Profile of Dolph Schluter

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Dolph Schluter explores the origin of species on Earth, an avenue of research he has pursued with persistence, creativity, and methodical precision for more than 40 years. Schluter has taken what for Darwin was mainly a thought experiment and applied modern experimental methods to provide scientific evidence of the process of natural selection on species' origins and the evolution of differences between species. He moved from field studies of Darwin's finches on the Galápagos Islands to experimental ponds filled with threespine stickleback fish on the University of British Columbia (UBC) campus, where he is a professor of evolutionary biology. Schluter was elected as a foreign associate of the National Academy of Sciences in 2017. His Inaugural Article (1) is a joint project with his long-time collaborator David Kingsley, with whom he has worked to discover key genes that underlie species differences among sticklebacks. In their Inaugural Article, Schluter, Kingsley, and colleagues point to a stickleback gene that appears to have a dramatic effect on fitness in adapting populations.

Evolving Interests

Schluter, a son of Dutch immigrants, grew up the second of five children in the suburbs of Montreal, Canada. The family lived in an English-speaking enclave west of Montreal where Schluter spent his childhood roaming through fields, woods, and ponds. "I used to bring home frogs and snakes and bugs," he says. "I was very interested in natural history."

His love of animals prompted Schluter's attendance at the closest school with a veterinary program, the University of Guelph in Ontario. There, his fascination with ecology and evolution began with an introductory

Dolph Schluter. Image credit: The Department of Zoology at the University of British Columbia/Sylvia Heredia.

This is a Profile of a member of the National Academy of Sciences to accompany the member's Inaugural Article, e1914889118, in vol. 118, issue 3.
Published Januray 11, 2021.

evolution course taught by Ronald Brooks. "I grew up in a Catholic community and there was something strangely compelling and interesting about the idea that we evolved from apes," he says.

Schluter began reading works by evolutionary biologists Ernst Mayr, Richard Dawkins, and Stephen Jay Gould. "These were powerful thinkers and I thought it was remarkable the progress you could make understanding how life evolved just by thinking very deeply about it and bringing in a few facts when necessary," he recalls.

Despite his budding interest in evolution, Schluter did not plan to continue his studies immediately after graduating. Instead, he accepted a job surveying mammals in the Athabasca tar sands in central Canada. Then, in his final semester, Brooks recommended Schluter attend a lecture by Bob Montgomerie, a PhD student at McGill University. Montgomerie described his work on territorial behavior in hummingbirds based on fieldwork in Mexico. "It was my first exposure to someone studying evolutionary biology in a field setting," says Schluter. "Not just thinking very deeply and writing about it, but actually studying costs and benefits of territorial behavior in a wild population."

Schluter asked Montgomerie if he needed an assistant. Montgomerie referred Schluter to his McGill University advisor and evolutionary biologist Peter Grant, now an emeritus professor at Princeton University. Schluter interviewed with Grant and learned about Grant's ongoing project studying Darwin's finches in the Galápagos along with his wife and collaborator Rosemary Grant, also now an emeritus professor at Princeton. Schluter decided that if Grant accepted him, he would get a Master's degree. If not, he would head to the tar sands.

Adapting on the Fly

Grant offered Schluter a research position and invited him to his new department at the University of Michigan, which did not offer a research Master's degree. So in the fall of 1977, Schluter enrolled as a PhD student. By January 1978, he had joined the Grants and a research assistant in the Galápagos. Thus began a multiyear quest to study adaptive radiation in Darwin's finches. Schluter used field observations and computer modeling to understand why the six species of ground finches on the Galápagos evolved from a common ancestor to possess unique characteristics. "I was trying to understand the overarching contribution that resources and resource competition between species played in the adaptive radiation of this seed-eating group of finches on the Galápagos," he explains.

Additionally, Schluter examined differences in beak size when two ecologically similar finches—in this case two species of seed-eating ground finch—evolved together, competing for resources on the same island, or in isolation, each living alone on an island. He found that finches living together were more different from each other than finches living alone, in large part because of the effect of resource competition (2). This study lent strong support for the concept of character displacement, which has since been verified in other species. The computer models also confirmed the hypothesis that food supply and competition among species determine morphological properties of finch communities (3).

Schluter continued similar work on the evolution of seed-eating finches during his postdoctoral stint at the University of California, Davis and at UBC. Working under University of California, Davis ecologist Thomas Schoener and UBC's Jamie Smith, he used museum collections to measure birds from Hawaii and the mainland, and spent time in the field in the American Southwest. Schluter later worked in East Africa (4). But the work discouraged him. "I thought that I could do comparisons [of birds] for decades and never get closer than I already had in understanding the role of competitive interactions between species and their evolution," he says.

Experimental Islands

Schluter wanted to find a system where he could do experiments on natural selection. "I was interested in experimental trials in which we could introduce to islands either species alone or together and ask whether competition between them occurred, and whether, if it occurred, it would change natural selection," he says.

By then Schluter was doing a 5-year university research fellowship that soon turned into a tenure-track faculty position at UBC. There, he learned about the threespine stickleback, a small fish that exists in oceans, freshwater lakes, and streams all over the northern hemisphere. UBC zoology professor J. Donald McPhail had found stickleback pairs in nearby small coastal lakes. The pairs of sticklebacks appeared to be distinct species: benthics, which are larger and feed on invertebrates in the mud close to shore, and limnetics, which are smaller, more slender, and feed in the open water on zooplankton (5).

"These species occur only in these tiny lakes that are about 10,000 years old," says Schluter. "And because they had evolved repeatedly, we could start to do comparative work and experiments that tested the role of natural selection in the origin of the species."

Along with big aquariums in his laboratory, Schluter constructed ponds on the UBC campus so he could experiment with the stickleback in a natural setting. He started with 13 ponds in 1991 and now has a new facility with 20 ponds. Because each stickleback species was adapted to a contrasting environment within a lake, Schluter could transplant fish from one environment to another and observe the effects. He found that phenotypic differences between the species made a huge difference in their ability to forage and grow in those environments (6). In addition, because the two species can mate and produce hybrids, he could test the fitness of these hybrids in both environments. "Hybrids aren't infertile," explains Schluter. "In the [laboratory] they do fine. But in the wild they fall between the niches of their parents and are mismatched in traits inherited in different mixtures from their parent species, so they don't do well in either environment." This work helped provide further evidence for Darwin's theory that natural selection drives the origin of species (7).

Another line of research examined how reproductive isolation might evolve. Schluter showed that benthics from one lake mate much more readily with benthics from another lake than they do with limnetics from another lake, and vice versa (8). "We call that pattern of repeated evolution of mating compatibilities under similar environmental conditions parallel speciation. We saw it in limnetic–benthic species pairs, and we also tested it with a global sample comparing the mating compatibilities of marine and stream-resident stickleback populations from around the world," says Schluter. "We see the same pattern and we think that part of the reason is that their behaviors evolved in concert with their similar phenotypes, which have evolved repeatedly."

Adding Genetics to the Mix

In 1998, David Kingsley and his then postdoctoral fellow Katie Peichel at Stanford University contacted Schluter. They wanted to explore the genetic basis of phenotypic differences between stickleback populations. Kingsley and Schluter have been collaborating ever since, uncovering the genetic basis of a number of the phenotypic differences between stickleback populations. In particular, the team has identified *PITX1*, which is associated with the loss of the pelvic girdle in certain stickleback species (9), and *EDA*, which is associated with differences in armor plating on sticklebacks (10).

In their Inaugural Article (1), Schluter and Kingsley examined the entire stickleback genome, looking for evidence of natural selection. They attempted to pin down genes that affect fitness in populations adapting to freshwater. To do so, they put hundreds of marine-freshwater hybrid sticklebacks into a pond and genotyped 220 females and 500 of their progeny, estimating which loci in females predicted the most offspring. They mapped that measurement of fitness in a standard design and found only one hit: *EDA*, the gene associated with armor plating. "Females that had two copies of the freshwater allele at that locus produced twice as many offspring on average as the females with two copies of the marine allele," Schluter says.

To help understand the finding, Kingsley and Schluter examined changes in the frequency of *EDA* over many generations in a population of stickleback introduced to a small lake in Alaska in the 1980s. The strength of selection on *EDA* is the same in the Alaskan lake as it is in the pond experiment. The finding suggests that *EDA* is a powerful target for natural selection in stickleback, but all the reasons are not yet known. "We know that *EDA* affects armor, a defensive trait, but we also know that it affects schooling behavior and other traits," says Schluter. "It's a highly pleiotropic gene."

Earlier work showed that the freshwater *EDA* allele exists in low frequencies in marine sticklebacks, suggesting that it is not a new mutation (10). This can help explain why freshwater stickleback that evolved far away from each other share the same mutation. "A lot of evolution happens over short timespans requiring no wait for new mutations," says Schluter. "Instead, many mutations originated a long time ago and are simply hanging out in low frequencies. With so much variation already present, natural selection can cause relatively rapid and repeated changes."

Although Schluter thinks that understanding evolution can help us understand and develop ways to preserve species in a rapidly changing world, his personal interest lies in understanding the origin of species. "I want to know why there are so many species and why there are more in the tropics than here. I'm really interested in how new species form, how they become different, how those differences allow many species to persist in an area, and how all the major patterns that we see when we look at Earth's species diversity evolved."

1 D. Schluter *et al*., Fitness maps to a large-effect locus in introduced stickleback populations. *Proc. Natl. Acad. Sci. U.S.A.*, 10.1073/pnas.1914889118 (2021).

2 D. Schluter, T. D. Price, P. R. Grant, Ecological character displacement in Darwin's finches. *Science* **227**, 1056–1059 (1985).

3 D. Schluter, P. R. Grant, Determinants of morphological patterns in communities of Darwin's finches. *Am. Nat.* **123**, 175–196 (1984).

4 D. Schluter, Character displacement and the adaptive divergence of finches on islands and continents. *Am. Nat.* **131**, 799–824 (1988).

5 D. Schluter, J. D. McPhail, Ecological character displacement and speciation in sticklebacks. *Am. Nat.* **140**, 85–108 (1992).

6 D. Schluter, Adaptive radiation in sticklebacks: Trade-offs in feeding performance and growth. *Ecology* **76**, 82–90 (1995).

7 T. Hatfield, D. Schluter, Ecological speciation in sticklebacks: Environment-dependent hybrid fitness. *Evolution* **53**, 866–873 (1999).

8 H. D. Rundle, L. Nagel, J. Wenrick Boughman, D. Schluter, Natural selection and parallel speciation in sympatric sticklebacks. *Science* **287**, 306–308 (2000).

9 Y. F. Chan *et al*., Adaptive evolution of pelvic reduction in sticklebacks by recurrent deletion of a *Pitx1* enhancer. *Science* **327**, 302–305 (2010).

10 P. F. Colosimo *et al*., Widespread parallel evolution in sticklebacks by repeated fixation of Ectodysplasin alleles. *Science* **307**, 1928–1933 (2005).