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Putting prey back together again: integrating predator-induced behavior, morphology, and life history

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Abstract The last decade has seen an explosion in the number of studies exploring predator-induced plasticity. Recently, there has been a call for more comprehensive approaches that can identify functional relationships between traits, constraints on phenotypic responses, and the cost and benefits of alternative phenotypes. In this study, we exposed *Helisoma trivolvis*, a freshwater snail, to a factorial combination of three resource levels and five predator environments (no predator, one or two water bugs, and one or two crayfish) and examined ten traits including behavior, morphology, and life history. Each predator induced a unique suite of behavioral and morphological responses. Snails increased near-surface habitat use with crayfish but not with water bugs. Further, crayfish induced narrow and high shells whereas water bugs induced wide shells and wide apertures. In terms of life history, both predators induced delayed reproduction and greater mass at reproduction. However, crayfish induced a greater delay in reproduction that resulted in reduced fecundity whereas water bugs did not induce differences in fecundity. Resource levels impacted the morphology of *H. trivolvis*; snails reared with greater resource levels produced higher shells, narrower shells, and wider apertures. Resource levels also impacted snail life history; lower resources caused longer times to reproduction and reduced fecundity. Based on an analysis of phenotypic correlations, the morphological responses to each predator most likely represent phenotypic trade-offs. Snails could either produce invasion-resistant shells for defense against water bugs or crush-resistant shells for defense against crayfish, but not both. Our use of a comprehensive approach to examine the responses of *H. trivolvis* has

provided important information regarding the complexity of phenotypic responses to different environments, the patterns of phenotypic integration across environments, and the potential costs and benefits associated with plastic traits.

Keywords Phenotypic plasticity · Trade-offs · Multiple traits · Multiple environments · Gastropod

Introduction

Nearly every organism is phenotypically plastic for some trait (Travis 1994) and many environmentally-induced phenotypic changes are adaptive strategies that permit organisms to improve their fitness (Pigliucci 2001). Such phenotypic plasticity has received a great deal of attention from ecologists and evolutionary biologists because it allows organisms to possess a wide range of ecological options (Clausen et al. 1948; Bradshaw 1965; Cook and Johnson 1968; Schlichting 1986; Sultan 1987; West-Eberhard 1989; Schlichting and Pigliucci 1998). While numerous types of plasticity exist, one of the most studied is predator-induced plasticity (Karban and Baldwin 1997; Tollrian and Harvell 1999).

Empirical investigations of predator-induced plasticity have documented an extensive list of prey responses to a diverse array of predators (Dill 1987; Sih 1987; Kusch 1993; Warkentin 1995; Kats and Dill 1998; Tollrian and Harvell 1999; Pettersson et al. 2000; Van Buskirk 2002). Behavioral responses to predators are particularly well documented and include reduced activity, increased use of refuges, and spatial avoidance (Snyder 1967; Schmitt 1982; Dodson 1988; Holomuzki and Hoyle 1990; Abrahams and Healey 1993; Kusch 1993; Turner et al. 1999; Sih 2004). Prey can also form morphological defenses such as body shape changes (Brönmark and Miner 1992; Kuhlmann et al. 1999; Van Buskirk and Schmidt 2000) and the growth of defensive spines (Krueger and Dodson 1981; Harvell 1986; Havel

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and Dodson 1987) that reduce predation rates. In addition to behavior and morphology, some prey respond to predators by altering life-history strategies. Prey that can achieve a size refuge from predators frequently delay reproduction in favor of more rapid growth (Crowl and Covich 1990) whereas prey that become more vulnerable with increased size typically reproduce earlier or at a smaller size (Riessen 1999; Barry 2000; Johnson 2001). In short, we have an impressive body of work that has examined how different prey species alter their traits in response to predators.

While past studies have shown that prey can alter a variety of traits in response to different predators, several authors have argued that to understand the complexity of adaptive phenotypic plasticity we must take a more comprehensive approach that includes more species, more environments (> 2), a larger number of traits, and several ontogenetic stages (Schlichting and Pigliucci 1998; Van Buskirk 2002; DeWitt and Langerhans 2003; Pigliucci 2003; Ghilambor et al. 2003; West-Eberhard 2003; Relyea 2004). A major tool in applying this approach has been phenotypic integration (Olson and Miller 1958; Schlichting 1989; Wagner and Schwenk 2000; West-Eberhard 2003; Pigliucci and Preston 2004). While definitions of phenotypic integration vary, Pigliucci (2003) broadly defined it as the pattern of functional, developmental, and/or genetic correlation (however measured) among different traits. As the definition implies, phenotypic integration can be viewed from a variety of perspectives (e.g., development, genetics) and can provide information concerning the functional relationships between traits, changes in phenotypic strategies over ontogeny, constraints on phenotypic responses, and the cost and benefits of alternative phenotypes. In predator-prey systems, phenotypic integration has provided important contributions to understanding the complexity of prey phenotypic responses to their predators (Kuhlmann et al. 1999; Tollrian and Dodson 1999; DeWitt and Langerhans 2003; Relyea 2004). The challenge is to undertake a comprehensive approach that examines a large number of traits and environments to obtain a more complete understanding of phenotypic integration.

Freshwater snails are highly conducive to the execution of a comprehensive approach to predator-induced plasticity. Snails exhibit predator-induced behavior (Snyder 1967; Alexander and Covich 1991b; Turner et al. 1999; DeWitt et al. 1999; McCarthy and Fisher 2000), morphology (Appleton and Palmer 1988; Trussell 1996; DeWitt 1998; DeWitt and Langerhans 2003), and life history (Crowl and Covich 1990; DeWitt 1998; Chase 1999). Additionally, snails have been utilized to address the functional relationship between traits (DeWitt et al. 1999), the effects of multiple predators (DeWitt and Langerhans 2003), and trade-offs among growth and reproduction (Chase 1999).

In this study, we reared the freshwater snail *Helisoma trivolvis* (hereafter referred to as *H. trivolvis*) under dif-

ferent food rations and predator environments (water bugs, *Belostoma flumineum*; and crayfish, *Orconectes rusticus*) to understand how prey alter their suites of defensive traits (behavioral, morphological, and life history) in a variety of predator and resource environments. Water bugs and crayfish were chosen because they use contrasting habitats and feeding strategies that may favor alternative phenotypes in the system. Crayfish are restricted to pond bottoms and consume *H. trivolvis* by shell chipping and crushing (J.T. Hoverman and R.A. Relyea, unpublished data). Therefore, crayfish should induce *H. trivolvis* to move higher in the water column and produce shells that are crush-resistant. In contrast, water bugs feed throughout the water column and consume snails via shell-invasion (Kesler and Munns 1989). Thus, water bugs should have no impact on *H. trivolvis* behavior (water bugs can search the entire water column) but induce the formation of invasion-resistant shells (i.e., shells that prevent water bugs from reaching the interior snail body). These hypothesized morphological responses to each predator likely represent trade-offs; snails cannot simultaneously produce shells that are both crush-resistant and invasion-resistant. In contrast to behavior and morphology, we expect the two predators to induce similar life history responses. Because predation rates decline as snail size increases (Alexander and Covich 1991a; Chase 1999), we expect *H. trivolvis* to delay reproduction and reach a larger size at reproduction at the cost of reduced fecundity (Tsitrone et al. 2003).

We tested the following hypotheses: (1) water bugs will not induce habitat shifts but crayfish will induce *H. trivolvis* to move to the surface; (2) water bugs and crayfish will induce opposite morphological defenses; (3) water bugs and crayfish will induce similar life-history responses; (4) snails will produce more extreme phenotypes with increased predator densities; and (5) decreased food rations will cause weaker antipredator responses, longer times to reproduction, smaller sizes at reproduction, and lower egg production.

Methods

Adult *H. trivolvis* were collected on 1 September 2002 from Geneva Pond no. 1, a semipermanent pond that contains water bugs but no crayfish or fish (located in northwestern Pennsylvania). In the laboratory, the adults were placed into 10-l plastic tubs filled with 7-l of carbon-filtered, UV-irradiated tap water to allow oviposition. Egg masses were laid over a span of 2 weeks and hatching began on 21 September 2002. Hatchlings were fed ground *Spirulina* fish food (OSI Marine Inc., CA, USA) ad lib. until the start of the experiment. Hatchlings were raised for 4 weeks until they were large enough to be transferred into the experimental containers.

The experiment began on 22 October 2002 using a randomized block design with a factorial combination of three resource levels and five predator treatments. The three resource levels were rations of *Spirulina* at 2.5, 5,

and 10% of mean snail mass per day. From previous experiments with *H. trivolvis*, a 10% food ration was found to be sufficient for normal growth and development (J.T. Hoverman and R.A. Relyea, unpublished data). Food rations were doubled when the snails doubled in biomass (averaged across groups). The five predator treatments were the following: no predator, one caged water bug, two caged water bugs, one caged crayfish, or two caged crayfish. The experimental blocks were four sets of shelves that differed in height and therefore, temperature. Thus, our 15 treatment combinations were replicated four times (one replicate per block) for a total of 60 experimental units. The experimental units were 10-l plastic tubs filled with 7-l of carbon-filtered, UV-irradiated tap water. Ten snails were added to each tub (mean mass \pm 1SE = 11 ± 2 mg). Twenty snails were set aside to assess 24-h survival after handling; survival was 100%. Snails were fed 3 times/week and the water was changed once per week to prevent fouling. The animal rearing room was held at 21°C and a 14:10 h day:night cycle.

Each tub was equipped with two predator cages constructed of a 180-ml plastic cup covered with a screen. Cages remained empty in tubs assigned the no-predator treatment. In tubs assigned predator treatments, either one or both cages held an individual predator (either a water bug or a crayfish). Water bugs were collected from several ponds near Geneva Marsh whereas crayfish were collected from Linesville Creek. *H. trivolvis* commonly coexist with these two predators in lakes, marshes, and ponds in western Pennsylvania (J.T. Hoverman, personal observation) Each predator was fed approximately 120 mg of snails 3 times/week. Empty cages were briefly lifted out of the water and then returned to the tubs to equalize disturbance among all tubs. Dead snails were removed from predator cages.

Late in the experiment (18 January 2003), several crayfish died and replacement crayfish were not available (due to the frozen conditions of their native habitat). Thus, we changed our method of producing predatory cues in the water. We removed all predators from the tubs and placed them in several separate tubs of water to serve as sources of predatory cues (one "cue tub" for each treatment). The cue tubs contained 4-l of water and either one or two predators were housed in cages and fed 120 mg of snail biomass 3 times/week. Each day, we transferred water from these cue tubs to the appropriate experimental tubs. For treatments assigned one predator, we added 60 ml of cue water from tubs with one predator; for treatments assigned two predators, we added 60 ml of cue water from tubs with two predators. For no-predator tanks, we added 60 ml of aged tap water. This later cue-tub protocol was approximately 10% of the cue concentration of the original caged predator design. However, reducing the strength of the predator cue late in the experiment would simply bias us against detecting a predator effect.

To quantify snail behavior, we made visual observations using scan sampling (Altmann 1974) on 18 January

2003. We recorded the percentage of snails that were within 3 cm of the water's surface, a commonly used measure of habitat choice in snails (Turner 1996; DeWitt 1998). We made ten observations on each tub and used the mean proportion from each tub as our response variable. In two tubs, the predators were dead on the day of observation. Thus, we excluded these tubs from our analysis.

To quantify snail life-history traits, we examined the time to reproduction, mass at reproduction, and the total number of eggs produced per snail. We defined time to reproduction as the number of days until the first egg mass appeared in a tub. We defined mass at reproduction for a tub as the average mass of the snails when the first egg mass appeared in a tub. The first egg masses were laid on 27 December 2002. By late February, most snail treatments contained eggs (except under the lowest food treatment). During this time (typically 3 times/week), we counted the number of eggs in each egg mass and the number of adult snails alive in the tub. After the masses were counted, we removed the masses from the tubs. We standardized the egg counts by dividing the values by the number of adult snails alive in each tub. We then used the standardized counts to calculate our response variables (the total number of eggs per snail). For all response variables, we used tub means.

The experiment was terminated after 4 months (21 February 2003). All snails were preserved in 10% formalin. Preserved snails were subsequently blotted dry, weighed for final mass, and measured using digital imaging software (Optimas Co., Bothell, WA, USA). With the snails resting on their umbilical side, we measured shell width and aperture width (Fig. 1). With the snails resting with their aperture up, we measured shell height, aperture height and shell thickness. Shell thickness was measured at the leading edge of the aperture.

Statistical analyses

In the analysis of morphological plasticity, we were interested in how shape changes independent of changes

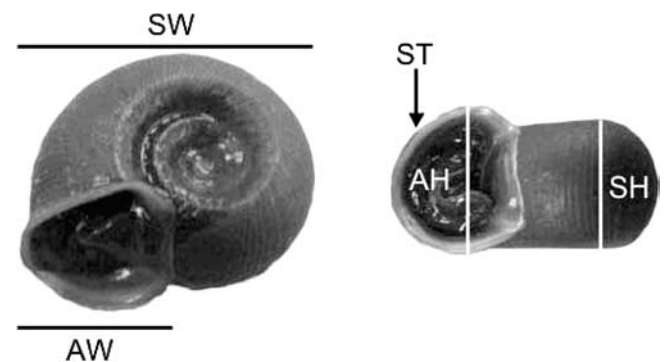


Fig. 1 Morphological dimensions measured on *Helisoma trivolvis*. *SW* shell width, *SH* shell height, *ST* shell thickness, *AW* aperture width, and *AH* aperture height

in overall size. We used analysis of covariance (ANCOVA) with mass as our covariate to correct for size (Darlington and Smulders 2001; Garcia-Berthou 2001). All traits were log transformed prior to analysis to improve the linearity of the relationship. A critical assumption in the ANCOVA procedure is that the treatments share a common slope of their regression lines. This was satisfied for all the traits except shell thickness. Upon closer examination, we found no relationship between shell thickness and mass. Therefore, we used the raw measurement of thickness in our analysis. For the remaining variables, we used the mass-adjusted group mean and residuals from the within-group regression to calculate each individual's size-adjusted value. For each morphological trait, we then calculated the mean response for each experimental unit and used this as our morphological response variable.

The data were divided into two analyses. In the first analysis, we began by conducting a principal components analysis (PCA) on the single behavioral trait (near-surface habitat use), the five morphological traits, and final mass (see Table 1). The first two principal components had eigenvalues greater than 1 and, thus, they were extracted for the analysis. For each tub, we calculated the mean PC-1 and PC-2 scores and subjected these tub scores to univariate analysis of variance (ANOVA) to examine the effects of block, treatments, and their interactions. We conducted separate ANOVAs for PC-1 and PC-2 because these variables are uncorrelated by definition. Because two tubs were missing values for near-surface habitat use (due to dead predators on the day of observation), they were excluded from the analysis. In the ANOVAs, the main effect of block (i.e., shelf height) and block interactions were not significant and not retained in the model; thus, their degrees of freedom and sums-of-squares were pooled with the error term. Mean comparisons were conducted using the Fisher LSD test.

In the second analysis, we examined the effects of the treatments on snail life history (i.e., time to reproduction, mass at reproduction, egg production) using only the 5% and 10% food rations because snails fed the 2.5% ration never reached reproduction in most tubs. We subjected the tub means to a PCA and only PC-1

had an eigenvalue greater than 1. Using the PC-1 scores for each tub, we used ANOVA to examine the effects of block, treatments, and their interactions. Block effects and their interactions were never significant; therefore, their degrees of freedom and sums-of-squares were pooled with the error term.

Although PCA can reveal overall patterns in multivariate data, some traits may not follow the general pattern of a particular principle component. In both analyses, most traits were well represented in the patterns depicted by the principle component scores (as indicated by communality values >0.6 ; McGarigal et al. 2000). However, both analyses presented some problems when interpreting the results. For five of the ten traits used in the study, the pattern of treatment means on the principal components did not adequately describe the treatment effect for the variables. Therefore, we conducted additional univariate ANOVAs on these traits. Our goal with this approach was to provide the reader with the most accurate picture of how all traits were affected by the treatments.

Trait correlations

We used correlation analysis to examine the degree of trait integration associated with *Helisoma's* responses to our treatments and to provide insights into possible phenotypic trade-offs across environments (Via and Lande 1985, 1987; Schlichting 1989). We constructed a Pearson correlation matrix of the ten traits across the 15 treatments. Because some tubs lacked reproductive data or behavioral data, the number of experimental units per trait ranged from 48 to 60. A Bonferroni correction was made for conducting the 45 possible correlations.

Results

Our first analysis started by conducting a PCA on snail behavior, morphology, and final mass. The first two principal components accounted for 68% of the variance in the data. PC-1 had an eigenvalue of 2.77 and accounted for 40% of the variance. Positive loadings on PC-1 were related to narrow and high shells, more use of surface habitats, and large final mass (Table 1). PC-2 had an eigenvalue of 1.98 and accounted for 28% of the variance. Positive loadings on PC-2 were related to high apertures, wide apertures, and thick shells (Table 1). We also examined final communality (how well the original variables were represented by the retained principal components; McGarigal et al. 2000). Most variables exhibited good agreement (communalities >0.6). However, near-surface habitat use, shell thickness, and final mass had relatively low values (0.48–0.59), suggesting that the retained principal components did not exhibit excellent agreement with these variables.

Using the scores for PC-1, we conducted a ANOVA to determine the effects of treatments and their interac-

Table 1 Principal component structure for the first two principal components from a PCA on the behavior, morphology, and final mass of *Helisoma trivolvis*

Variable	PC-1	PC-2	Final communality
Near-surface habitat use	0.772	0.025	0.597
Shell width	-0.676	0.551	0.760
Shell height	0.864	0.184	0.780
Shell thickness	0.450	0.572	0.529
Aperture height	0.332	0.813	0.770
Aperture width	-0.423	0.810	0.835
Final mass	0.693	0.015	0.481

Final communalities are shown for each variable

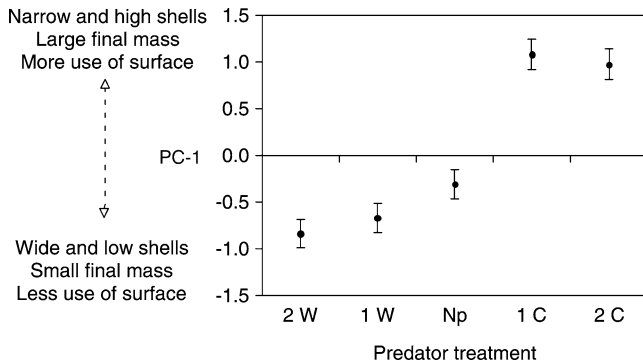


Fig. 2 The effects of caged predators on principal component scores generated from a PCA on behavior, morphology, and final mass of *Helisoma trivolvis*. Treatments are abbreviated as follows: 2 W 2 water bugs, 1 W 1 water bug, Np no predator, 1 C 1 crayfish, 2 C 2 crayfish. PC-1 accounted for 39.6% of the variation in the data set. Data are least-squares means \pm 1SE

tions. There was a significant effect of predators ($F_{4,43} = 32.8$, $P < 0.0001$) and food ($F_{2,43} = 9.4$, $P > 0.0001$) but no predator-by-food interaction ($F_{8,43} = 0.5$, $P = 0.489$). Based on mean comparisons, snails reared at the 2.5% food ration had marginally lower scores (i.e., wider and lower shells, less use of surface habitats, and smaller final mass) compared to snails reared at 5% ($P = 0.065$). Both the 2.5% and 5% food rations had smaller scores compared to snails reared at 10% ($P \leq 0.016$). Among the predator treatments, snails reared with crayfish had higher scores (i.e., narrower and higher shells, more use of surface habitats, and larger final mass) than snails reared without predators ($P \leq 0.0001$; Fig. 2). Snails reared with water bugs had similar scores (one water bug, $P = 0.107$) or lower scores (two water bugs, $P = 0.021$) than snails reared without predators. Snails reared with crayfish had higher scores compared to snails reared with water bugs ($P < 0.0001$). Within each predator species, there were no differences between snails reared with one or two predators ($P \geq 0.453$).

Using the scores for PC-2, we conducted a second ANOVA to determine the effects, treatments and their interactions. There were no significant effects of predators ($F_{4,43} = 2.2$, $P = 0.084$), food ($F_{2,43} = 3.0$, $P = 0.063$), or the predator-by-food interaction ($F_{8,43} = 0.5$, $P = 0.864$).

For most traits, the PCA and ANOVA analyses adequately described the shifts in snail traits. However, for three traits (near-surface habitat use, shell height, and aperture width), a more complete understanding of the responses to water bugs and crayfish was obtained by also examining the univariate ANOVAs. When we examined shell height and near-surface habitat use more closely, we confirmed that crayfish induced increases in both traits compared to the no-predator treatments ($P \leq 0.0001$), but we found that water bugs did not ($P \geq 0.358$). In addition, we found no food effect for habitat use ($P = 0.397$). Despite the lack of significant effects for PC-2, we detected significant univariate effects

of predator and food treatments on aperture width ($P \leq 0.0001$ and $P = 0.033$, respectively). Snails reared with water bugs developed wider apertures than snails reared with no predators or crayfish ($P \leq 0.005$), but there was no difference between the no-predator and crayfish treatments ($P \geq 0.5$). Snails reared at the 10% food ration produced wider apertures than snails reared at 2.5% and 5% ($P \leq 0.05$) but there was not a difference between snails reared at 2.5% and 5% ($P = 0.569$).

In the second analysis, we examined snail life history responses (time to reproduction, mass at reproduction, and egg production) using only the 5% and 10% food rations. From the PCA, only the first principal component was extracted (eigenvalue = 2.02) and it accounted for 68% of the variance in the data. Positive loadings on this component were related to long time to reproduction, large size at reproduction, and less egg production (PC loadings = 0.933, 0.673, and -0.837 , respectively; communalities = 0.871, 0.453, and 0.700, respectively).

The ANOVA on this life history principle component (PC-1) found significant effects of predators ($F_{4,27} = 8.9$, $P < 0.001$) and food ration ($F_{1,27} = 28.0$, $P < 0.001$) but no predator-by-food interaction ($F_{4,27} = 2.0$, $P = 0.122$). Snails reared at higher food rations reproduced earlier, at a smaller size, and produced more eggs (i.e., lower scores; Fig. 3). Based on mean comparisons, snails reared with crayfish and water bugs reproduced later, at a larger size, and produced fewer eggs (i.e., higher scores) than snails reared without predators ($P \geq 0.036$). Snails reared with one water bug had lower scores than snails reared with one or two crayfish ($P \leq 0.050$). Snails reared with two water bugs were not different from snails reared with two crayfish ($P = 0.153$) but had lower scores than snails reared with one crayfish ($P = 0.013$). Within each predator species, there were no differences between snails reared with one or two predators ($P > 0.26$).

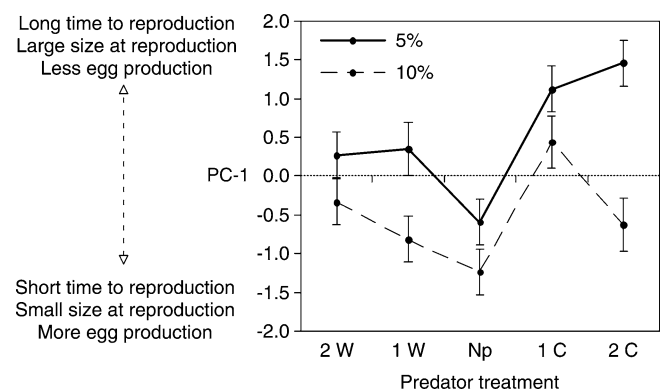


Fig. 3 The effects of caged predators and food ration (Spirulina at 5% (●) or 10% (◻) of snail's mass/day) on the first principal component generated from a PCA on *H. trivolvis* life history (time to reproduction, size at reproduction, and egg production). Treatments are abbreviated as follows 2 W 2 water bugs, 1 W 1 water bug, Np no predator, 1 C 1 crayfish, 2 C 2 crayfish. PC-1 accounted for 67.5% of the variation in the data set. Data are least-squares means \pm 1SE

In this analysis, mass at reproduction had a low communality value (0.45). Once again, we felt that a more complete understanding of the responses to water bugs and crayfish was obtained by also examining the univariate ANOVA for this trait. Predator treatments had a significant univariate effect on mass at reproduction ($P \leq 0.0001$) while food ration ($P = 0.459$) and the predator-by-food interaction did not ($P = 0.111$). In agreement with the PCA, snails reared with water bugs and crayfish were larger at reproduction than snails reared without predators ($P \leq 0.002$). In slight contrast to the PCA, snails reared with water bugs were not different from snails reared with crayfish size at reproduction ($P \geq 0.166$). A more accurate understanding of egg production was also possible with an univariate ANOVA. Consistent with the PCA, snails reared with crayfish produced fewer eggs relative to snails reared without predators. However, we found no differences between snails reared with water bugs compared to snails reared without predators egg production ($P \geq 0.768$). This suggests that the rate of egg deposition in snails reared with water bugs was greater than those reared without predators because there was less time to deposit the eggs (due to the delay in reproduction).

Trait correlations

Our analysis of phenotypic correlations was conducted across all 15 treatments of the experiment (Fig. 4). *H. trivolvis* displayed 15 significant correlations out of 45 possible correlations (Bonferroni-corrected $P \leq 0.00512$) suggesting a high level of integration among morphology, behavior, and life history. Across environments,

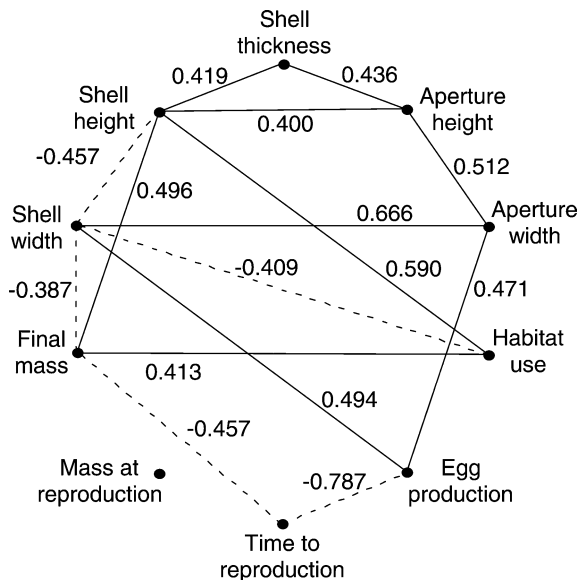


Fig. 4 Trait correlations across predator treatments and food rations. All morphological responses are size-independent except shell thickness. Solid lines indicate positive trait correlations, whereas dashed lines indicate negative trait correlations. Only correlations with Bonferroni corrected $P \leq 0.00512$ are shown

wide shells were associated with wide apertures, low shells, small final mass, less use of surface-habitat, and greater egg production. High shells across environments were associated with large final mass, high apertures, thick shells, and more use of the surface. Five of the fifteen significant correlations were negative suggesting possible phenotypic trade-offs in the system. For example, high shells were associated with narrow shells, large final mass was associated with delayed reproduction, and delayed reproduction was associated with low egg production.

Discussion

Our study explored the ability of a prey species to use multiple traits and trait types (i.e., behavior, morphology, and life history) in response to a range of predators and resource levels. The results demonstrated that *H. trivolvis* changed life history and morphology in response to resources and changed behavior, morphology, and life history in response to predators. Moreover, the particular suite of defenses was dependent on predator identity.

Recent studies have shown that prey are capable of simultaneously altering suites of traits in the presence of predators and these responses can be predator-specific (Tollrian and Dodson 1999; Relyea 2001a; DeWitt and Langerhans 2003; Ghalambor et al. 2003). In our study, we examined prey responses to two predators that induce unique suites of morphological and behavioral traits. For example, water bugs induced no change in habitat use whereas crayfish induced greater use of surface habitats. Further, water bugs induced wide shells whereas crayfish induced narrow and high shells. Interestingly, the predators induced slightly different life-history changes; compared to snails living without predators, crayfish induced delayed reproduction, larger size at reproduction, and fewer eggs whereas water bugs induced delayed reproduction and larger size at reproduction but a similar number of eggs. Thus, *H. trivolvis* has the ability to alter large suites of traits that are predator-specific.

Behavioral responses to predators have been well-documented in many prey taxa (Sih 1987; Lima and Dill 1990; Tollrian and Harvell 1999). In snails, the most common antipredator behavior is spatial avoidance (Snyder 1967; Alexander and Covich 1991a; Turner 1996; DeWitt et al. 1999; McCarthy and Fisher 2000; Rundle and Brönmark 2001). For instance, predators that feed in the water column (i.e., fish, insects, and turtles) typically induce snails to seek benthic refuges whereas predators that feed in the benthos (i.e., crayfish, lobsters, crabs, and starfish) typically induce snails to move toward the surface. Consistent with previous studies, we found that crayfish induced *H. trivolvis* to move toward the surface. The extensive work of Snyder (1967) demonstrated that although some snail species respond to water bugs by burrowing into substrates, *H. trivolvis* does not exhibit this response. This is consistent with our observations.

However, it is possible that other antipredator behaviors may occur within more complex habitats (e.g., rock crevices, macrophytes, and substrates).

Over the last two decades, numerous studies have documented predator-induced morphological defenses across a variety of aquatic taxa (Schmitt 1982; Gilbert and Stemberger 1984; Havel 1987; Appleton and Palmer 1988; Brönmark and Miner 1992; Trussell 1996; Van Buskirk et al. 1997; DeWitt 1998; DeWitt et al. 2000; Relyea and Werner 2000). In freshwater snails, our knowledge of predator-induced morphological plasticity has come solely from snails with a spiral morphology (DeWitt 1998; Krist 2002) that is produced by secreting whorls around a central body axis resulting in a spire (see Fig 10.2 in Brown 1991). Importantly, our study examined planorbid snails that have a different coiling pattern; they secrete shell material in a spiral with the whorls lying in a single plane (Fig. 1). Additionally, physids and planorbids differ in the shape of the aperture (i.e., the “generating curve” for the shell; oval vs. round, respectively; Raup 1962). Given these differences in shell morphology, we might expect the function of predator-induced morphological responses in physids and planorbids to be quite different. We found that crayfish induced *H. trivolvis* to develop relatively narrow and high shells but no changes in aperture shape. These responses may reflect the mode of attack by crayfish. Snyder (1967) found that for crayfish consuming a variety of snail species, “the mode of attack is ‘patient’ chipping away at the shell with the mandibles until the soft parts are reached” (p. 93). For our species of crayfish (*O. rusticus*), we have found that predation on *H. trivolvis* is entirely via shell chipping and crushing and never via shell entry (J. T. Hoverman and R. A. Relyea, unpublished data). Thus, a likely explanation for the observed responses is that *H. trivolvis* is attempting to increase the roundness of the entire shell, which would increase overall shell strength (Rundle and Brönmark 2001; DeWitt et al. 2000). In contrast, crayfish typically attack physids via shell entry and induce physids to produce more elongate shells and apertures that restrict shell entry (DeWitt et al. 2000; DeWitt and Langerhans 2003). Interestingly, physids and planorbids have similar responses to crayfish in that they have greater expansion parallel to the coiling axis versus perpendicular to the axis. However, the function of those responses may be extremely different; greater parallel expansion in physids produces an elongate invasion-resistant shell whereas in planorbids it produces a round crush-resistant shell. Clearly, additional work is necessary to address the functional morphology of *H. trivolvis* responses to crayfish.

In past studies of freshwater snails, fish and crayfish have received the majority of the empirical attention as predators since they are dominant in permanent waters. However, water bugs can be a significant source of snail mortality, especially in habitats lacking fish (Kesler and Munns 1989). Water bugs feed on snails by grasping the shell in their forelegs, plunging their stylet down into the

aperture, and piercing the soft tissue of the snail. This shell-invading tactic is fundamentally different from the shell crushing/chipping tactics displayed by crayfish; thus, we expected the morphological defenses induced by water bugs to be fundamentally different from those induced by crayfish. *H. trivolvis* behaviorally responds to water bug predation by retracting the body into the shell away from the stylet. To enhance this defensive strategy, *H. trivolvis* should increase the distance that the water bug must reach inside the shell before contacting the body. In our study, water bugs induced relatively wide shells and apertures, which should increase this retraction distance. Preliminary work on predation rates by water bugs has shown that *H. trivolvis* reared with water bugs for 2 weeks and then exposed to lethal water bugs suffered 37% predation whereas snails reared without predators suffered 63% predation (J.T. Hoverman and R.A. Relyea, unpublished data). Therefore, the changes in shell shape induced by water bugs appear to be adaptive defenses against water bugs. Because water bugs and crayfish generally induce opposite morphological defenses, the two predators may help maintain selection for plastic morphology in *H. trivolvis*.

Based on life-history theory, size-selective predation on small individuals should favor rapid growth and delayed reproduction whereas predation on large individuals should favor slow growth and early reproduction (Stearns and Koella 1986; Roff 1992; Stearns 1992; Abrams and Rowe 1996). Empirical support for these predictions has come from a variety of taxa (fish, Reznick and Endler 1982; *Daphnia*, Spitze 1992; amphipods, Wellborn 1994; tadpoles, Warkentin 2000). In freshwater snails, crayfish and water bugs selectively consume small snail size classes (Alexander and Covich 1991b; Chase 1999). As a consequence, snails typically delay reproduction and allocate resources to growth in the presence of these predators (Crowl and Covich 1990; Chase 1999; DeWitt 1998). In our study, crayfish and water bugs induced longer times to reproduction and greater mass at reproduction. Interestingly, snails reared with water bugs had a greater rate of egg deposition than snails reared without predators (i.e., less time to produce the same number of eggs). In contrast, crayfish, which induced longer delays in reproduction than water bugs, laid fewer eggs. Reduced egg production may have simply occurred because we stopped the experiment before the completion of the reproductive period, thereby restricting the length of time possible for egg deposition. Over longer time periods, snails in the crayfish treatments might eventually equalize their fecundity as seen with the water bug treatments. Alternatively, snails in the crayfish treatments may have laid fewer eggs because they were allocating additional resources to egg size to permit offspring to more quickly reach a size refuge (Roff 1992; Stearns 1992; Oksanen and Lundberg 1995), form morphological defenses, or as a consequence of behavioral responses (DeWitt 1998). Predator induction of a longer time to reproduction and greater mass at reproduction has been documented in

other snail studies (Crowl 1990; Crowl and Covich 1990; DeWitt 1998; Chase 1999), but data on egg production have not been presented (both Crowl and Covich (1990) and DeWitt (1998) collected egg data but did not formally present the data). Our egg data not only suggest that crayfish-induced snails experience lower fecundity, but that these shifts in prey life-history traits (i.e., egg production) may have important long-term effects on snail population sizes.

Effects of predator density and resource levels

The magnitude of predation risk can be an important factor in the induction of prey phenotypes. Many prey species respond to the presence of increased predator density by producing more extreme phenotypes (Loose and Dawidowicz 1994; Kusch 1995; Relyea 2004b). In freshwater snails, several studies using large experimental venues (wading pools and 38-l aquaria) have shown that the magnitude of snail defenses increases with predation risk (Turner 1997; McCarthy and Fisher 2000). In our study, increased predator density had little impact on *H. trivolvis* phenotypes. However, given the small size of our experimental units (10-l plastic tubs), it is likely that the water was saturated with chemical cues. Additional research with *H. trivolvis* must be conducted before definite conclusions can be drawn.

There is a growing appreciation that the antipredator responses of prey can depend upon resource levels or competition (Werner and Anholt 1996; Relyea 2002; Weetman and Atkinson 2002; Relyea and Hoverman 2003; Relyea 2004b). We examined predator-induced responses of *H. trivolvis* at three different food rations (2.5, 5, and 10% of snail body mass). We found that greater resource levels resulted in larger snails that have relatively high and narrow shells and wide apertures. Consistent with previous studies that have either experimentally increased resources (Eisenberg 1970; Chase 1999) or observed snails living in mesotrophic versus eutrophic habitats (Eversole 1978; Brown 1985), we found that higher food rations also increased fecundity, decreased the time to reproduction, but did not affect the mass at reproduction. Contrary to our expectations and the work of Chase (1999), we detected no interaction between resource level and predator treatment on *Helisoma's* behavior, morphology, or life history. The discrepancies between Chase (1999) and our study could be due to a variety of protocol differences including different experimental venues (laboratory vs. outdoor mesocosms), types of resource manipulation (food additions vs. nutrient additions), and measures of size (mass vs. shell size).

What have we learned by taking a comprehensive approach to predator-induced plasticity?

Several researchers have called for a more comprehensive approach to examining phenotypic plasticity

because it allows a more detailed examination of prey responses (Schlichting and Pigliucci 1998; Pigliucci 2003, DeWitt and Langerhans 2003; Ghalambor et al. 2003; West-Eberhard 2003; Relyea 2004). Prey typically experience different species of predators that have different feeding strategies and can favor different prey defenses. In addressing how prey respond to different predators, the primary focus has been on behavioral defenses (Sih 1987; Relyea 2003). Such an approach may overlook the importance of other trait changes that can be deployed in place of, or in addition to, behavior (Relyea 2001a, b). By conducting a more comprehensive study to characterize how prey alter a large number of traits, we were able to document the formation of predator-specific suites of responses. The next step in plasticity research will be to determine the relative importance of each of these responses in reducing predation rates and the functional relationships among different traits (e.g., trait compensation or complementation; DeWitt et al. 1999).

A more comprehensive approach can help us evaluate the costs and benefits of predator-induced responses. Embedded in the theory of plasticity evolution is the assumption that no single phenotype is optimal in all environments (Dudley and Schmitt 1996). Therefore, there should be costs associated with antipredator responses. In both plants and animals, the cost of induced defenses is typically reduced growth or fecundity in predator-free environments (Karban and Baldwin 1997; Kats and Dill 1998; Tollrian and Harvell 1999; Relyea 2002). In snails, morphological defenses reduce predation rates at the cost of slower growth (Appleton and Palmer 1988). We found that induced defenses against crayfish in *H. trivolvis* came at the cost of reduced fecundity and potentially a lower intrinsic rate of population increase (r). Thus, we were able to identify potential costs associated with crayfish-induced responses by including multiple life-history traits.

By examining the integration of the traits with correlation analyses, we can also assess the basis of phenotypic trade-offs across environments in our system. For instance, there were a large number of significant correlations among the morphological traits suggesting that *H. trivolvis* could produce shells that are either wide or high, but not wide and high. Thus, the morphological defenses induced by one predator (e.g., water bugs) may result in greater susceptibility to the other predator (e.g., crayfish). While this hypothesis clearly needs to be tested in our system, research on other snail species have confirmed this prediction. For example, crayfish and fish generally induce opposite behaviors (near-surface habitat use vs. refuge use) and morphology (elongate apertures vs. round aperture) in physid snails (DeWitt 1998; Turner et al. 1999; DeWitt et al. 2000; Turner et al. 2000) and snails that respond to one predator can become more susceptible to the other predator (DeWitt et al. 2000; DeWitt and Langerhans 2003). Possible constraints on shell shape have been discussed previously by Raup (1966) and Gould (1980) who demonstrated that

extant snail species exist only in a small portion of the possible morphological space (but see Schlichting and Pigliucci 1998 for a critique). In sum, future work that addresses the underlying causes of phenotypic correlations (e.g., genetic correlations) may provide us with important information to address phenotypic trade-offs and evolutionary responses to predator environments.

Conclusion

Phenotypic plasticity is an expanding field of ecological and evolutionary research and a recent emphasis on more comprehensive studies has inspired researchers to explore suites of trait changes when an organism is exposed to different environments. In our comprehensive approach to understanding *H. trivolvis* plasticity, we found that *H. trivolvis* can alter a wide range of traits and that the suite of responses is environment-specific. Such a comprehensive approach provides important information regarding the complexity of phenotypic responses to different environments, the patterns of phenotypic integration across environments, the potential costs and benefits associated with the phenotypic responses, and potential effects of predators on long-term population dynamics. In short, a more comprehensive approach can provide a more complete understanding of prey responses to predators.

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