



Predator diet and prey behaviour: freshwater snails discriminate among closely related prey in a predator's diet

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Chemical cues are commonly used by prey to assess predation risk. Prey typically respond to predator cues by altering behaviour, but their response may depend on predator diet. There are few data on how predators feeding on prey types spanning a continuous gradient of relatedness affect prey behaviour. Here I present the results of a study evaluating the relationship between predator diet and prey behaviour. We presented two species of freshwater gastropods with caged crayfish fed one of five diets and compared them with a no-predator control. Diets included conspecific prey, congeners, prey in the same order, and two prey taxa in different phyla. We monitored behaviour and growth over 3 weeks. Predators feeding on conspecifics induced a large increase in the refuge use of both prey species. Refuge use was highly contingent on predator diet, as one snail species responded only to predators feeding on conspecifics and the other species responded only to predators feeding on conspecifics and congeners. Neither snail species responded to predators feeding on prey taxa in a different genus. Snail behaviour did not depend on the degree of ecological overlap with diet items, but behaviour was related to the degree of phylogenetic similarity. There was no evidence that diets of an intermediate relatedness induced an intermediate response. Instead, prey responded to the diet gradient in a threshold manner. Growth responses were generally concordant with behavioural responses. The overall effect of predators on prey in nature depends on how variation in predator diet translates into altered prey phenotypes.

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A host of studies show that environmental variation can induce dramatic changes in individual phenotypes as organisms adjust their behavioural, life-historical, morphological or physiological traits in an adaptive manner (Pigliucci 2001; DeWitt & Scheiner 2004). With respect to phenotypic plasticity, perhaps the most studied form of environmental variation is predation risk (Tollrian & Harvell 1999). Predators pose a formidable challenge to prey, as effective antipredator traits typically are quite costly (DeWitt et al. 1998; Tollrian & Dodson 1999), but a failure to avoid predation levies the ultimate penalty—death. Thus, antipredator traits that are used only when predators are present (e.g. inducible defences) offer the advantage that prey can invest in costly defences only when necessary. One key condition necessary for the evolution of inducible

defences is the presence of reliable, high-quality information regarding predation risk (Bronmark & Pettersson 1994; Harvell & Tollrian 1999; Gabriel et al. 2005).

In aquatic environments, reception of chemical stimuli released by predators and injured prey is the primary mechanism by which most taxa gather information about the threat of predation (Dodson et al. 1994; Chivers & Smith 1998; Kats & Dill 1998). A number of studies show that the nature of these chemical cues depends on the identity of the consumed prey, as predators feeding on distantly related prey species generally induce a weaker antipredator response than do predators feeding on conspecifics (reviewed in Chivers & Mirza 2001). The dependence of prey responses on predator diet has important implications for the study of inducible defences and has been the focus of a number of recent studies (e.g. Mathis & Smith 1993; Bronmark & Pettersson 1994; Chivers & Smith 1998; Chivers et al. 2002; Schoeppner & Relyea 2005; Sullivan et al. 2005).

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Although the dependence of inducible defences on predator diet is established, most studies have limited their diet comparisons to diets distantly related to the target prey versus diets conspecific to the target prey (Schoeppner & Relyea 2005), leaving several important questions unanswered. These questions include: (1) How specific are prey responses to variation in the diet of predators? Because there are almost no studies of predators feeding on diets of closely related prey (e.g. congeners), it is not known if diets of closely related prey will induce a strong shift or a weak shift in prey phenotype. A consideration of the specificity of prey response, in relation to the predator's diet breadth, can yield insight on the degree to which diet-based responses are adaptive. (2) What is the shape of the relationship between variation in the relatedness of the consumed diet and prey responses? Prey may respond in a graded manner to declining relatedness of the predator's diet, or prey may show an abrupt shift at some threshold level of diet relatedness. (3) What form of relatedness is most useful in predicting prey responses? Relatedness can be defined in various ways, including phylogenetic similarity (the degree of evolutionary divergence; Chivers & Mirza 2001) or ecological similarity (coexistence in space and time; Mathis & Smith 1993; Schoeppner & Relyea 2005; Sullivan et al. 2005).

Here I evaluate the role of predator diet in the induction of antipredator defences by two species of freshwater snails, *Helisoma trivolvis* and *Physa gyrina*. *Helisoma trivolvis* and *P. gyrina* use chemical cues to detect predators (Snyder 1967; Covich et al. 1994) and in response alter their morphology, life history, and behaviour (Crowl & Covich 1990; Alexander & Covich 1991; Turner 1996; Chase 1999; Turner et al. 2000; Hoverman et al. 2005) when these chemical cues are perceived. Studies with freshwater snails have shown that exposure to injured prey, unfed predators, or predators feeding on unrelated prey induces a weak response, or no response at all, relative to predators feeding on conspecifics (Turner et al. 2006). However, Turner et al. (2006) presented predators with just two alternate diets, and the full role of diet in mediating the antipredator response of freshwater snails remains poorly understood.

This study consists of two independent experiments, one examining the effect of predator diet on the habitat use and growth of *H. trivolvis* and another examining the effect of predator diet on habitat use and growth of *P. gyrina*. *Helisoma trivolvis* and *P. gyrina* are geographically widespread and among the most abundant of the North American gastropods (Eversole 1978; Jokinen 1987; Dillon 2000). Changes in snail grazing rates have important food-web consequences because gastropods regulate periphyton productivity and standing crops in lakes and streams (Lowe & Hunter 1988; McCormick & Stevenson 1989; Rosemond et al. 1993). Thus, shifts in the behaviour of *H. trivolvis* or *P. gyrina*, induced by variation in predator diet, may have important consequences for the ecology of littoral communities (e.g. trait-mediated indirect interactions; McCollum et al. 1998; Bernot & Turner 2001). Here I evaluate the relationship between predator diet and the induction of antipredator defences by freshwater snails. The larger goal of the study is to understand better the potential scope for trait-mediated indirect interactions in littoral food webs.

METHODS

We tested the influence of predator diet on the induction of antipredator defences by stocking the target species (*H. trivolvis* or *P. gyrina*) into outdoor mesocosms and exposing them to caged predators in one of five diet treatments or a no-predator control treatment. We selected predator diets so as to provide graded levels of phylogenetic overlap with the target species. In both experiments we exposed the targets, in order of declining phylogenetic relatedness, to (1) predators fed prey conspecific to targets, (2) predators fed a different species in the same genus, (3) predators fed prey in the same order, but a different family, or (4 and 5) predators fed one of two diets of prey in different phyla.

For the first experiment, with *H. trivolvis* as the target, predator diets were *H. trivolvis*, *Helisoma anceps*, *Physa acuta*, oligochaete worms (the red earthworm *Lumbricus*), or coenagrionid damselfly (*Enallagma* spp.) larvae (treatments 1, 2, 3, 4 and 5 above). *Physa gyrina* was the target prey in the second experiment, and predator diets were *P. gyrina*, *P. acuta*, *H. trivolvis*, oligochaete worms (*Lumbricus*), or coenagrionid damselfly larvae.

This design also allows a test of the ecological similarity hypothesis, as the relative frequency of local coexistence of the diets and targets varies independent of the relative phylogenetic similarity of diets and targets. For example, both experiments used diet treatments of annelids and arthropods. Annelids are more closely related to gastropods than are arthropods (Kim et al. 1996), but damselflies have a larger ecological overlap with pond snails than do *Lumbricus*. Considering the first experiment, our survey data show that target *H. trivolvis* coexists much more often with *P. acuta* than with *H. anceps* (personal observation), and thus the ecological similarity hypothesis predicts that *H. trivolvis* should respond more strongly to the *P. acuta* diet. A similar test of among-gastropod ecological similarity is not possible in the second experiment, as target *P. gyrina* has low overlap with both *H. anceps* and *P. acuta* (personal observation).

The predator used in both studies was the decapod crayfish *Cambarus bartoni* (Fabricius). Crayfish have a broad diet, but are important predators of snails (Hanson et al. 1990; Lodge et al. 1994; Nyström et al. 1999; Hobbs 2001) and are known to induce shifts in the life history and behaviour of *H. trivolvis* and *P. gyrina* (Alexander & Covich 1991; Covich et al. 1994; Chase 1999; Turner et al. 1999; Turner 2004; Hoverman et al. 2005). Full induction of antipredator defences in freshwater snails occurs only when a predator is actively feeding on prey (Turner et al. 2006). Thus, each mesocosm assigned to a predator treatment contained a single crayfish (18- to 25-mm carapace length) held in a cage built from slotted polyvinyl drainpipe (10 cm diameter) covered on the ends with mesh screening. The resulting crayfish density (1.0 crayfish/m²) was somewhat lower than is typical of lake ecosystems (Garvey et al. 2003). Mesocosms assigned to the no-predator control treatment held an empty predator cage. As the caged crayfish were fed and resided within the mesocosms, targets were exposed to chemical and perhaps mechanical cues associated with predation, but suffered no direct mortality. The

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