Population differentiation: adaptation vs. plasticity

The origin and nature of population differentiation is a major question in evolutionary ecology. In many cases, populations differ for traits that are selectively important. Often, this divergence is advantageous, and confers a local fitness advantage. Adaptive population divergence may be caused by either local adaptation, or by phenotypic plasticity.

One major contributor to population differentiation is local adaptation. When populations are locally adapted, the native population has higher fitness than the non-native population, in all of the environments studied. Local adaptation is based on genetic differences between populations, and is shaped by selection.

Phenotypic plasticity can also contribute to population differentiation, however. If populations are measured under natural conditions, then differences in the environment may contribute to differentiation. Phenotypic plasticity can be considered “adaptive” if the plasticity increases fitness under the local conditions; that is, if an individual responds to an environmental cue in a way that increases fitness in that environment.

Trinidadian guppies have been a study system for population differentiation and local adaptation for some time. These guppies live in pools and rivers; lower water basins often include predators that feed on the guppies, while higher ones generally do not. Migration between environments is rare. Thus, some populations of guppies have experienced predation for many generations, while others have not. Predation regime has repeatedly led to population divergence for many traits. Previous studies have indicated local adaptation for life history, morphology, and behavioral traits. It has also become apparent, however, that many of these traits are plastic, and that environmental cues from predators can alter them as well.

Torres-Dowdell *et al*. investigated whether plasticity in response to predators was adaptive, and the relative roles of plasticity and local adaptation. The authors asked three questions:

- **What is the degree to which plastic responses to predator presence explain population differentiation?**
- **Do populations differ in the magnitude of plasticity?**
- **What is the role of plasticity during local adaptation?**

The researchers collected gravid females from sample sites, raised a generation under controlled lab conditions, and then performed the experiment on the next generation. They collected from four sites, using replicate populations from two watersheds; from each, they collected from a low site (with predators) and a high site (no predators).

Torres-Dowdall, J., C. A. Handelsman, D. N. Reznick, and C. K. Ghalambor. 2012. Local adaptation and the evolution of phenotypic plasticity in trinidadian guppies (poecilia reticulata). Evolution; international journal of organic evolution 66:3432-3443.

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In both watersheds, guppies originally occupied the lower, predator-prone environments; in each, they then independently colonized the higher pools. Thus, we can consider the predator environment to be ancestral and the non-predator environment to be derived.

The goal of this study was to look at both genetic differences between high and low populations and plasticity induced by the presence of predators. They looked at one behavioral trait (position in the water) and two morphological traits (size at maturity and head size/shape); all three are believed to affect fitness when predators are present, and all three were known to be plastic.

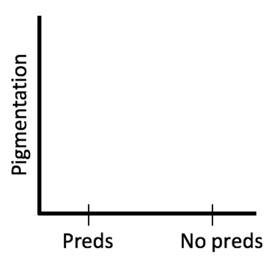
What type of experiment would you need to perform to investigate whether there is a genetic basis for population divergence for these traits? How would you set it up?

What type of experiment would you set up to see whether there's an environmental basis?

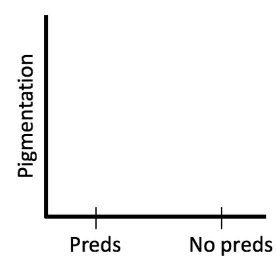
What is the benefit of using populations from two watersheds instead of just one?

Imagine that, in natural populations, populations with predators were always less intensely pigmented than populations without. In an experiment, someone raises fish from a predator-prone population and fish from a non-predation population in both environments. Sketch in a graph of what you might expect to see if the following situations were true:

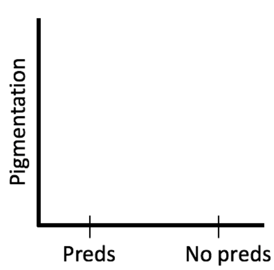
a. Genetic variation, but no plasticity



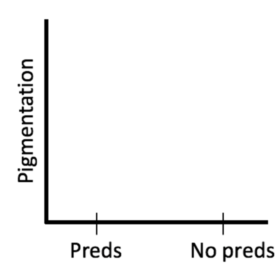
b. Genetic variation and adaptive plasticity



c. Plasticity, but no genetic variation



d. Genetic and plasticity, and non-predator populations have a higher degree of plasticity



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The researchers raised guppies from each of the four populations in two conditions: with and without predator cues. They then measured their traits of interest in the offspring raised under those divergent conditions.

For all of the following figures, if the error bars overlap, the differences are not significant.

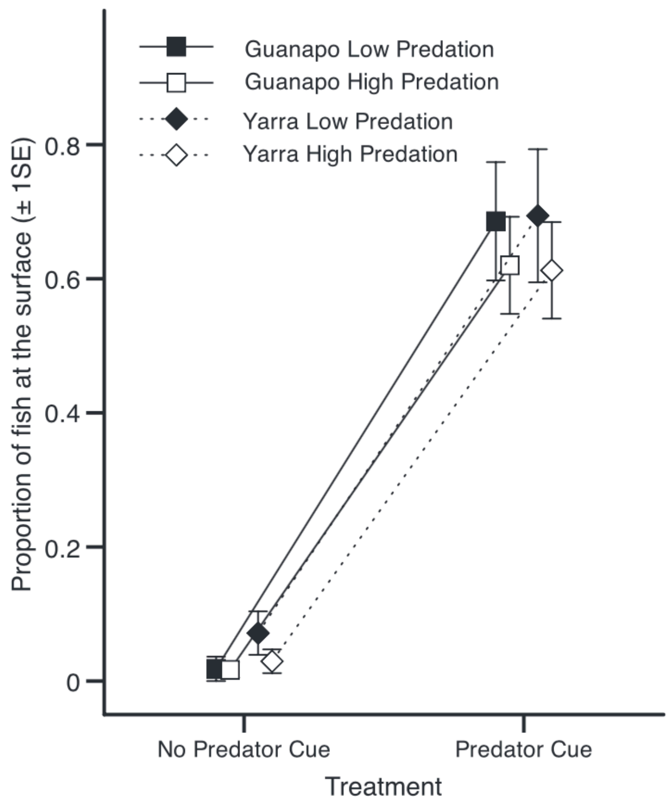

Figure 1. Mean and SEs of proportion of fish at surface from low- (filled symbols) and high- (open symbols) predation regimes from the Guanapo (square symbols) and the Yarra (diamond symbol) drainages reared in the presence or absence of predator cues. Symbols are slightly displaced to facilitate visualization of the error structure.

Figure 1 shows the results for water column position. Positioning near the surface is hypothesized to increase survival when predators are present, although data has not been specifically collected to support this.

Is there plasticity for this trait? Is it adaptive?

Is there genetic differentiation for this trait?

Do populations differ in the amount of plasticity?

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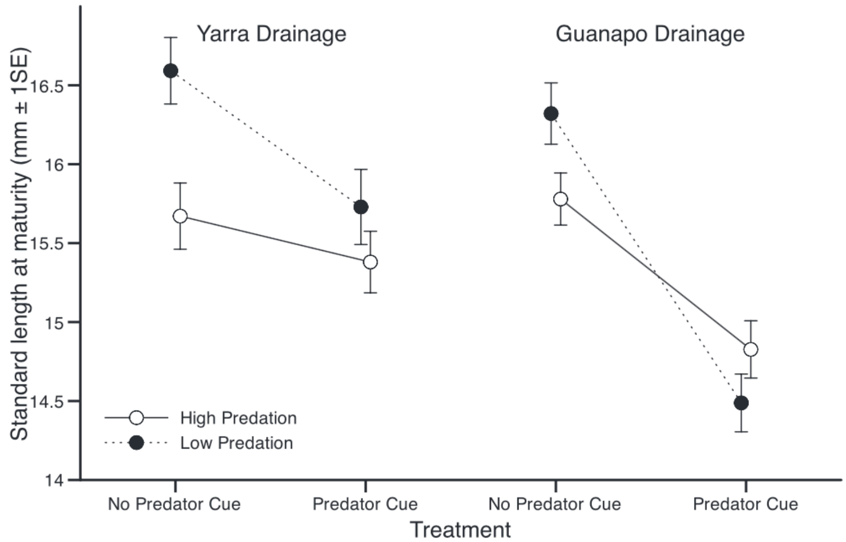

Figure 2. Mean and SEs of standard length at maturity from low- (filled symbols) and high- (open symbols) predation regime guppies reared in the presence or absence of predator cues. The right panel depicts fish from the Guanapo drainage, and the left panel depicts fish from the Yarra drainage. Symbols are slightly displaced to facilitate visualization of the error structure.

Figure 2 shows mean size for each population under the two treatments. Being larger has been shown to be advantageous in the absence of a predator, but being smaller is better when predators are present.

Is there genetic variation for the trait? Is it consistent in all environments?

Is there plasticity? Is it adaptive?

Are the populations consistent in the degree of plasticity?

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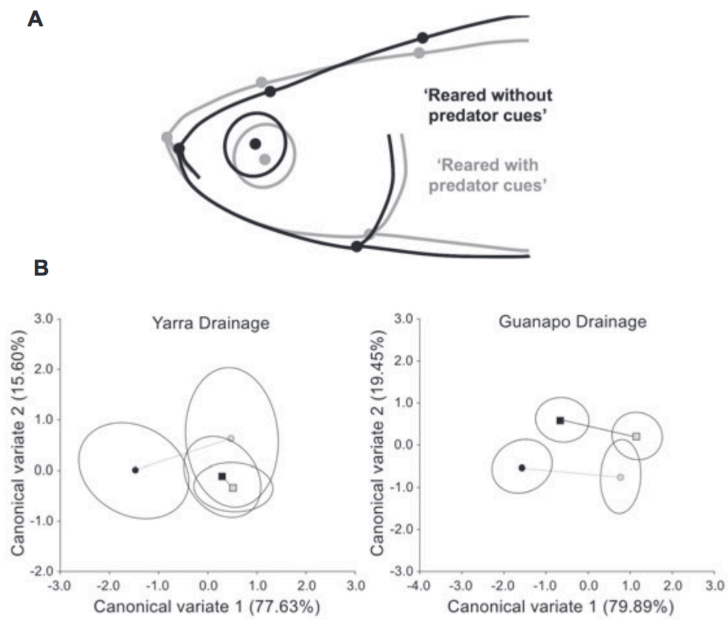

Figure 3. (A) Changes in head shape due to the effect of rearing environment identified by discriminant function analysis (Klingenberg 2011). When reared in the presence of predator cues, guppies develop a more fusiform head shape (gray lines). In the absence of predator cues, the angle from the rostrum to the posterior terminus of the head increased (black line). Solid circles represent landmarks used for morphological analysis. (B) Mean and 95% confidence ellipses for CV1 and CV2 scores from low- (circles) and high- (squares) predation regime guppies reared in the presence (gray symbols) or absence (black symbols) of predator cues. Analyses were performed for each drainage separately. Note that low-predation genotypes responded more strongly to the treatment than the high-predation genotypes, and that the 95% confidence ellipses overlap for the high- and low-predation populations in the presence of the predator cue, but not in its absence.

Figure 3 shows head shape. Because head shape and size is composed of multiple measurements, the data are shown differently. An analysis (called PCA) identifies the variables that sum up the most important measurments. The first of these combined variables (canonical variate 1) is on the X-axis, while the combined variable that explains the next largest amount of variation is on the Y-axis. A point on the graph shows the relative position for a combination of traits that sum up variation in head size/shape. Points that are close on the graph have similar head shapes. Different populations and conditions are indicated by the symbols. The ovals represent confidence intervals; if they overlap, the difference is not significant.

Is there genetic variation for head shape? Is it consistent across environments?

Is there plasticity? Is it adaptive?

Are populations consistent in the degree of plasticity?

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The authors began this experiment with three main questions:

What is the degree to which plastic responses to predator presence explain population differentiation?

Both genetics and plasticity can contribute to population differentiation.

Which trait(s) varied genetically between populations?

Which trait(s) were plastic?

Was there G x E? Put another way, were genetic differences consistent across environments?

For two of the traits, genetic variation for the trait was only present in one environment. Which environment? What patterns do you see?

Putting together all of this information, what can you say about the relative contributions of adaptation and plasticity?

Do populations differ in the magnitude of plasticity?

The degree of plasticity itself may have a genetic basis; thus, it may vary between populations. For the traits that demonstrated G x E, was there variation in the magnitude of plasticity? (look at the slopes of the reaction norms).

Remember that the low populations (with predators) are ancestral and the high populations (no predators) are derived. Did plasticity increase or decrease with invasion of the upper part of the watershed?

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What is the role of plasticity during local adaptation?

The previous question feeds right into this one. Theory predicts that when populations move into a novel environment, a high degree of plasticity can increase the changes of survival under new directional selection. Local adaptation takes time (allele frequencies have to change, and as we know that can take many generations), and populations may go extinct while waiting; plasticity, however, can act almost instantly.

It's hypothesized that staying near the surface of the water would be advantageous when predators are present, but that venturing deeper (and so being able to feed at all depths) would benefit fish when predators are not present. If there was directional selection for deeper foraging in non-predator environments, but no plasticity for the trait, what differences (if any) would you expect to see between high and low populations?

Is that expectation what was observed? What do these results suggest about the role of plasticity in colonizing a new environment?

The magnitude of plasticity may be a genetically-determined trait that is under selection itself. If that is the case, then when a species invades a new environment, there could be selection for increased or decreased plasticity (theoretical arguments have been made either way). Looking at the populations that were more plastic, can you see any patterns? Do these patterns indicate that either increased or decreased plasticity may be favored in a new environment?

Putting together all of the results from this study, are there general conclusions that you can draw about the roles of genetic adaptation and plasticity in population differentiation?