millions of years. In biology terms, the question is whether microevolution is the same as macroevolution.

One well known macroevolutionary event is the specialization of lizards on Caribbean islands. Lizards have evolved into 150 different species spread across these islands. Losos and his colleagues write that their lizard experiment suggests that macroevolution is simply microevolution observed over a much larger time period.

Punctuated equilibrium proponents suggest that a given species may remain unchanged for millions of years until some event shakes up the ecosystem, causing rapid evolution. Since the lizards on all 14 islands evolved as expected, Futuyma states that "it means you don't need to invoke a complicated hypothesis of this type."

The rate of evolutionary change is measured in units called darwins. Darwins provide a measure of the proportional change in a given organ over time. Changes typically seen over millions of years in the fossil record usually amount to 1 darwin or less. The transplanted lizards evolved at rates of up to 2000 darwins.

"Darwin thought that natural selection had to be slow and gradual," Losos said. "I think it is clear he was mistaken. In some cases change can be very rapid."

The results of the experiment echo observations made in the 1980s of one species of Finch on one Galapagos island. Over a ten year period there were three major swings in the ecosystem of the island. At the start of the observation period, there were two morphs of the Finch, a large beaked morph and a small beaked morph. One change in the ecosystem favored the large beaked morph over the small beaked morph, with the latter nearly becoming extinct. A second change in the ecosystem favored the now nearly extinct small beaked morph, and within a short time it was the dominant morph, with the large beaked morph on its way to extinction. Finally, the ecosystem shifted again, and populations stabilized. Today, a third morph has appeared, with a beak intermediate between the large and small beaked morphs. Over a ten year period, three natural selection events occurred, suggesting that evolutionary change might be more rapid than ever before suspected.

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Article #3

Preying For Rapid Evolution

The discovery, reported in the Sept. 30 issue of the journal *Nature*, shows that environmental degradation can be reduced when the affected animals evolve quickly, according to Cornell biologist Nelson G. Hairston Jr.

"It appears that ecological events that we think of as occurring relatively quickly -- such as nutrient enrichment of a lake -- can be influenced by the rapid evolution of the animals that are affected," says Hairston, a professor of environmental science. "If these little crustaceans hadn't changed with the times, their kind might not have survived." Hairston co-authored the *Nature* report with Winfried Lampert, director of the Max Planck Institute for Limnology in Plšn, Germany.

In less than 30 years, as Germany's Lake Constance suffered environmental degradation from phosphorus pollution, populations of tiny crustaceans called Daphnia found more and more toxic cyanobacteria (also called "blue-green algae") mixed with their favorite food, a more edible type of algae. So the crustaceans adapted to handle a less nutritious food that would have seriously stunted the growth of their ancestors, and they became one of the important, natural controls for toxic cyanobacteria in the lake.

The research, carried out at the Germany institute, documented the crustaceans' express-style evolution by hatching a series of dormant Daphnia eggs that were found, level by level, in lake-bottom sediments in a state of "diapause." Diapausing animals, such as certain insects and crustaceans, can suspend their growth and development for years or even centuries during periods of unfavorable conditions.

In Hairston's Cornell laboratory, researchers already had learned how to awaken 300-year-old crustacean eggs. Working at Lake Constance, the biologists needed to go back only 37 years, beginning with Daphnia eggs that were deposited on the lake bottom in 1962, to trace the clever crustaceans' evolution. They hatched Daphnia eggs that piled up year after year in sediments, then reared the crustaceans to adulthood in the laboratory and offered them cyanobacteria from the lake. Cyanobacteria produce high concentrations of the hepatotoxin, microcystin-LR.

Daphnia with 1960s genes -- before Lake Constance became so polluted and cyanobacteria were so plentiful -- couldn't stomach the modern meal. But by the late 1970s -- just a decade later -- Daphnia had become much more adept at living on a diet laced with the toxic algae. And Daphnia hatched from eggs deposited between the 1980s and the 1990s were found to retain this ability.

DNA tests of Daphnia grown from eggs that were deposited over the years revealed that crustaceans that couldn't cope easily with cyanobacteria were virtually eliminated from the population; all that remain today are cyanobacteria eaters, even though the toxic bacteria still aren't particularly nutritious.

"Strong natural selection can lead to rapid changes in organisms, which can, in turn, influence ecosystem processes," the biologists concluded in their article.

Other authors of the Nature report, titled "Dormant eggs record rapid evolution," are Lawrence J. Weider, Max Planck Institute for Limnology; Ursula Gaedke, Limnology Institute, University of Constance; Cami L. Holtmeier, David M. Post and Jennifer A. Fox, graduate students in ecology and evolutionary biology at Cornell; Janet M. Fischer, postdoctoral fellow at Cornell; and Carla E. Caceres, a former graduate student in Hairston's laboratory and now a biologist at the Illinois Natural History Survey's Center for Aquatic Ecology. At Cornell, Hairston (pronounced "HAHRS-ton") is the Frank H.T. Rhodes Professor of Environmental Science.

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Article #4

By E. S. Benson

If it is your unlucky lot in life to be prey, you can take some consolation in the fact that evolution has granted you a few helpful tricks. If you are a rabbit, your nearly 360-degree vision will help you spot an approaching predator. If you are a turtle, your shell will protect you. Less comfortingly, to humans at least, if you are an agricultural pest or disease-causing bacteria, you may be resistant to the insecticides and antibiotics arrayed against you.

Developing such defenses usually takes thousands or even millions of years. But a recent study by ecologists at Cornell University suggests that under certain conditions, evolution can move so fast, occurring in months rather than millennia, that it alters the population cycles of both predators and prey.

The Cornell scientists' research began when they noticed something strange about the population dynamics of two tiny organisms harvested from a nearby lake: green algae and the multicelled creatures called rotifers that prey on them. In a classic predator-prey system, the two species are supposed to go through alternating cycles of high and low population, with one species lagging behind the other by exactly one quarter-cycle.

In the test tubes, however, the rotifers and algae weren't behaving according to the model. Instead, their populations were increasing and decreasing exactly out of phase. When rotifers were at their peak, algae were at their minimum, and vice versa.

The researchers examined a number of possible causes for the unusual behavior, such as the effects of crowding or nutrient deficiency, but only one explanation-rapid evolution of rotifer-resistant algae-exactly predicted the dynamics of the relationship.

"We think that somehow the algae made themselves indigestible," said Nelson Hairston Jr., one of the study's authors. "They figured out how to pass straight through the rotifer gut without being digested and survived to make lots more of themselves."

This is not the first recorded appearance of rapid evolution. In 1999, Hairston and his colleagues published a paper showing that plankton in a polluted European lake had become resistant to toxic bacteria in less than a decade. Other scientists have reported rapid evolution in hatchery-raised salmon.

But the pace of the evolution in this study-it took less than a month in most cases-was extraordinary. And because the evolutionary change occurred in a test tube, where external factors could be carefully controlled, the scientists were able to demonstrate that evolution was the only viable explanation.

As a result, the study is "an almost textbook example of how science should be done," said Peter Turchin, a population geneticist at the University of Connecticut.

It also serves, Turchin noted, as a challenge to ecologists studying population dynamics, most of whom have, until now, assumed they could safely ignore evolution in their models.

The study could even have implications beyond the world of population ecologists. Outside the lab, as inside, humans seem to be one of the main causes of rapid evolution, said Stephen Palumbi, a marine geneticist at Stanford University. By causing widespread changes in the natural environment-whether through suburban sprawl, the use of antibiotics, or other changes-we create intense selection pressure. One result, said Palumbi, is rapid evolution of organisms that suit the new environment-including those, such as antibiotic-resistant diseases, that are directly opposed to our interests.

The cost of rapid evolution can even be measured in dollars. Palumbi estimated that the annual "evolution bill," the total cost to U.S. agriculture and health care, is at least \$50 billion and probably greater than \$100 billion. And the social costs, while harder to calculate, may be even more significant. Skyrocketing medical expenses, he noted, are partly due to the need to develop ever-more powerful drugs for resistant diseases.

Article #5

Rapid Evolution Rampant at Sea

by Hans G. Dam, Ph.D.

Professor of Marine Sciences, the University of Connecticut

By some accounts, almost half of all Americans believe that evolution is just a theory, not a fact. This is perhaps the most pervasive and dangerous misconception about the wondrous process that has shaped life as we know it. Another misconception, one that even Charles Darwin held to some extent, is that because evolution proceeds at a snail pace we cannot witness it in action. As author Steven R. Palumbi points out in his readable *The Evolution Explosion*, both of these misconceptions are dismissed by examples of “antibiotic resistance, the triumph of HIV over antiviral drugs,... and resistance of insects to nerve gas pesticides” all of which have happened in a few decades. Similarly, in his book *the Beak of the Finch*, Pulitzer Prize-winner Jonathan Weiner describes how evolutionary biologists are documenting evolution as it occurs among the celebrated Galápagos finches that inspired Darwin to formulate his famous theory of natural selection.

Most examples of rapid evolution are from land studies. But aquatic scientists are quickly realizing that rapid evolution is also rampant at sea. For instance, selective removal of large fish in commercial fisheries has led to dramatic changes in the size of some species. A delicious example (bad pun intended) is the 30% decrease in the mean size of pink salmon caught off British Columbia, Canada, since the 1950's, a fact documented by fisheries biologist W.E. Ricker.

Pink salmon are born in freshwater streams, spend their youth at sea and return after two years, when they mature, to their native streams to spawn. The return to the spawning grounds is such a Herculean effort that after spawning, the wasted salmon die. In this life-history pattern, salmon put all their eggs in one basket and the stakes for leaving offspring are immense. Fishermen have figured out this life cycle and understand that it is better to catch the salmon before they are physically wasted; hence, they set their gill nets on the path of salmon trying to return to their spawning grounds.

Because larger fish are more likely to be retained in fishing nets, reduction in average adult size has occurred over time in finfish like this Pacific salmon, as a result of selection against fast-growing individuals.

Because pink salmon returning to a spawning ground are all two years old, larger individuals are those that have grown faster. Unfortunately for these fast growers, they are disproportionately retained in the gill nets. Relatively few of these fast-growing salmon ever get the chance to reach their spawning grounds to reproduce. In contrast, the slow-growing and smaller salmon pass through the nets to reach their spawning grounds, where they can produce offspring. Over the years, the proportion of slow-growing individuals has increased in the population, leading to a decrease in mean size of the fish caught in the gill nets. In this salmon story, we can reason that the reduction

in fish size with time has resulted from selection against fast-growing individuals, a case of natural selection. Natural selection is one of the main mechanisms of evolution.

The salmon story illustrates the essential ingredients for natural selection to occur: 1) variation in traits among individuals in a population (in this case size at maturity, which is driven by growth rate), 2) differential reproduction (here, slow-growing smaller individuals leave more offspring than fast-growing ones-larger ones), 3) Inheritance of traits (size at maturity is passed between generations). Furthermore, the salmon story also illustrates a common feature to many historical sciences; that is, the phenomena of interest are inferred after the fact. It is possible, however, to predict the outcome of evolution and to carry out experiments to test these predictions. For instance, one prediction that has been confirmed experimentally by microbiologists is the evolution of bacterial strains resistant to antibiotics.

A practical lesson for us all is that without understanding the evolutionary history of populations, we will be hard-pressed to come up with effective management plans for living marine resources.

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