Part VI

Evolution

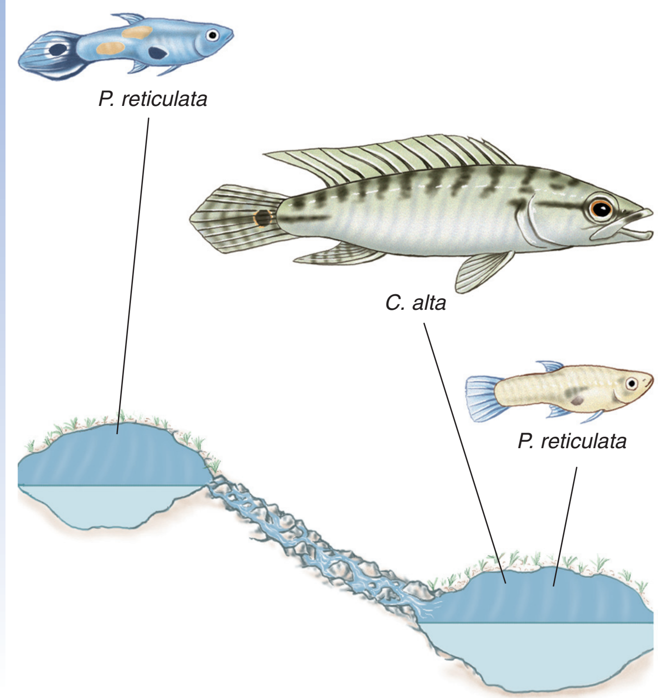
Catching Evolution in Action

To study evolution, biologists have traditionally investigated what has happened in the past, sometimes many millions of years ago. To learn about dinosaurs, a paleontologist looks at dinosaur fossils. To study human evolution, an anthropologist looks at human fossils and, increasingly, examines the "family tree" of mutations that have accumulated in human DNA over millions of years. For the biologists taking this traditional approach, evolutionary biology is similar to astronomy and history, relying on observation and deduction rather than experiment and induction to examine ideas about past events.

However, evolutionary biology is not entirely an observational science. In recent years many case studies of natural populations have demonstrated that in some circumstances evolutionary change can occur rapidly. In these instances, it is possible to establish experimental studies to directly test evolutionary hypotheses. Although laboratory studies on fruit flies and other organisms have been common for more than 50 years, it has only been in recent years that scientists have started conducting experimental studies of evolution in nature.

To conduct experimental tests of evolution, it is first necessary to identify a population in nature upon which selection might be operating. By manipulating the strength of the selection, an investigator can predict what outcome selection might produce, then look and see the actual effect on the population.

Guppies offer an excellent experimental opportunity. The guppy, *Poecilia reticulata*, is found in small streams in Venezuela and the nearby island of Trinidad. In Trinidad, guppies are found in many mountain streams. One interesting feature of several streams is that they have waterfalls. Amazingly, guppies are capable of colonizing portions of the stream above the waterfall. During flood seasons, rivers sometimes swell, reducing the depth of waterfalls. During these occasions, guppies may be able to jump these barriers and invade pools above waterfalls. By contrast, not all species are capable of such dispersal and thus are only found in these streams below the first waterfall. One species whose distribution is restricted by waterfalls is the pike cichlid, *Crenicichla alta*, a voracious predator that feeds on guppies and other fish.

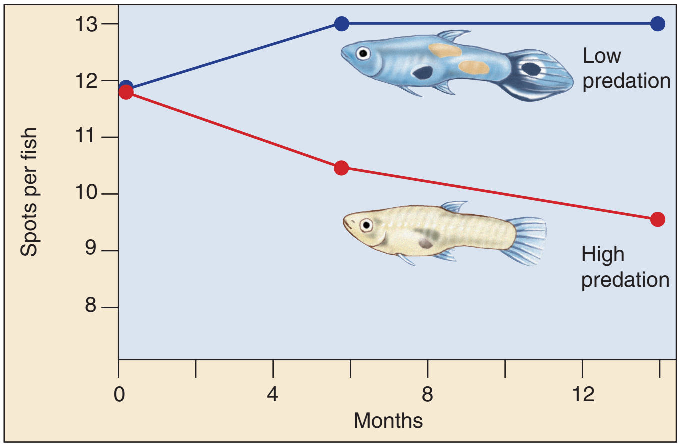


The evolution of protective coloration in guppies. In pools below waterfalls where predation is high, guppies (*Poecilia reticulata*) are drab colored. In the absence of the highly predatory pike cichlid (*Crenicichla alta*), guppies in pools above waterfalls are much more colorful and attractive to females. The evolution of these differences can be experimentally tested.

Because of these barriers to dispersal, guppies can be found in two very different environments. In pools just below the waterfalls, predation is a substantial risk and rates of survival are relatively low. By contrast, in similar pools just above the waterfall, few predators prey on guppies. As a result, guppy populations above and below waterfalls have evolved many differences. In the high-predation pools, guppies exhibit drab coloration. Moreover, they tend to reproduce at a younger age.

The differences suggest the action of natural selection. Perhaps as a result of shunting energy to reproduction rather than growth, the fish in high-predation pools attain relatively smaller adult sizes. By contrast, male fish above the waterfall display gaudy colors and spots that they use to court females (see figure above). Adults there mature later and grow to larger sizes.

Evolution does not offer the only explanation for these observations. Perhaps, for example, only very large fish are capable of jumping past the waterfall to colonize pools. If this were the case, then a founder effect would occur in which the new population was established solely by individuals with genes for large size.



Evolutionary change in spot number. Guppies raised in the low-predation environment had a greater number of spots, whereas selection in more dangerous environments, like the predator-filled pools, led to less conspicuous fish (*above left*). The same results are seen in field experiments in pools above and below waterfalls (*above right*).

The Experiments

The only way to rule out such alternative possibilities is to conduct a controlled experiment. A classic set of laboratory and field experiments carried out by John Endler in the late 1970s (now at the University of California, Santa Barbara) first attempted to demonstrate that natural selection was acting on these Trinidad guppies.

Laboratory Experiment. Endler constructed a series of ten large artificial ponds in a laboratory greenhouse, with size and color of gravel designed to mimic the different background patterns found in the natural streams of Trinidad. In each pond he raised a diverse population of guppies, mixing the ten populations as they grew so that all the populations had a similar range of genetic diversity.

He then added cichlid predators (*C. alta*) to four of the pools and killifish (which rarely prey on guppies) to another four, with the remaining pools left as "no predator" controls. The populations were then allowed to evolve with or without predators.

Field Experiment. In a parallel field experiment, Endler captured drab guppies from a stream they shared with cichlid predators, and released them upstream above a waterfall where there were no cichlids or guppies.

As a key follow-up, David Reznick of the University of California, Riverside, reexamined the evolving population of Trinidad guppies 11 years after its initial transfer by Endler from a high-predation community to a low-predation one.

Results

Laboratory Experiment. Fourteen months after adding the predator fish to the ponds (which corresponds to 10 guppy generations), Endler compared the populations (see graph). The guppies in the killifish and control pools were indistinguishable, all brightly colored. In contrast, the surviving guppies in the pike cichlid pools were drab in coloration. Predation greatly reduced bright coloration in guppies.

Field Experiment. Two years after transferring the drab guppies to a predator-free environment—that is, after 15 generations of relaxed selection pressures—the drab color patterns of the guppy population had shifted toward the more complex and colorful pattern typical of guppy populations living where there are no predators.

Endler's initial field results offer an exciting but sketchy picture of evolution in action. Many questions immediately suggest themselves. Is color pattern the only trait under selection by predation? What about the number of offspring, and their growth rate? Can we actually measure how fast selection is acting?

These questions were addressed in an extensive follow-up analysis by David Reznick of the University of California, Riverside, Frank and Ruth Shaw of the University of Minnesota, and Helen Rodd of the University of California, Davis. They reexamined the guppy population 11 years after transfer, examining a wide array of characters designed to reveal not only the physical appearance of the guppies, but also their investment in reproduction.

Reznick's team found that the descendants of the transplanted guppies were not only more brightly colored, they matured at a later age and were larger in size than the control population living below the barrier waterfall with cichlid predators. They also produced fewer but larger offspring per litter, devoting a smaller proportion of their resources to reproduction. In a word, their life histories had evolved to resemble that of guppies living in low-predation or predator-free communities.

The speed of evolutionary change is measured in darwins, the proportional amount of change per unit time. Reznick's team estimates the guppies evolved at a rate of up to 45,000 darwins. By comparison, rates of change measured in the fossil record are only one-tenth to 1 darwin. Apparently evolution can sometimes act very fast.