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David Reznick talks with *ScienceWatch.com* and answers a few questions about this month's Emerging Research Front Paper in the field of Environment/Ecology.

Article: Effect of extrinsic mortality on the evolution of senescence in guppies
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SW: Why do you think your paper is highly cited?

This paper was a comparative study of aging in fish derived from natural populations that experience differences in mortality rate. I looked at populations that either do or do not live with predators and have shown in earlier work that those that live with predators suffer higher mortality rates. Evolutionary theory predicts that they should have a higher rate of senescence.

My study is probably cited because it is a good example of testing predictions of evolutionary theory in natural populations, but more so because the outcome of the experiment was the opposite of what the classical evolutionary theories predict. My results thus provide a good incentive to consider the much larger diversity of theory that is now available for how the aging process should evolve, since some of these new ideas make predictions that are consistent with what I found.

SW: Does it describe a new discovery, methodology, or synthesis of knowledge?

The results are a new discovery in the sense that they are probably the best available documentation of the evolution of the aging process in a fashion that departs so dramatically from the predictions made by Medawar and Williams during the 1950s.

SW: Would you summarize the significance of your paper in layman's terms?

Two classic papers, one by Peter D. Medawar ("An unsolved problem of biology," H.K. Lewis & Co., London, 1952) and one by George C. Williams ("Pleiotropy, natural selection, and the evolution of senescence," *Evolution* 11: 398-411, 1957) made similar predictions for how and why lifespan should evolve. They predicted that organisms which experience low extrinsic mortality rates, meaning a low risk of mortality attributable to external factors like predators or disease, will evolve longer lifespans. These predictions have prevailed through all subsequent discussions of lifespan and why some organisms live longer than others.

"My research shows in various ways that evolution is a fast process that can have large impacts on our day-to-day lives."

We tested these predictions in populations of guppies from natural environments, in which they experience very different mortality rates, because they either do or do not live with predators. Our results were the opposite of what these classical theories predict. Guppies derived from sites where they co-occur with predators, and where we had already shown they experience much higher mortality rates, lived longer and reproduced more successfully into advanced ages than guppies from sites where they do not live with predators and have much greater life expectancies.

SW: How did you become involved in this research and were any particular problems encountered along the way?

I am an evolutionary ecologist and I began my research on guppies some 30 years ago. I chose them because prior research had demonstrated that there were natural differences among populations in the risk of predation. They live in mountain streams on the Caribbean island of Trinidad that are steep and have many waterfalls; the waterfalls are often barriers to the upstream dispersal of predators but not guppies, so I can often find populations found close to one another in very similar habitats that have very different mortality rates. I also chose guppies as they are a good organism for laboratory research because they are so easy to rear and breed.

I wanted to apply predictions from evolutionary theory to the study of natural populations and to do experiments in nature. I have done so, sometimes treating streams as if they were giant test tubes by introducing guppies or predators to a section of stream where they were not previously found. In this way I have been able to manipulate mortality rates and study the evolution of life history traits, including age at maturity, the number of offspring produced, offspring size, and reproductive effort.

I have also been able to quantify the intensity of selection and rate of evolution in nature. My results were among the earliest to show that the rate of evolution that we see in real time can be many thousands, even millions, of times faster than had been inferred as rapid evolution in the fossil record. My colleagues joke that my choice of study has followed my own development, since offspring size and maturity came first, then reproductive effort and finally senescence.

SW: Where do you see your research leading in the future?

Our unusual results suggested that there were environmental interactions with the presence of predators that were modifying how guppies evolved in response to predators. For example, while predators kill guppies, they also lower population density and increase resource availability for the lucky survivors. It is this sort of interaction that can account for our results. We now have a very well-funded, multi-investigator grant to study the interaction between ecological and evolutionary processes that was suggested by the results of this paper.

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For the record, the study of such interactions is an emerging subdiscipline. Ecology and ecological theory are traditionally done with the implicit assumption that the organisms that participate in ecological interactions do not evolve. The reason this is done is that it was assumed that the rate of evolution is so much slower than the rate at which organisms interact that it could be safely ignored.

My results show that this is not the case. This means that interacting organisms can change their environment and that the changing environment can, in turn, alter the kind of selection that these organisms are exposed to, such that the outcome is not what would be predicted from traditional ecological theory. The reason these interactions are of possible importance is that including them can improve ecology as a predictive science.

SW: Do you foresee any social or political implications for your research?

My research shows in various ways that evolution is a fast process that can have large impacts on our day-to-day lives. This is not new, since we already know about the evolution of insecticide or antibiotic resistance, but this work shows that the effects are more pervasive. For example, my work has helped to show that the commercial exploitation of fish as a source of food has almost certainly caused the fish to evolve, even over the course of decades. The kinds of evolution that have occurred have in turn caused them to be less useful as a source of food because they mature at an earlier age and smaller size and often have lower growth rates.

With regard to aging, we have discovered natural populations that differ in the rate of aging. They provide excellent material for studying the genetics of the aging process that is different from the sorts of organisms that are now used for this purpose. We currently study the genetics of lifespan and aging in lab lines of model organisms like mice, fruit flies, nematodes, and yeast that are the product of long-term laboratory culture and are often screened for new mutations that affect lifespan.

We can instead offer organisms that have naturally evolved differences in lifespan, which means that these differences have evolved under the constraints of success in the real world. The differences in conditions may mean that the genetic mechanisms that cause longer lifespan are entirely different from those that are discovered in laboratory studies. Characterizing them may then give us very different ideas about how and why aging occurs. No one has pursued work on guppies from this perspective, but perhaps that lies in the future.

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Keywords: extrinsic mortality, evolution of senescence in guppies, predictions made by Medawar and Williams during the 1950s, mountain streams, Trinidad, waterfalls, barriers to the upstream dispersal of predators, interaction between ecological and evolutionary processes.

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