

A Tale of Two Species

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—G Brennan



Drs. Catherine L. Peichel and Matthew E. Arnegard in the artificial pond at the University of British Columbia.

Image courtesy Dr. Matthew E. Arnegard

The process of speciation is complex and poorly understood. Many studies have investigated individual phenotypes that may provide a competitive advantage; however, interactions between several different traits are likely required for an organism to adapt to a new and complex environment (Orr, H.A., 2005). In a recent study published in *Nature*, Drs. Matthew E. Arnegard and Catherine L. Peichel (Human Biology and Basic Sciences Divisions) led an international collaboration with Dr. Dolph Schluter (University of British Columbia), using a unique combination of the threespine stickleback fish model system and artificial ponds to demonstrate that multiple unlinked genetic loci across the genome contribute to the adaptation of these fish to either inshore or open water lake habitats.

The researchers focused on two species of threespine stickleback fish coexisting in Paxton Lake, British Columbia, Canada. These species inhabit either inshore niches (benthic) or open water niches (limnetic). Benthic and limnetic species pairs have independently evolved five separate times in lakes in British Columbia as marine sticklebacks invaded freshwater habitats ~12,000 years ago and diversified to exploit the different food resources in these two niches (Schluter, D., 1994). While

they rarely interbreed in the wild, hybrids between these two species are viable in the laboratory. However, hybrid offspring are outcompeted by the parental species in their respective niches.

To investigate the genotypic and phenotypic contributions to the adaptations of these two species, the researchers mated the two species in the laboratory. The researchers then introduced 40 of the resulting first generation offspring, F_1 hybrid fish, into an artificial outdoor pond replicating the benthic and limnetic habitats found in Paxton Lake (see picture). This artificial habitat is a new and powerful way to test the genetic basis of a complex phenotype (habitat performance) in a natural environment with competition for resources. F_2 hybrid juvenile fish, the generation of offspring from the F_1 hybrid fish, were recovered from this lake before their first winter. Using body size as a measure of feeding performance, the researchers found that the largest individuals segregated into two groups with either a predominantly benthic- or limnetic-like foraging pattern. The smallest individuals were outcompeted for more common food resources and suffered a growth disadvantage.

To understand the genetic basis of these adaptive differences, the researchers identified several functional morphological traits underlying diet and habitat adaptation and conducted quantitative trait locus (QTL) mapping on them. These traits mapped to more than half the chromosomes in the stickleback genome, a surprising amount of genetic divergence considering the relatively young age of these species. The relative contributions of these loci to the overall performance of the fish were largely additive, and the genetic loci did not strongly interact with each other. This finding is in contrast to the strong epistatic genetic interactions leading to speciation through intragenomic conflict, e.g. interactions between parental genes that in the offspring lead to hybrid sterility, suggesting that there are differences in the genetic mechanisms underlying diverse modes of speciation.

However, some evidence for interactions between traits was revealed by phenotypic analysis of the smallest individuals in the study. This group inherited poorly matched combinations of traits such as a benthic-like upper jaw and a limnetic-like lower jaw. This combination of traits reduced their feeding efficiency relative to larger individuals with matched upper and lower jaw structures. Notably, these individuals would have performed well in standard laboratory settings; this functional difference could only be detected in the new experimental pond system that contained the divergent habitats to which the parental species are adapted. This environmentally-elicited epistatic interaction between the traits "suggests that despite clear differences in the genetics of the two types of speciation, there is a deep similarity that unites them," said Dr. Peichel.

This study is the first to make connections across three mechanistic levels essential to Darwin's hypothesis of speciation, relating (1) how well individuals perform when using and acquiring resources from different habitats to (2) the subset of "component traits" responsible for variation in individual performance, and (3) connecting these phenotypes to their underlying genetic factors. "Given that performance is context-dependent and emerges from a large number of underlying component traits we expect that a similar genetic architecture will hold true for other types of whole organism performance. One possible example is human athletic performance, [in which] many structural, physiological, and life-history traits contribute to athletic performance in general, yet the

exact suite of component traits underlying athletic prowess should depend on which sport is being played," said Dr. Arnegard.

[Arnegard ME, McGee MD, Matthews B, Marchinko KB, Conte GL, Kabir S, Bedford N, Bergek S, Chan YF, Jones FC, Kingsley DM, Peichel CL, Schluter D](#). 2014. Genetics of ecological divergence during speciation. *Nature*. Epub ahead of print, doi: 10.1038/nature13301.

See also: [Orr HA](#). 2005. The genetic theory of adaptation: a brief history. *Nat Rev Genet*. 119-27.

See also: [Schluter D](#). 1994. Experimental evidence that competition promotes divergence in adaptive radiation. *Science*. 798-801.