

When Should Prey Respond to Consumed Heterospecifics? Testing Hypotheses of Perceived Risk

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In aquatic systems, a long-standing question is why chemical cues from some diets consumed by a predator induce strong anti-predator responses in prey while other diets induce weak or no responses. We performed an experiment to determine if strong prey responses to particular predator diets are due to prey being closely related to the predator's diet (i.e., phylogenetic relatedness) or due to prey coexisting with the predator's diet and thereby sharing a risk of predation. We compared the behavior of Gray Treefrog tadpoles (*Hyla versicolor*) to cues from a dragonfly nymph (*Anax junius*) that consumed either conspecific Gray Treefrogs, one of six diets that commonly coexist with Gray Treefrogs (spanning a wide range of phylogenetic relatedness), or one diet that is closely related to Gray Treefrogs but has an allopatric range that has not overlapped for at least 20,000 yrs. We found that tadpoles could discriminate among the diets and that the magnitude of behavioral response supported the hypothesis of diet phylogenetic relatedness and refuted the hypothesis of diet coexistence.

PREY use a wide range of behaviors to decrease their encounter rates with predators and hence increase their survival (Lima and Dill, 1990). Because the use of anti-predator behavior often comes at the cost of reduced growth and reproduction compared to individuals that do not display the behavior (Sih, 1980; Anholt and Werner, 1995), threat-sensitivity theory predicts that organisms should exhibit responses that are commensurate with the magnitude of predation risk faced (Helfmann, 1989). To accomplish this, prey must be able to perceive their current predation risk and balance the cost of defense with other requirements (e.g., foraging or finding a mate). While many organisms use environmental cues (chemical, mechanical, visual) to detect their predators and make decisions about allocation to defensive behaviors (Tollrian and Harvell, 1999; Venzon et al., 2000), we still lack an understanding of what aspects of the cues are important in communicating information about predation risk.

In aquatic systems, prey generally assess predation risk via chemical cues released by both the predator and the consumed prey (Larsson and Dodson, 1993). Predators emit chemicals, termed “kairomones,” that the prey use to determine which species of predator is present and which defenses should be induced to reduce their risk of being killed (behavior, morphology, or life history). The specificity of kairomones has been confirmed by showing that different predator species induce different behavioral responses, either in the magnitude or type of traits induced (Turner et al., 1999; DeWitt et al., 2000; Relyea, 2001a, 2001b). Prey also respond to chemicals from other injured prey (termed “injury-released alarm cues”) or consumed prey (termed “dietary cues”; Wisenden, 2000). Prey often exhibit the strongest behavioral defenses when the predator consumes a diet of conspecific prey (Wilson and Lefcort, 1993; Schoeppner and Relyea, 2005). However, when predators consume heterospecific prey, the behavioral defenses of prey can vary in strength (Smith, 1992; Chivers and Mirza, 2001). To explain the wide range of responses to different predator diets, two hypotheses have been proposed: ecological coexistence and phylogenetic relatedness (Parker and Shulman, 1986; Chivers and Mirza, 2001).

The ecological-coexistence hypothesis posits that prey should respond strongly to injury-released alarm cues or dietary cues from coexisting heterospecifics and respond weakly to such cues from non-coexisting heterospecifics (Chivers and Mirza, 2001). This hypothesis assumes that responses to heterospecific cues are a result of natural selection favoring the ability to detect and respond to cues that provide information about a shared predator (i.e., if you are being eaten, I am in danger too). Under this scenario, the predator consumes two different species of prey with similar probabilities and, therefore, cues from the consumed heterospecifics are interpreted (via innate or learned mechanisms) as representing a level of risk that is similar to the risk posed when the predator consumes conspecifics. Several studies have supported this hypothesis by demonstrating that closely related, coexisting prey induce similarly strong defenses (Chivers and Smith, 1998; Mirza et al., 2003). However, few studies have examined whether closely related, non-coexisting prey also induce strong defenses. Such a result would allow us to reject the ecological-coexistence hypothesis.

The phylogenetic-relatedness hypothesis posits that prey should respond strongly to injury-released alarm cues or dietary cues from closely related heterospecifics but respond weakly to such cues from distantly related heterospecifics (Parker and Shulman, 1986; Mathis and Smith, 1993; Sullivan et al., 2003; Schoeppner and Relyea, 2005). This hypothesis is based upon the premise that closely related prey produce similar chemical cues and, therefore, should induce similar behavioral defenses. Therefore, cues from two species that are allopatric, but of similar phylogenetic relatedness to a target species, should induce similar defenses. In one of the most extensive tests of the phylogenetic-relatedness hypothesis to date, Schoeppner and Relyea (2005) exposed Gray Treefrog tadpoles (*Hyla versicolor*) to chemical cues from a wide range of predator diets and found that the magnitude of anti-predator responses decreased as phylogenetic relatedness of the diet decreased. However, because all of the diets used in that study coexisted with Gray Treefrog tadpoles, it remains unclear if the cues from the closely related diets (i.e., other

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species of amphibians) induced strong responses because they were closely related (and thereby emit similar cues) or because they coexisted (and thereby interpret the cues from any conspecific or heterospecific prey as indicating that a predator is present and poses a high level of risk). Of course, there is the possibility that both phylogenetic relatedness and coexistence are important and prey use both sets of information in making their defense decisions.

To distinguish between the ecological-coexistence and phylogenetic-relatedness hypotheses, we need to include closely related predator diets that do and do not coexist with the responding species. We addressed this question in a laboratory experiment in which we exposed Gray Treefrog tadpoles to a variety of treatments where we fed larval dragonflies several different diets. We quantified Gray Treefrog activity in each environment and tested the following hypotheses: 1) prey can discriminate among a wide range of predator diets; 2) behavioral defenses will be stronger when predators consume closely related prey and weaker when predators consume distantly related prey; and 3) behavioral defenses will be stronger when predators consume closely related, coexisting prey and weaker when predators consume closely related, non-coexisting prey.

MATERIALS AND METHODS

We exposed Gray Treefrog tadpoles to chemical cues from caged dragonfly naiads (*Anax junius*, which coexist with Gray Treefrogs) that were fed different species of prey. We employed a randomized block design in which we exposed tadpoles to nine different treatments that were replicated ten times for a total of 90 experimental units across two spatial blocks (i.e., laboratory shelves). The nine treatments consisted of the following: no predator, a caged and starved dragonfly, caged dragonflies fed one of six diets that coexist with Gray Treefrog larvae (Gray Treefrog larvae; Spring Peeper larvae, *Pseudacris crucifer*; Wood Frog larvae, *Rana sylvatica*; Spotted Salamander larvae, *Ambystoma maculatum*; libellulid dragonfly naiads, *Sympetrum internum*; and freshwater snails, *Physa acuta*), and caged dragonflies fed a diet that is closely related to Gray Treefrogs but does not coexist (Pacific Treefrog larvae, *Pseudacris regilla*). The starved predator treatment was included to control for the effect of the predator alone on tadpole behavior. Pacific Treefrogs were selected because they are closely related to Gray Treefrogs (confamilial) but the two species have allopatric ranges. Pacific Treefrogs are restricted to the west coast from British Columbia south through California extending east into Montana, Idaho, and Nevada, while Gray Treefrogs are found on the east coast from south Ontario through north Florida and extending west into Manitoba, Oklahoma, and central Texas (Behler and King, 1991).

We conducted the experiment in the laboratory using 10-L plastic tubs filled with 7 L of filtered well water. To ensure that the hatchling tadpoles were kept predator-naïve, we collected 18 pairs of amplexed frogs from Mallard Pond (Crawford County, PA) on 11 May 2004 and allowed them to oviposit in laboratory tubs containing aged well water. We reared the hatchlings outdoors in covered wading pools and fed them rabbit chow *ad libitum*. From these hatchlings, we randomly selected ten tadpoles for each tub (initial mean mass \pm 1 SE = 105 \pm 6 mg). Each tub also contained a 250-mL opaque plastic cup covered with a mesh screen, which served as the predator cage. Such cages reduce but do not eliminate the potential for visual cues of a predator's

presence. For tubs assigned a predator treatment, we added a single late-instar dragonfly naiad. We fed each predator 300 \pm 10 mg of the assigned diet; for the no-predator control treatment, we added an empty cup. To protect against problems of predators emitting chemical cues from different diets consumed prior to the experiment, we fed the assigned diets to the dragonflies for at least two weeks prior to the start of the experiment. Dragonflies assigned the "starved" treatment were not fed for one week prior to the experiment.

We added the tadpoles and caged predators to the tubs on 11 July 2004 (between 1600 and 1700 hrs). We observed tadpole activity the next morning between 1000 and 1200 hrs. Using scan sampling (Altmann, 1974), we counted the number of tadpoles moving (i.e., swimming or feeding) in each tub to determine the proportion of active tadpoles. During the 2-hr observation period, we performed ten observations on each tub and used the mean observation from each tub as our response variable. This is a standard technique that has proven successful in a large number of past studies (Relyea, 2001a, 2003a). We analyzed tadpole activity using an analysis of variance (ANOVA) in which we looked for the effect of predator treatment and block on tadpole activity. After detecting an overall treatment effect to control the experiment-wise error rate, we conducted pairwise comparisons using Fisher's LSD test.

RESULTS

The ANOVA found a significant effect of the treatments ($F_{8,71} = 19.8$, $P < 0.01$) but no significant block effect ($F_{1,71} = 1.1$, $P = 0.269$) or block-by-treatment interaction ($F_{8,71} = 1.4$, $P = 0.227$). Therefore, the block and block-by-treatment degrees of freedom were pooled into the error term. Based on mean comparisons, the strongest reduction in activity occurred when predators consumed any of the amphibian diets (Fig. 1). There were no differences among these amphibian diet treatments ($P > 0.125$), but the treatments had significantly lower activity than the no-predator treatment, the starved-predator treatment, and both diets of insects and snails ($P < 0.01$). The libellulid diet induced intermediate tadpole activity that was weaker than the response to the amphibian diets ($P < 0.01$) but stronger than the response to the snail or starved dragonfly diets ($P \leq 0.031$). Both the freshwater snail diet and starved-predator treatment were not different from the no-predator control ($P \geq 0.368$).

DISCUSSION

Our results provide evidence that chemical cues from conspecific prey (Gray Treefrogs), closely related, coexisting prey (Spring Peepers), and closely related, non-coexisting prey (Pacific Treefrogs) all induced nearly identical anti-predator behavior in Gray Treefrog tadpoles. Moreover, the cues from consumed Pacific Treefrog tadpoles induced activity reductions that were not significantly different from those induced by all of the coexisting amphibian species. These results are consistent with a previous experiment that supported the predictions of the phylogenetic-relatedness hypothesis but lacked any allopatric diets (Schoeppner and Relyea, 2005). The current experiment suggests that the cues emitted by predators consuming different species of amphibians must be quite similar (especially among confamilial amphibians), whereas the cues emitted by predators

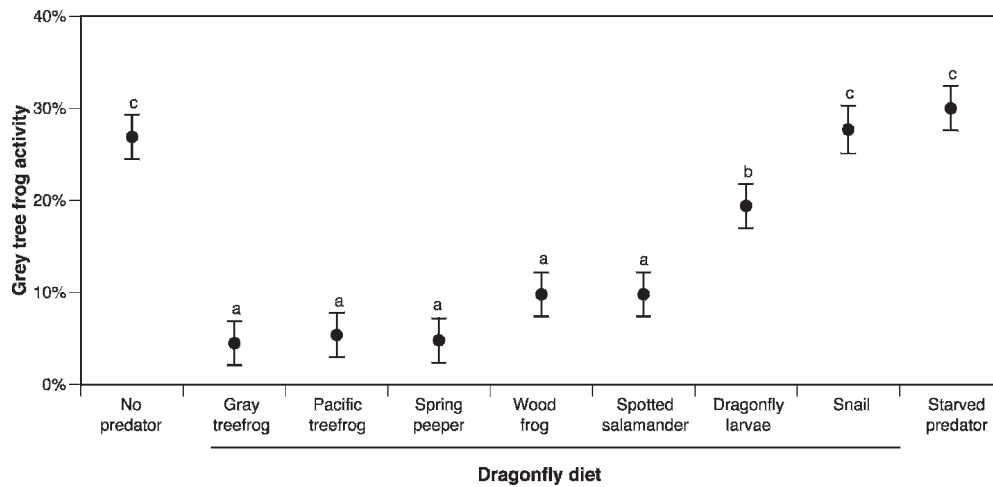


Fig. 1. Activity of Gray Treefrog tadpoles in response to no predator cues, cues from a starved predator, or cues from caged dragonflies that had consumed one of seven different diets. Each treatment was replicated four times with ten tadpoles in each experimental unit. Data are means \pm 1 SE, and different letters indicate significantly different means based on Fisher's LSD.

consuming insects or snails, which induced weaker responses, must be quite different from amphibians. Because we were able to include only one closely related allopatric diet, further studies that include multiple allopatric diets should be conducted to ensure that this result is a general phenomenon and not unique to the taxa that we used.

While the phylogenetic-relatedness hypothesis is strongly supported in tadpoles, not all taxa support this hypothesis. For example, Parker and Shulman (1986) found that the induction of hiding behavior in seven species of sea urchins in response to injury-released alarm cues was not consistent with either the phylogenetic-relatedness or ecological-coexistence hypotheses. Alarm cues from more closely related sea urchins and coexisting sea urchins did not always induce hiding. Similarly, in experiments using fishes, injury-released alarm cues from closely related heterospecifics did not induce behavioral responses while damage-released alarm cues from more distantly related species did induce behavioral responses (Commens and Mathis, 1999; Chivers et al., 2000). While these results could indicate that phylogenetic relatedness is not a consistent predictor of prey responses to heterospecific cues in other taxonomic groups, there are several methodological differences between our work and previous work addressing the role of phylogenetic relatedness that may account for the differences among the findings (including diet identity, cue type, the previous predator experience of the target animals, and the degree of phylogenetic relatedness among the diets).

The equivocal support for the two hypotheses in the literature may be explained in part by the identity of the diets chosen. Some dietary cues may provide "mixed information" if the diet used is also a predator or potential prey of the focal animal whose behavior is being observed (Petranka, 1989; Wildy et al., 1999; Mirza et al., 2003). If the diet fed to a predator is itself a predator of the focal species, the focal species may detect and respond to kairomones emitted by the diet and injury-released alarm cues emitted by the diet. As a result, the target prey could respond strongly to the diet regardless of phylogenetic relatedness (Mirza et al., 2003). In contrast, if the diet is a potential prey item for the focal species, the focal species may respond to the cues by increasing its foraging rather than exhibiting anti-predator behavior (Petranka, 1989; Wildy et al., 1999).

One of the diets used in our study provides a good example of this issue. The *Sympetrum* dragonfly is a small predator that can only consume small tadpoles and induce weak tadpole defenses (Relyea, 2003b). We found that tadpoles responded to the *Sympetrum* diet with activity that was lower than the no-predator and starved-predator treatments but higher than any of the amphibian diets. Because this small dragonfly species can be a tadpole predator, we cannot rule out that some fraction of the activity reduction could have been caused by kairomones possessed by *Sympetrum* in addition to the injury-released alarm cues from *Sympetrum* when consumed by the larger *Anax* dragonfly. This illustrates the importance of only using diets that cannot also potentially emit cues that can serve as kairomones or food cues to the target prey.

When considering the evidence for the phylogenetic-relatedness hypothesis, we must also consider whether experiments were performed using damaged prey or consumed prey. For example, the phylogenetic-relatedness hypothesis is well supported in tadpole studies (Wilson and Lefcort, 1993; Laurila et al., 1997; Schoeppner and Relyea, 2005) but not well supported in fish studies (but see Mirza and Chivers, 2001a for suggestive data in salmonids). However, most amphibian studies use cues from consumed prey (i.e., dietary cues), whereas most fish studies use cues from crushed fish skin (i.e., injury-released alarm cues; Chivers and Mirza, 2001). This difference in protocol may be critically important because in some groups (e.g., amphibians) crushed prey can induce much weaker anti-predator behaviors, making responses to crushed prey much more difficult to detect (Schoeppner and Relyea, 2005). To determine whether the lack of consistency across taxa is due to taxonomic group or experimental protocol, we need to conduct experiments across numerous taxonomic groups and directly compare the effects of cues from crushed versus consumed diets (Ferrari et al., 2007).

The tadpoles used in our study were predator-naïve and demonstrated that their responses to dragonflies consuming tadpoles were largely innate. However, many experiments that document prey defensive behaviors in response to chemical cues have used wild-caught prey. Numerous studies have shown that prey can learn to respond strongly to heterospecific cues once the target has simultaneously

encountered the heterospecific and conspecific alarm cues (Chivers and Smith, 1994; Chivers et al., 1996; Wisenden and Millard, 2001; Mirza and Chivers, 2001b, 2003; Chivers et al., 2002). When animals can learn to associate alarm cues from heterospecifics with predation risk, the behaviors of experienced prey no longer reflect previous selection for responses to cues that reliably predict risk. It is likely that many organisms respond innately to some cues (i.e., cues from conspecifics and heterospecifics that have cues that are structurally similar) while they learn to respond to other cues (cues from heterospecifics that are also consumed by a common predator), and both types of responses are important in producing effective anti-predator defenses. Therefore, in evaluating the phylogenetic-relatedness or the ecological-coexistence hypotheses, we must recognize that these two types of responses (innate and learned) generate different predictions about the expected patterns of responses. The phylogenetic-relatedness hypothesis predicts that prey should respond innately to cues from heterospecifics and any cue that is structurally similar to the conspecific alarm cue. If prey can learn that other cues communicate information about predation risk, then the innate pattern of responses may be obscured when organisms with previous predation experience are tested. Using prey that have previous experience with predation cues is also a concern because such prey may have formed morphological defenses and, as a result, no longer use behavioral defenses (Relyea, 2003a). Therefore, it is crucial that we understand how experience affects prey responses to chemical cues and consider the effect of such experience on the predicted behavioral responses.

When testing the phylogenetic-relatedness hypothesis, we must also consider our subjective definitions of “closely related” versus “distantly related.” For example, in studies of fish responses to predators eating a variety of heterospecifics (different species of fish), diets that diverged approximately 250 mya relative to the focal species have been classified as “distantly related” (Commens and Mathis, 1999; Mirza and Chivers, 2001a; Mirza et al., 2001). However, in studies of amphibian responses to predators eating a variety of heterospecifics (from amphibians to invertebrates), diets that diverged 250 mya relative to the focal species have been classified as “closely related” (i.e., the amphibian diets of Schoeppner and Relyea, 2005), whereas diets that diverged 900 mya have been classified as “distantly related” (i.e., the invertebrate diets of Schoeppner and Relyea, 2005). A strong anti-predator response to the heterospecific diet would be interpreted as rejecting the phylogenetic-relatedness hypothesis under the first scenario, but supporting the phylogenetic-relatedness hypothesis under the second scenario. In one of the most extreme examples of phylogenetically distant diets, Nolte et al. (1994) found stronger responses by a variety of mammals when they were exposed to the urine of coyotes (*Canis latrans*) that had been fed meat versus fruit. These studies highlight the fact that if a study focuses on a more narrow range of relatedness, it could miss the point at which the alarm cues become too dissimilar and the prey responses weaken. For example, if we had considered only the amphibian diets in this study, we would have concluded that predator diet had no effect on prey behavior. Therefore, a more rigorous evaluation of the phylogenetic-relatedness hypothesis requires that diets span a wide range of relatedness based on a

standardized measure (such as divergence time or degree of genetic difference) to make comparisons among studies more meaningful.

This study demonstrated that anuran larvae can discriminate among predator diets and that the pattern of discrimination supported the phylogenetic-relatedness hypothesis and refuted the ecological-coexistence hypothesis. However, it is important to note that our experiment only contained a single allopatric diet; more allopatric diets need to be investigated to assess the generality of this result. The ambiguous support for the two hypotheses in non-amphibian systems likely results from differences in the range of relatedness used, the use of crushed versus consumed diets, the inclusion of “mixed information” cues from diets that also can function as predators or food of the focal prey, and differences in the role of cue learning among systems. As we begin to explore these issues more fully and combine our insights with a knowledge of the chemical composition of alarm cues and predator kairomones, we will better understand how chemical cues communicate information about predation risk.

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