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Evidence for contemporary evolution of behavioural responses to introduced fish

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Introduced predators are a major driver of worldwide biodiversity loss. However, if endemic prey are not rapidly extirpated by invaders, they may evolve antipredator traits that promote coexistence with invaders. We studied antipredator behaviours in fish-naïve and fish-exposed populations of Cascades frog tadpoles, *Rana cascadae*, to test the hypothesis that fish-exposed populations have evolved stronger defensive behaviours. We raised tadpoles from field-collected eggs in fish-free aquaria, and performed behaviour assays to quantify their behaviours with and without fish scent cues. Fish scent induced strong decreases in activity and increases in refuge use in both population types, potentially indicating a persistent ancestral response to fish. Populations co-occurring with fish were constitutively less active and in refuges more than naïve populations in the absence of cues, but had a smaller plastic decrease in activity and a smaller increase in refuge use when exposed to cues. Weakening of the antipredator response in fish-invaded populations may be a signal of contemporary evolution towards optimization of time spent foraging versus the fitness costs of time spent avoiding predation.

Humans are modifying environments worldwide at an unprecedented rate. While evolution is most commonly discussed in terms of hundreds or thousands of generations, examples of rapid evolution (occurring within 10–20 generations) caused by human modifications have been uncovered in numerous systems (reviewed in Carroll, Hendry, Reznick, & Fox, 2007; Stockwell, Hendry, & Kinnison, 2003; Strauss, Lau, & Carroll, 2006). Evolutionary change will occur at faster rates if there is strong directional selection on a highly heritable trait with a high degree of variation within the population. However, rapid evolution is only possible if the selection pressure is not so strong as to cause the species to go extinct before evolution can occur (Stockwell et al., 2003). Amphibians across the globe are often threatened by introduced fishes (reviewed in Kats & Ferrer, 2003), but their capacity to evolve appropriate responses has rarely been tested. Here we explore whether anuran larvae may evolve behavioural responses to introduced predatory fish.

Non-native species are one of the leading causes of endemic species extinctions worldwide and are often a driver of contemporary evolution (Latta, Bakelar, Knapp, & Pfrender, 2007). Given the ubiquity of non-native species and the political and practical problems associated with their removal, it is wise to learn more about the evolutionary potential that native organisms may have for developing coexistence with invaders (Carroll, 2011). If evolution over ecological timescales allows a threatened prey species to adapt to an invasive predator for long-term coexistence, understanding contemporary evolution may be important in native species conservation.

Naïve prey may not have the physical or behavioural defences to cope with novel predators and may not be able to recognize them as predators (Schlaepfer, Sherman, Blossey, & Runge, 2005; Sih et al., 2010). While many organisms have generalized responses to all predators, it is often more advantageous to have specific responses based on predator identity (Relyea, 2001a). When an invasive predator is so novel that no similar predator currently exists, a prey's generalized defences may become useless, or the prey may fail to recognize the threat and initiate these defences (Sih et al., 2010). However, if there is at least some defensive response and an associated benefit, introduction of predators provides a very strong force of selection towards antipredator

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behaviours in their prey. This may cause evolution on ecological timescales to result in rapid development of predator response where virtually none previously existed.

Larval anurans are an excellent system in which to look for contemporary evolution of responses to predators because their responses to native predators have been researched extensively (e.g. Ferrari, Wisenden, & Chivers, 2010; Hokit & Blaustein, 1995; Kats, Petranka, & Sih, 1988; Laurila & Kujasalo, 1999; Lawler, 1989; Smith, Boyd, Dayer, & Winter et al., 2008). Studies of tadpole responses to novel predators have yet to show consistent patterns. Kats et al. (1988) showed that amphibian larvae that normally did not coexist with fish did not show antipredator behaviours when exposed to fish chemical cues. More recently, Vredenburg (2002) showed that tadpoles of *Rana muscosa* did not respond to introduced fish cues but did respond to cues from sympatric snakes. Similarly, Paoletti, Olson, and Blaustein (2011) found no response from *Rana boylii* to invasive fish but did find a response to native predatory newts, and Smith, Boyd, et al. (2008) found no response from two species of tadpoles to a non-native mosquitofish. However, some amphibians with more generalized responses did respond to an introduced fish when they already had inherent responses to native fishes (Bosch, Rincon, Boyero, & Martinez-Solano, 2006; Smith, Burgett, Temple, Sparks, & Winter, 2008), although others did not (Garcia, Thurman, Rowe, & Selego, 2012). Most promisingly, there is evidence for contemporary evolution of antipredator behaviours in tadpoles when exposed to evolutionarily novel predatory bullfrog tadpoles (Kiesecker & Blaustein, 1997) and to novel predatory crayfish (Nunes, Orizaola, Laurila, & Rebelo, 2014).

Evolution of antipredator responses may take several forms. Traits that may be under selection pressure include behaviours such as activity (Richardson, 2001) and refuge use (Kats et al., 1988), chemical defences (Benard & Fordyce, 2003; Kats et al., 1988), changes to growth rate (Relyea & Werner, 1999), changes to body morphology (Relyea, 2001a) and shorter time to metamorphosis (Werner, 1986). The expression of these traits can vary as well. Differences in traits may be due to phenotypic plasticity that is induced by the presence of a predator, or to constitutive changes towards greater antipredator traits that are expressed whether or not the predator is present (Relyea, 2002; Van Buskirk, 2000).

Antipredator responses may not evolve if they are accompanied by high costs of predator avoidance. Reduction of activity, increased time spent in refuges or increased vigilance are common antipredator traits in anurans (as well as in many other taxa), but these traits may come at the cost of decreased time spent foraging and slower growth rates (Lima, 1998; Relyea & Werner, 1999; Werner, 1986). Therefore, while evolution of antipredator behaviours can be beneficial in some situations, such evolution may be slowed or prevented by associated fitness costs. The 'threat sensitivity' hypothesis predicts that antipredator behaviour should optimally be proportional to the threat presented by the predator (Helfman, 1989).

Predator–prey theory predicts that prey will spend more time immobile and/or in refuges when predators are present (Sih, 1987). If overall risk is very high, prey may constitutively minimize conspicuous behaviours even in the absence of immediate predator cues, as would occur with fast, mobile predators or high predator density (Sih, 1987). Rapid evolution could favour constitutive activity reduction if tadpoles do not recognize sensory cues emitted by predators, such as odour, shape or motion. However, if tadpoles can sense the predator quickly and predation levels are moderate, evolution could favour the ability to plastically reduce activity only in the presence of cues (Clark & Harvell, 1992). Alternately, the tadpoles may already respond to fish because of a general response to predators that includes fish or an ancestral response specifically to fish. If predation risk from fish is relatively low and the ancestral response to fish is high, the threat sensitivity hypothesis would predict that the presence of fish could drive selection of a reduced antipredator response to compensate for excessive time lost foraging.

In this study, we tested whether a native prey species, the Cascades frog, *Rana cascadae*, has evolved antipredator behaviours in response to brook trout (*Salvelinus fontinalis*) introduced into fishless mountain lakes. These fish can cause sweeping changes in native prey communities (reviewed in: Knapp, Corn, & Schindler, 2001; Pilliod & Peterson, 2000). However, eradication is difficult and may create controversy. Successful trout removal can require several years of effort (Pope, 2008; Vredenburg, 2004), and trout fishing is important to many rural economies (Deisenroth, Bond, & Loomis, 2012). Therefore, in addition to its relevance to behavioural evolution, the study has the practical aspect of exploring the extent to which native species can evolve to coexist with these invaders. The experimental animals for this work were native to the Klamath and Cascades Mountains where there are hundreds of historically fishless lakes now stocked with trout. *Rana cascadae*, a species of special concern in California, U.S.A. (Jennings & Hayes, 1994), does not usually breed in lakes that contain fish; however, there are a handful of lakes with brook and/or rainbow trout (*S. fontinalis*, *Oncorhynchus mykiss*) where it does breed successfully (Hartman, Pope, & Lawler, 2014; Pope, 2008). These lakes have been stocked with fish for over 80 years (California Department of Fish and Wildlife, 2011), which corresponds to approximately 20 *R. cascadae* generations (Briggs & Storm, 1970). Contemporary evolution of antipredator defence has been shown in *R. cascadae's* congener, *Rana aurora* (Kiesecker & Blaustein, 1997) and in the Iberian waterfrog, *Pelophylax perezi* (Nunes et al., 2014), so there may be the potential for contemporary evolution in populations of *R. cascadae* that have coexisted with introduced trout in recent history.

We quantified activity level, refuge use, time to metamorphosis and size at metamorphosis of *R. cascadae* tadpoles collected from lakes with and without fish. Activity reduction has previously been shown to be an antipredator behaviour in *R. cascadae* (Hokit, Grant, & Blaustein, 1995), and refuge use is an antipredator response in numerous other amphibian larvae (Kats et al., 1988; Kiesecker & Blaustein, 1997). A field study of *R. cascadae* showed that tadpoles were more likely to occur in shallower water in lakes with fish; however, it was unclear whether this was due to tadpoles choosing shallower water or to fish removing tadpoles from deeper water (Hartman et al., 2014). Because *R. cascadae* did not coexist with fish before the last ice age (10 000 years ago) (Welsh, Pope, & Boiano, 2006), we hypothesized that *R. cascadae* from fish-naïve populations would have little or no antipredator response to fish. Because of strong selection pressure caused by predation, we predicted that populations of *R. cascadae* that have co-occurred with fish for many generations would show greater activity reduction and increased refuge use when exposed to fish chemical cues compared to fish-naïve populations. We also predicted shorter times to metamorphosis and smaller size in fish-exposed populations. Shorter times to metamorphosis may provide escape from aquatic predators, although often at the cost of smaller size at metamorphosis, which may have fitness consequences (Benard & Fordyce, 2003; Werner, 1986).

METHODS

We collected *R. cascadae* eggs from six lakes in the Trinity Alps Wilderness, Trinity County, California, U.S.A. on 18–19 May 2013, when eggs were all below Gosner stage 18 (Gosner, 1960). All bodies of water above 1500 m in elevation were historically fish-