Parental Programming of Development and Behavior in Threespine Stickleback *Gasterosteus aculeatus* of Lake Mývatn, Iceland

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Introduction

An organism's development and life history is influenced by multiple factors, including parental programing of its phenotype. Offspring phenotype can be affected by parents either through genetics, learned behavior, or via transgenerational plasticity. Furthermore, both maternal and paternal effects can act independently on an organism, or together (Bell et al., 2018) Threespine stickleback (*Gasterosteus aculeatus*) are an important model organism for studying the impact of genetics and environment on behavior and morphology. Stickleback display a remarkable amount of phenotypic diversity (Kristjánsson et al., 2002; Millet et al., 2013; Einarsson et al., 2004). This includes both genetic diversity, as well as a high degree of phenotypic plasticity. Much research has been conducted exploring phenotypic plasticity, the ability for an organism to alter its phenotype in response to its environment within its lifetime (Denver and Middlemis-Maher, 2010; Kishida et al., 2010; Klemetsen, 2010). However, there is increasing interest in transgenerational plasticity (TGP), wherin plastic responses to environmental conditions are passed down to offspring (Hellmann et al., 2020; Richter-Boix et al., 2014; Bell and Hellmann, 2019; Shama et al., 2014). This concept holds particular importance in the face of rapid environmental change, because it allows organisms to evolve without relying on actual genetic changes.

As mentioned above, stickleback display a high amount of phenotypic variation between and within habitats. Populations often form species pairs, with two or more morphs coexisting in a single body of water via niche partioning. In lake Myvatn, two morphs exist, the "mud" and "lava" morphs, defined mainly by habitat type, as well as morphology and behavior (Kristjánsson et al., 2002; Millet et al., 2013). Different sections of lake Myvatn act as distinct habitats (referred to as the North (Warm) and South (Cold) basins), and so the sticklebacks can also be distinguished by habitat of origin (Millet et al., 2013; Einarsson et al., 2004). Millet et al. (2013) in particular found that there was a large difference in size between sticklebacks from different habitats, with those of the North basin being larger ($\geq$ 55mm) and of different age classes than those of the South. They posit that these differencee could be due to differences in life history strategies between the populations, or plasticity in response to resources. Interestingly, they also note that North basin stickleback have larger spines than those of the South basin, possibly owing to differences in abundance of gape-limited predators, which occur at rates of up ten times higher in the North basin than the south (Millet et al., 2013).

While we know that plasticity in traits does occur in lake Mývatn stickleback, there is little data on whether this plasticity is transgenerational. Indeed, much of the research on TGP in stickleback has been performed on oceanic populations, and thus TGP in freshwater stickleback represents a current gap in our knowledge of the ecology and evolution of these organisms (Shama et al., 2014). Evidence from marine stickleback suggests that TGP does occur, although it varies between populations (Shama et al., 2014; Heckwolf et al., 2018; Kozak and Boughman, 2012). Research by Kozak and Boughman (2012) found that TGP led to increased shoaling behavior in response to predators by limnetic morphs of stickleback in British Columbia, while Benthic morphs did not show evidence of TGP. This is particularly interesting the the context of lake Mývatn, because as noted above, different subpopulations of stickleback occur in regions with different predator abundances. Particularly in the North basin, where predator abundance is much greater than the South, we could expect to see TGP acting to alter antipredator behavior. Other research has implications for responses to climate change. Heckwolf et al. (2018) investigated adaptive and nonadaptive TGP in marine stickleback in response to changes in salinty. They found that directional selection of nonadaptive TGP accelarated the evolutionary response in offspring, but that it was dependent on life stange and the particular environmental factor they are exposed to. In the context of lake Mývatn, the different basins apply different environmental factors to the sticklebacks living in them (in terms of different temperatures, prey and predator abundances, and seasonal dynamics) and thus the evolutionary selection on TGP might be altered.

Familial genetic effects can also range in heritability. Bell et al. (2018) investigated the heritability of parental behavior (Specifically, fanning of eggs) by male stickleback and found strong heritability of the trait. Furthermore, they concluded that a strong amount of genetic variation could lead the evolvability of the fanning trait. Offspring of male stickleback that expirience predation risk have shown to grow smaller and spend less time in the open (Bell et al., 2016; Stein and Bell, 2014) Female stickleback have also been shown to pass on phenotypic information to their eggs. An RNAseq study analyzing female sitckleback found that eggs from mothers exposed to predators had faster development times, as well as major epigenetic changes and alterations to non-coding genes during development (Mommer and Bell, 2014; Bell et al., 2016). These epigenetic changes, along with phenotypic plasticity, blur the line between true genetic changes and evironmentally-mediated ones.

Major questions I want to address:

- Do lake Mývatn stickleback experience morphological/behavioral TGP in response to food and predator presence, temperature, and salinty? Are maternal or paternal effects stronger?
- How does TGP impact eco-evolutionary dynamics within lake Mývatn? Specifically, does TGP contribute to sympatric speciation of morphs?
- Do Mývatn stickleback obtain familial information primarily through genetics or inherited plastic effects?

Methods

I will use a half-sibiling common garden expiriment to assess TGP in Mývatn stickleback. Stickleback will be collected from seperate basins of the lake, the North, or cold shore, and the South, or warm shore. Sticklebacks from both shores will then be crossed using standard methods laid out by Schluter.

Half-sibling split clutch designs have been used previously to examine the effects of indirect fitness in parasite resistance, as well as TGP in response to temperature in marine stickleback (Barber et al., 2001; Ramler et al., 2014).

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