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Phenotypic plasticity in response to fine-grained environmental variation in predation

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Summary

1. In nature, organisms experience environmental variability at coarse-grained (inter-generational) and fine-grained (intra-generational) scales and a common response to environmental variation is phenotypic plasticity. The emphasis of most empirical work on plasticity has been on examining coarse-grained variation with the goal of understanding the costs and benefits of plastic responses in response to a particular environment.

2. In this study, we investigated the effects of fine-grained variation in predation on the inducible defences of larval wood frogs (*Rana sylvatica*) by widely altering the density and feeding schedule of caged predators (*Dytiscus* spp.) while holding average predation constant.

3. We found that predator cues induced change in tadpole behaviour, morphology, and mass. Surprisingly, however, temporal variation in predation did not cause the tadpoles to alter their activity (compared to a constant predation treatment) or mass. Temporal variation in predation did alter tadpole tail depth, but only when experiencing our most extreme variation treatment in which the predators were fed once every 8 days. Under these conditions, the predator-induced tadpole tail was less extreme compared to environments containing constant predation.

4. While a number of previous studies have examined behavioural responses of prey to temporal variation in predation risk without holding average predation constant, this appears to be the first test of temporal variation *per se*. As in previous studies of organism responses to temporal variation in resources, our results suggest that fine-grained environmental variability can affect the expression of phenotypically plastic traits, but our tadpoles appear to be generally unresponsive to this fine-grained variation for many of their traits.

Key-words: inducible defence, amphibian, mesocosm, risk variation, trait lability

Introduction

Few organisms live in static environments but instead experience fluctuations in both biotic and abiotic factors. These fluctuations can affect their fitness and limit their distribution. When there are reliable environmental cues, many organisms exhibit phenotypic plasticity in response to changes in their environment and improve their performance (Pigliucci 2001; West-Eberhard 2003; DeWitt & Scheiner 2004). Most empirical work on phenotypic plasticity has focused on how organisms respond to a constant exposure to different environments. This approach has produced a wealth of knowledge about the costs and benefits of phenotypic plasticity when organisms experience variable environments across generations (i.e. coarse-grained environmental variation; Schlichting & Levin 1984; Lively 1986; van Tienderen 1990; Sultan & Bazzaz 1993; Tollrian 1993; Dudley & Schmitt 1996; Pigliucci *et al.* 1997; Relyea 2004). In nature, however, organisms often encounter substantial environmental variation within their lifetimes over both space and time (i.e. fine-grained environmental variation). If fine-grained variation encompasses the same range of environments as coarse-grained variation, then organisms that express the 'wrong' phenotype may suffer the same range of fitness costs that favour plasticity in coarse-grained environments, but for shorter periods of time (i.e. some fraction of the lifetime). Therefore, fine-grained variation may have substantial effects on individual fitness. As a result, selection should favour individuals that can adjust their phenotypes in response to fine-grained environmental variation. If organisms can detect and respond to fine-grained variation, then understanding these effects will be particularly important for extrapolating experimental results to the interpretation of phenotypic patterns observed in nature.

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Surprisingly few studies of phenotypic plasticity have directly manipulated fine-grained variation. The majority of empirical work has addressed the effects of temporal variation in resource levels (Wayne & Bazzaz 1993; Kacelnik & Bateson 1996; Winn 1996; Siems & Sikes 1998; Ali & Wootton 1999; Novoplansky & Goldberg 2001; Miner & Vonesh 2004; Englemann & Schlichting 2005; Ruehl & DeWitt 2005) or predation risk in animals (Hamilton & Heithaus 2001; Sih & McCarthy 2002; Van Buskirk *et al*. 2002; Pecor & Hazlett 2003; Foam *et al*. 2005). However, because most of the above studies were not designed to examine temporal variation *per se*, most studies that have manipulated temporal variation in the environment have simultaneously altered the average environment that the organism experiences. For example, several tests of the risk allocation hypothesis (Lima & Bednekoff 1999) have been conducted to determine how prey behavioural defences are affected by fluctuating periods of high and low predation risk compared to a constant high-risk predator environment (Hamilton & Heithaus 2001; Sih & McCarthy 2002; Van Buskirk *et al*. 2002; Pecor & Hazlett 2003; Laurila *et al*. 2004; Foam *et al*. 2005). Thus, individuals in the fluctuating-risk treatment not only experience greater fine-grained variation in predation risk, but also a lower average risk compared to individuals in the constant high-risk environment. To address the effects of temporal variation *per se*, we need to manipulate fine-grained variation while holding the average experience constant among treatments. The only studies to manipulate temporal variation *per se* have been studies of resource variation (Wayne & Bazzaz 1993; Siems & Sikes 1998; Novoplansky & Goldberg 2001; Miner & Vonesh 2004; Englemann & Schlichting 2005).

The effects of fine-grained variation on an organism's traits will depend on whether the induced responses are reversible or irreversible. If induced traits are irreversible, then organisms with induced traits obviously cannot respond to future environmental changes. When traits are reversible, the pattern of response to temporal variation will depend on whether responses are threshold (all-or-none) or graded. For threshold responses, organisms would be limited to switching between alternative trait states and the observed response to temporal variation will depend on the last environment encountered. For graded responses, organisms can produce a wide range of possible phenotypes, and the final phenotype exhibited will depend on the intensity of the variation, how individuals interpret variation over time, and how frequently the environment changes (i.e. whether it is longer than the time required for adjusting the trait, Padilla & Adolph 1996; Gabriel 1999; Gabriel *et al*. 2005). Thus, behavioural traits, which can be rapidly induced, should be modified quickly and track fine-grained variation to produce a phenotype that is continuously suited to the environment. In contrast, morphological traits, which require longer times for induction and reversal (Van Buskirk 2002b; Relyea 2003), may be less sensitive to temporal environmental variation.

We examined the effect of fine-grained variation on larval anurans (i.e. tadpoles), a system that has become well documented for its plasticity in response to predators (Smith & Van Buskirk 1995; Laurila & Kujasalo 1999; Lardner 2000; Relyea 2001, 2002a,b; Laurila *et al.* 2002; Van Buskirk 2002a,b). Inducible defences are well-studied and can show continuous and reversible responses to changes in predation risk (Van Buskirk 2002b; Van Buskirk & Arioli 2002; Relyea 2003, 2004; Schoeppner & Relyea 2008), making tadpoles a prime candidate for studying the effects of temporal variation on plasticity. By observing how behaviour, mass, and morphology are affected by temporal variation in predation (while holding average predation constant), we asked whether tadpole phenotypes were affected by fine-grained environmental variation. Given that tadpoles are known to have graded responses to predation (Relyea 2001, 2004; Schoeppner & Relyea 2008), we predicted that tadpole behaviour would be more sensitive to temporal variation in predation compared to tadpole mass and morphology.

Materials and methods

We conducted the experiment at the Pymatuning Laboratory of Ecology's Aquatic Research Lab located in northwestern Pennsylvania in the spring of 2003. We used a completely randomized design with nine treatments replicated five times for a total of 45 experimental units. Our goal was to expose tadpoles to predator environments that varied over time but had the same average amount of predation on tadpoles (i.e. the average mass of prey consumed per predator). Variation in predator consumption of tadpoles in nature is unknown; therefore, our goal was to create variation in a variety of ways. Our nine treatments included a no-predator control, a 'constant-predation' treatment in which four caged predators were each fed 100 mg every day, and seven treatments in which we created fine-grained variation in predation. First, we varied the frequency that four predators were fed: (i) 200 mg every 2 days, (ii) 400 mg every 4 days, or (iii) 800 mg every 8 days (*Dytiscus* larvae can consistently consume up to 800 mg of tadpoles within 1 day). Second, we varied the amount that four predators were fed on a set time schedule. Using a 2-day feeding schedule, we rotated four predators through cycles of 100, 200, and 300 mg of prey ('100–200–300, 2 days'); using a 4-day feeding schedule, we rotated four predators through cycles of 100, 400 and 700 mg ('100–400–700, 4 days'). Third, we varied the number of predators. For this treatment, we rotated through cycles of 2, 4, and 6 caged predators (feeding the predators 200 mg of prey every 2 days or 400 mg of prey every 4 days). Over a 24-day period, we could cycle through three or four rounds of each type of temporal variation while averaging the same amount of prey consumed per predator per day.

The experimental units were 800-L pond mesocosms (cattle watering tanks) designed to simulate the types of ponds in which these amphibians are typically found. Each mesocosm contained 700 L of aged well water, 200 g leaf litter, 15 g rabbit chow (as an initial food source), and an aliquot of pond water containing algae and zooplankton. Because up to six predators were added to some tanks, we placed six predator cages into each tank. The cages were constructed of 10-cm black plastic drainpipe covered on both ends with a fibre glass mesh screen which allowed the predator cues to diffuse into the tank. Depending on the treatment, each cage was either empty or contained a single larval beetle (*Dytiscus* sp.). All mesocosms were covered with shade cloth lids to prevent colonization by other organisms. The wood frog tadpoles were collected from two populations (Shrub pond and Staub pond; 10 egg masses/population) as newly

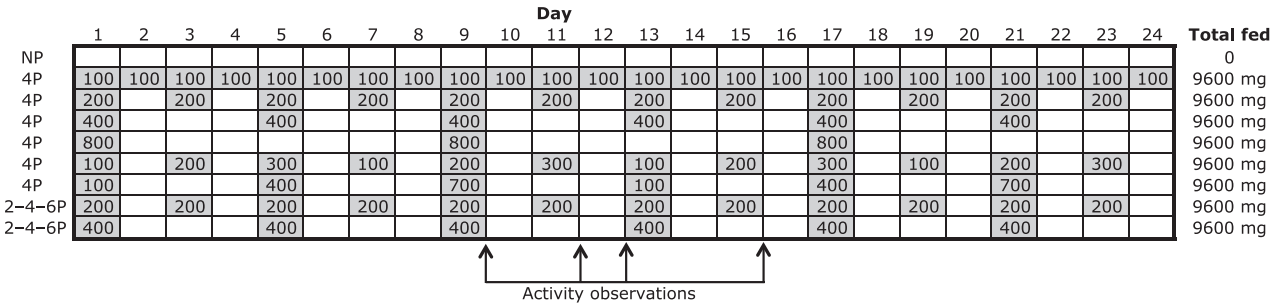

Fig. 1. A schedule of the predator feeding regimes over 24 days. The left hand column indicates the number of constant or variable predators. The right-hand column reflects the total mass of prey fed to predators in each mesocosm (prey mass × number of predators × number of feedings). Arrows indicate the four dates during which behavioural observations were made.

laid egg masses on 28 March 2003. The eggs were hatched and the tadpoles were reared in pools containing aged well water. The wood frogs were fed rabbit chow *ad libitum* before the experiment. Using a mixture of tadpoles from the two populations, we added 30 tadpoles to each mesocosm on 9 May 2003 (initial mean mass ± SE = 139 ± 5 mg). The predators were fed the following day (defined as 'day 1' of the experiment; Fig. 1).

Behavioural observations were conducted during the middle 8-day cycle of predator feeding. We counted the number of tadpoles that were moving (i.e. swimming or feeding) and divided this number by the 30 tadpoles that were in each tank to obtain the proportion of active (i.e. moving) tadpoles in each tank (Relyea & Werner 1999; Relyea 2002d, 2004; Schoeppner & Relyea 2008). The alternative approach of dividing the number of active tadpoles by the total number of tadpoles observed in the tanks provided similar results. We began observations the day after all of the predators were fed (i.e. day 9) and continued to conduct observations until day 15 so that we could capture tadpole behaviour as the predation treatments varied over that 8-day period. The number of observations per tank was as follows: seven observations on day 9, seven observations on day 11, six observations on day 12, and six observations on day 15. The activity data were analysed with a repeated-measures analysis of variance (rm-ANOVA). When a significant effect was found, we conducted pairwise comparisons using Fisher's LSD test.

After 24 days, all tadpoles were removed from the mesocosms and preserved in 10% formalin for subsequent morphological measurements (mean survival = 93 ± 0·2%). Tadpole morphology was measured using an image analysis system (Optimas Bioscan; Bothell, Washington, DC). We weighed each tadpole and then measured seven morphological dimensions: body depth, length, and width; tail muscle depth and width; and tail length and depth (see Fig. 1 in Relyea 2000). Because the tadpole's body is round, we placed a glass plate under the tadpole's tail to bring both structures into the same plane of focus and ensure that we obtained an undistorted lateral image.

Because we were interested in the effects of the treatments on tadpole shape independent of tadpole mass, we first performed a multivariate analysis of covariance (MANCOVA; using tadpole mass as a covariate) and then saved the residuals. Before performing the MANCOVA we log-transformed the data when necessary to improve the linearity of the relationship between each trait and mass. A requirement when making size-adjustments is that there were no mass × treatment interactions for any of the traits, indicating that the regression lines for each trait were parallel among treatments. To produced mass-independent estimates of each trait for every tadpole, we added the residuals saved from the MANCOVA to the estimated marginal means of each treatment as detailed in a number of past studies (McCoy *et al*. 2006; Schoeppner & Relyea 2008). This produces mass-independent estimates of tadpole shape for each tadpole. We then averaged the mass-adjusted morphological dimensions for all tadpoles in a tank, and then used these tank means, along with mean tadpole mass, as our response variables in MANOVA to examine the effects of the treatments (we excluded two tanks from the analysis because they represented significant outliers). When significant multivariate effects were found, we conducted univariate tests. If the univariate tests were significant, we used Tukey's HSD test to make pairwise comparisons among treatment means. Of primary interest were comparisons between the no-predator treatment and the eight treatments containing predators and between the constant-predation treatment (i.e. 100 mg fed to each of four predators every day) the variable predation treatments.

Results

We found significant effects of the predator treatments on the tadpole traits (Fig. 2). In the repeated-measures ANOVA on tadpole activity, we found a significant effect of predator treatment ($F_{8,34} = 45{\cdot}8$, $P < 0{\cdot}001$), time ($F_{3,102} = 87{\cdot}0$, $P < 0{\cdot}001$), and a treatment × time interaction ($F_{24,102} = 2{\cdot}2$, $P = 0{\cdot}003$). As a result, we then examined the effects of the treatments on each observation day. On all four observation days, mean comparisons indicated that tadpoles were always more active in the treatments lacking predators than in any of the eight treatments containing predators ($P < 0{\cdot}001$). However, there were never any differences between the constant predation treatment and any of the seven variable-predation treatments ($P > 0{\cdot}3$).

There was a significant multivariate effect of the treatments on wood frog mass and morphology (Wilks' $F_{64,162} = 3{\cdot}6$, $P < 0{\cdot}001$). The multivariate effect was caused by univariate effects of mass, tail depth, tail length, body length, and body width ($P \leq 0{\cdot}04$ for all tests; Fig. 3); there were no univariate effects of body depth, muscle depth, or muscle width ($P \geq 0{\cdot}1$).

When we conducted mean comparisons on mass, we found that tadpoles were smaller in all of the eight treatments containing predators compared to the no-predator treatment ($P \leq 0{\cdot}001$). Compared to the constant-predation treatment (i.e. 100 mg of prey fed every 1 day), tadpole mass was not different from any of the variable predation treatments ($P > 0{\cdot}3$).

Mean comparisons on relative tail depth indicated that tadpoles had deeper tails in all eight treatments containing predators compared to the no-predator treatment ($P \leq 0{\cdot}001$).

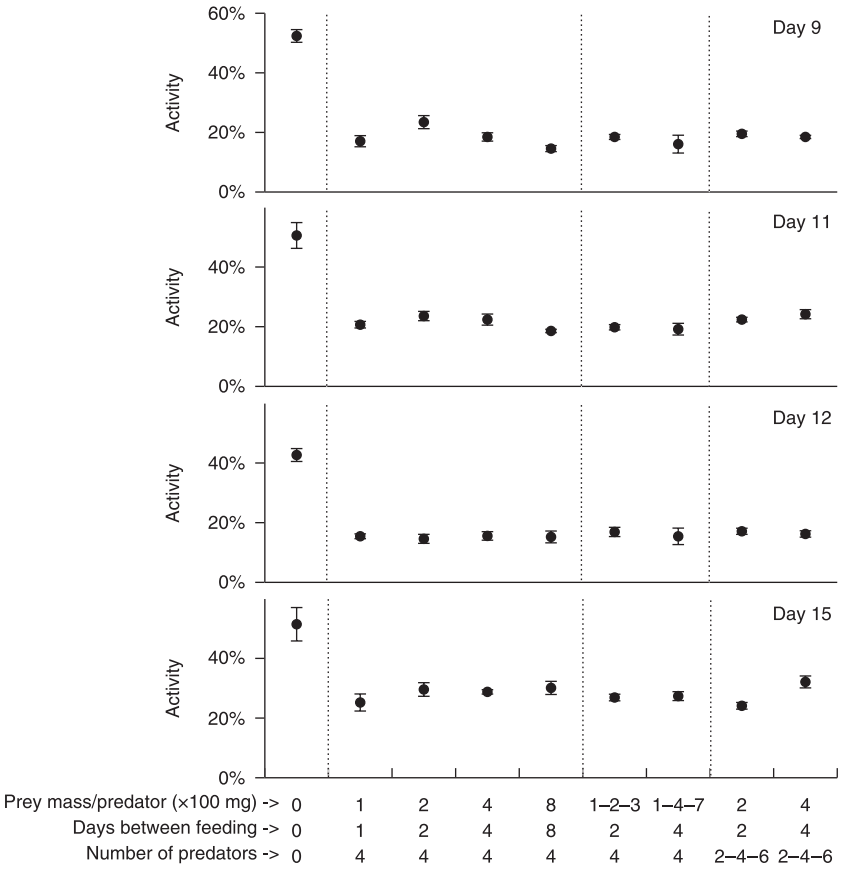

Fig. 2. Wood frog tadpole activity in response to variable predation risk on four different days (means ± 1 SE). In all predator treatments, tadpoles experienced an average predation rate of 100 mg prey/predator/tank/day but varied in the amount and frequency that predators were fed or the number of predators that were fed.

Whereas the constant-predation treatment induced 16% deeper tails than the control, tadpoles raised with predators fed 800 mg every 8-day treatments had 5% shallower tails than the constant-predation treatment ($P = 0{\cdot}006$). The remaining variable-predation treatments did not differ from the constant-predation treatment ($P > 0{\cdot}18$).

In the mean comparisons on relative tail length, tadpoles in the no-predator treatment had relatively longer tails than tadpoles in any of the eight treatments containing predators ($P \leq 0{\cdot}007$). Compared to the constant-predation treatment, variation in predation had no effect on tail length ($P \geq 0{\cdot}5$).

In comparing relative body length among treatments, we found that tadpoles raised without predators had relatively longer bodies than any of the eight treatments containing predators ($P \leq 0{\cdot}001$). However, compared to the constant-predation treatment, variation in predation had no effect on body length ($P \geq 0{\cdot}7$).

When we conducted mean comparisons on tadpole body width, we found that, compared to the no-predator treatment, body width was not different in any of the predator treatments ($P > 0{\cdot}2$). Moreover, there were no differences between the constant-predation treatments and any of the variable predator treatments ($P > 0{\cdot}3$).

Discussion

In this study, we found that tadpoles altered their phenotypes in response to predation and in response to fine-grained variation in predation. The fine-grained variation produced no differences in tadpole behaviour or mass and only one difference in tadpole morphology. The predator-induced phenotypic changes were generally consistent with past experiments and are thought to be adaptive in tadpoles. The combination of reduced activity and the development of deeper tails and shorter bodies lowers the risk of predation but at the cost of slower growth due to reduced time spent foraging, the induction of relatively smaller mouthparts, and the induction of relatively shorter, presumably less efficient, intestines (Skelly 1992, 1994; Relyea 2001, 2002c,d; Van Buskirk 2002b, Relyea & Auld 2004, 2005). Many of these traits are under selection by predator and no-predator environments (Van Buskirk *et al.* 1997; Van Buskirk & Relyea 1998; Relyea 2002a) and, at least in wood frogs, have a heritable basis (Relyea 2005).

We predicted that tadpole behaviour would track fine-grained variation in risk such that periods of high predation would induce lower activity while periods of low predation would induce higher activity. We observed tadpole behaviour at four periods during the course of the 8-day feeding cycle in the middle of the experiment and found no differences between the constant-predation treatment and any of the seven variable-predation treatments. It was particularly striking that even when predators were only fed once every 8 days, tadpole activity did not increase 7 days after the feeding. This result contradicts the predictions made by the risk allocation hypothesis (Lima & Bednekoff 1999) which predicts that prey

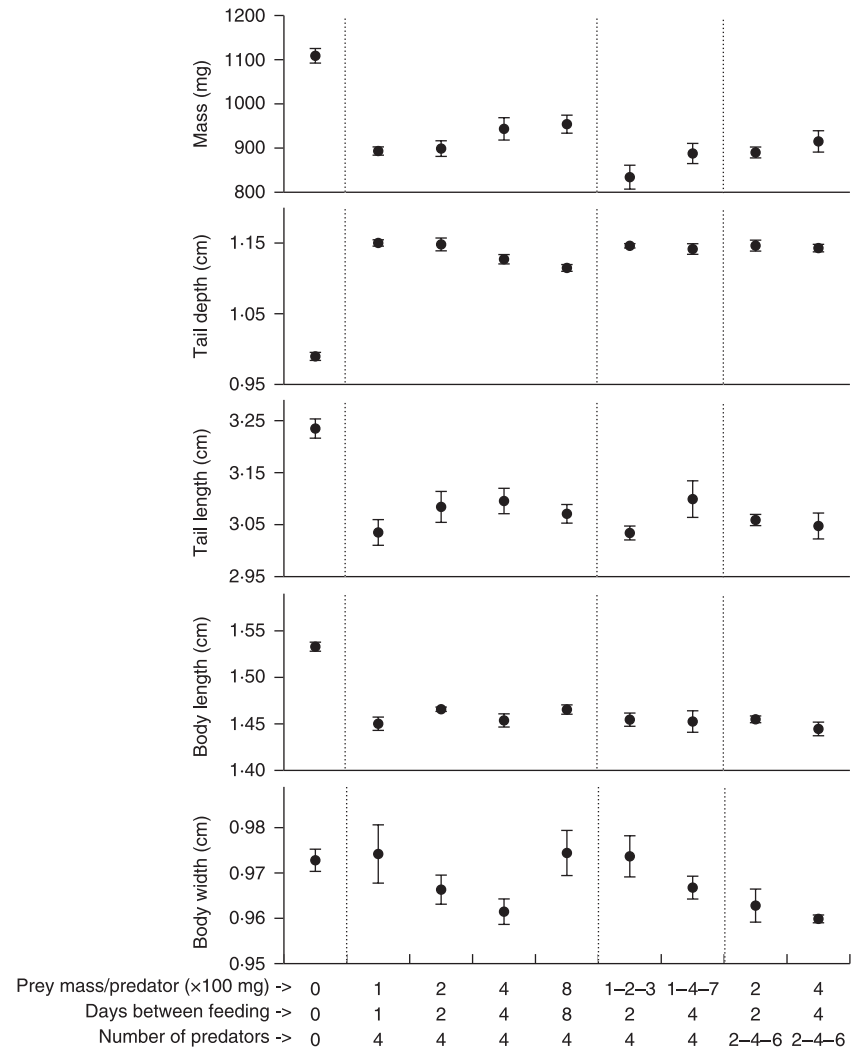

Fig. 3. Wood frog tadpole mass and relative morphology in response to variable predation risk after being exposed to 24 days of different predation environments (means ± 1 SE). In all predator treatments, tadpoles experienced an average predation rate of 100 mg prey/predator/tank/day but varied in the amount and frequency that predators were fed or the number of predators that were fed.

experiencing variable risk should forage more during periods of low risk and less during periods of high risk compared to prey reared in constant low or high risk environments, respectively. In our experiment, we found no differences in tadpole behaviour among the treatments that differed in the proportion of time they spent in higher risk environments. In another test of the risk allocation hypothesis using tadpoles, Van Buskirk *et al*. (2002) found that tadpoles also did not behaviourally respond to increased proportion of time at risk. They proposed that the lack of response was due to the tadpole's ability to maintain high growth rates under high predation risk, and that the risk allocation hypothesis may only apply in situations where some minimum growth requirement cannot be met in the high-risk environment. It is also possible that one would not observe responses consistent with the risk allocation hypothesis if prey were already maximizing their foraging in the constant-low-risk environment.

The lack of behavioural response to predators fed 800 mg every 8 days suggests either that the behavioural responses of the tadpoles are not reversible, the chemical cues did not break down over time, or the predators continued to emit cues for 8 days after being fed. Previous experiments have demonstrated that behavioural responses are quickly reversible when tadpoles are moved from predator to no-predator environments (Relyea 2003; Fraker 2008) and our past work on leopard frog tadpoles (*Rana pipiens*) has found that predator cues emitted by other invertebrate predators (larval *Anax junius*) break down and do not induce behavioural changes after 24 h (R. A. Relyea, unpublished data). In addition, Peacor (2006) has also shown that chemical cues from larval dragonflies that have been aged for 2 days no longer cause bullfrog tadpoles to alter their behaviour. In another example, chemical cues from sunfish induce weak behavioural defences in snails (*Physa acuta*) after being aged for 24 h and have no effect after being aged for 41 h (Turner & Montgomery 2003). Hence, our best current estimates from a number of aquatic taxa are that chemical cues from predators completely break down within 1–2 days after being produced.

The duration that predators continue to produce chemical cues is an open question. In deriving our hypotheses, we assumed that the primary pulse of chemical cues associated with predation would be released during the first day. If predators actually release chemical cues over a longer period of time, then prey in the shorter periods of variability (e.g.,

predators feeding every 2 days) may not have experienced fluctuations in cues that were different from the constant-risk treatment. Given that the chemical cues have never been identified in the tadpoles (nor most other taxa), there is no way to quantify the duration of cue production. However, we can draw upon data from studies that have observed tadpole responses to starved predators. In these studies, starved predators (dragonfly naiads) sometimes induce behavioural and morphological responses in tadpoles, but responses appear to depend on the length of time that the predator has been starved and the size of the experimental venue (Anholt *et al.* 1996; Van Buskirk & Arioli 2002; Schoeppner & Relyea 2005). For example, larval dragonfly nymphs (*A. junius*) that were fed 300 mg of tadpoles and then not fed for > 4 days induce no defensive responses in larval tree frogs (*Hyla versicolor*; Schoeppner & Relyea 2005). Further, *Anax* fed 150 mg of prey and then subsequently starved for 2 days induce intermediate morphological defences in larval pool frogs (*Rana temporaria*; Van Buskirk & Arioli 2002). Given that tadpole behavioural responses are rapidly reversible and that any cue produced is expected to break down with 1–2 d, our experiment suggests that dragonflies fed a very large amount of prey (e.g., 800 mg) continue to emit chemical cues for a relatively long period of time (i.e. 7 days).

We predicted that morphological defences would be affected by fine-grained variation when the periods between changes in the risk were longer than the time needed to alter the morphology. Given that uninduced individuals require approximately 4 days to develop morphological defences that are equivalent to an individual that has experienced continuous predation risk (Van Buskirk 2002b; Relyea 2003), we predicted that the tadpoles exposed to longer periods between predation events would respond by producing less extreme defences. This hypothesis was only supported for relative tail depth and only in response to the most extreme variation in predator feeding frequency (i.e. predators fed 800 mg of prey once every 8 days). This demonstrates that tadpoles can respond to fine-grained variation, but the responses are limited to particular traits and require fairly extreme environmental variation.

Prey may not be inclined to respond to very short-term changes in predation because such short-term changes may be a poor indicator of actual predation risk (Fraker 2008). If predators produce chemical cues for a short period while they digest their prey, and then do not produce cues while they are hunting, tadpoles that immediately increase activity when they detect decreases in cue concentrations would be more likely to encounter the predator when it resumes hunting. If this were the case, tadpoles that increase their activity immediately following a decrease in cue concentration would have lower survival than tadpoles that behaved more cautiously. Therefore, the lack of a behavioural response to fine-grained temporal variation may be adaptive, because over evolutionary time the prey that have ignored short-term fluctuations in risk would have survived better. However, this is less likely to be the case when fluctuation in risk occurs over longer time scales (4–8 days) because the lost growth opportunities of being overly cautious would be more substantial. Indeed, the tail depth response to 8-day temporal variation suggests that prey do not ignore temporal variation on these longer time scales.

The effects of fine-grained variation in predation risk on prey morphology have important implications for interpreting the phenotypic patterns observed in nature. In this experiment, we found that tadpoles exposed to some types of fine-grained variation in risk produced 5% shallower tails than tadpoles in the constant-risk environment. Particularly in scenarios where both the predator and prey colonize habitats every year (vernal pools or species with complex life cycles) predation risk will vary with the relative density and size distributions of both the predator and the prey. Therefore, in nature, tadpoles likely experience fine-grained variation in the chemical cues that indicate predation. If fine-grained variation is the norm, then the magnitude of the defences observed in constant-risk experiments may over-estimate what is achieved in nature. Given that phenotypes are often viewed as the product of balancing conflicting demands (i.e. growth and defence), less intense defences are often interpreted as indicative of increased competition. This experiment has shown that the magnitude of the defence can also be decreased by fine-grained variation in predation and care must be taken when interpreting phenotypic differences observed in nature. Given that deeper-tailed tadpoles survive predation better (Van Buskirk *et al.* 1997; Van Buskirk & Relyea 1998), we interpret the weaker tail depth response with predators eating only once every 8 days as indicating that the tadpoles are perceiving a lower mean predation risk and balancing the need for defence with the need for growth. The precise magnitude of increased risk associated with possessing a 5% shallower tail (i.e. exposure to predation every 8 days versus constant predation) is unknown.

While this study focuses on the effects of variability *per se* on inducible defences, it is in accordance with the findings of previous work examining the effects of temporal variation in resources on an individual's phenotype. In all studies to date that have manipulated fine-scaled variation while holding the average environment constant, at least one trait was affected by environmental variability. In animals, sea urchin larvae had longer feeding arms and fathead minnows had longer guts when food availability was varied (Siems & Sieks 1998; Miner & Vonesh 2004). In plants, both Wayne & Bazzaz (1993) and Novoplansky & Goldberg (2001) found that total biomass was lower when resources were more variable (light and water respectively). In addition, Novoplansky & Goldberg (2001) found that variable water conditions altered competitive hierarchies among species particularly at low overall resource levels. Additionally, Englemann & Schlichting (2005) found that fine-grained variation in water availability affected bolting date, plant height, and survival; however, the effects of variability were only observed when overall water availability was low. Overall, these results indicate that fine-grained environmental variability is important to the expression of phenotypically plastic traits.

Conclusions

Previous work has shown that when prey experience temporal variability in predation they often respond by altering their behaviour (Hamilton & Heithaus 2001; Sih & McCarthy 2002; Van Buskirk *et al*. 2002; Pecor & Hazlett 2003; Laurila *et al*. 2004; Foam *et al*. 2005). However, these studies have simultaneously varied both variation in predator environment and average predator environment. In this experiment, we demonstrated that prey behaviour and mass were not affected by fine-grained variation in predation *per se* while morphology can be affected by fine-grained variation in predation. These results contradict the conventional wisdom that traits which can be altered quickly should track temporal environmental change while traits which cannot be altered quickly should not be affected by fine-grained temporal variation. The results also highlight the need to understand how prey make their phenotypic decisions in regard to temporal variation in predation and to determine the extent of temporal variation in risk that the prey actually encounter in nature. Moreover, our study supports previous research on fine-scaled variation in resources which has shown that fine-scaled temporal variation decreases the magnitude of the induction of plastic traits. Increased investigation into fine-grained environmental variation is certainly needed to determine the extent to which such variation is important to the ecology and evolution of phenotypic plasticity.

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