Predator Cues during the Egg Stage Affect Larval Development in the Gray Treefrog, *Hyla versicolor* (Anura: Hylidae)

M. J. Smith, M. M. Drew, M. Peebles, and K. Summers

The presence of predators can induce changes in the morphology and behavior of the potential prey. In this study, we examined the effects of different predator-induced changes in water chemistry experienced during the egg stage on larval development in the Gray Treefrog, *Hyla versicolor*. The potential predators of amphibian eggs and tadpoles used in this study included larval odonates, crayfish, and leeches. Tadpoles from eggs exposed to leech-induced changes in water chemistry were consistently smaller throughout their larval development than the tadpoles in the control and other potential predator treatments. Size at metamorphosis did not differ significantly among treatments, but the tadpoles in the leech treatment were significantly older at metamorphosis than tadpoles in the other treatments. These results highlight some of the potential fitness consequences for larval *H. versicolor* that received predator cues during the egg stage.

Predator-prey relationships have been an important source of selection in many, if not all, species. In the case of amphibians, the presence of predators during the aquatic life-history stages can not only induce modification in the switch-points of the prey from egg to tadpole and tadpole to froglet (Chivers et al., 2001) but can also bring about changes in tadpole morphology and behavior (Relyea, 2001). Morphological responses to the potential of predation can include changes in size and shape (Relyea, 2002) as well as color (LaFiandra and Babbitt, 2004). Behavioral responses may include a reduction in activity and spatial avoidance (Relyea and Werner, 1999).

Because amphibians have complex life histories that include both aquatic and terrestrial stages, carry-over effects from the one stage to the next are possible. For example, several studies have now found a link between the metamorphic phenotype, which reflects the outcomes of the aquatic stages, and the maturation phenotype (e.g., Altwegg and Reyer, 2003; Berven, 1990; Semlitsch, 1988). In some species, individuals that are smaller at metamorphosis may be less likely to survive to maturity (Smith, 1987) and may mature at an older age (Berven, 1990) or a smaller size (Altwegg and Reyer, 2003). The fitness consequences of survival to the reproductive life-history stage are obvious. However, even for those that do survive, size and age at maturity may also be important factors affecting lifetime reproductive success. For females, small size at metamorphosis may increase age at maturity (Berven, 1990) and for some species can also influence an individual’s ability to compete with other males during the reproductive phase and to attract females (Halliday and Tejedo, 1995).

Thus, the many factors that can influence an individual phenotype during the amphibian aquatic stage may in turn initiate trade-offs for which there can be an array of emergent consequences. First, as described above, small size at metamorphosis may be a disadvantage that can be carried on through life (Altwegg and Reyer, 2003; Semlitsch, 1988). However, the multitude of threats and stresses that can be experienced during the aquatic stages (e.g., predation, pond drying, and density effects) may be such that metamorphosing at a smaller size could increase the probability of current survival.

Much work has focused on the many factors that affect the larval life-history stage in amphibians (e.g., Wilbur, 1977; Travis, 1983; Van Buskirk and Saxer 2001). Fewer studies, however, have looked at factors during the egg stage that later influence fitness (e.g., Laurila et al., 2002; Chivers et al., 2001; Schalk et al., 2002). From the work that has been done, predation pressures experienced during the egg stage can affect time of hatching and size at hatching (Laurila et al., 2002; Chivers et al., 2001; but see Anderson and Petranka, 2003). If the hatching phenotype can influence the metamorphic phenotype, as has been shown under some circumstances in other species (e.g., Semlitsch and Schmiedehausen, 1994), then predation cues experienced during the egg stage could have far reaching fitness consequences.

In the frog *Hyla versicolor*, the presence of