

REPORT

Having the guts to compete: how intestinal plasticity explains costs of inducible defences

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Abstract

Predators commonly induce phenotypic changes that make prey better at surviving predation at the cost of reduced growth. While we have a good understanding of how trait changes affect predation risk, we lack a mechanistic understanding of why predator-induced phenotypes differ in growth. Using two mesocosm experiments, we combined phenotypic plasticity theory with predictions from optimal digestion theory to demonstrate that intra- and interspecific competition induced relatively long guts while predators induced relatively short guts. The longer guts induced by competition appear to be an adaptive response that allows more efficient digestion and more rapid growth whereas the shorter guts induced by predators appear to result from a tradeoff of building larger tails in predator environments at the cost of smaller bodies. By combining these two bodies of theory, we now have a much better understanding of the mechanisms that cause the phenotypic trade-offs that select for inducible defences.

Keywords

alimentary tract, inducible defence, phenotypic plasticity, *Rana sylvatica*, trade-off.

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INTRODUCTION

Understanding how environmental heterogeneity impacts the phenotypes of organisms is one of the leading challenges for ecologists and evolutionary biologists. A tremendous amount of work has shown that environmental variation can induce dramatic changes in the traits of organisms and many of these phenotypically plastic changes appear to be adaptive (Schlichting & Pigliucci 1998; Pigliucci 2001). At the same time that numerous empirical examples of phenotypic plasticity have appeared, there has been a simultaneous increase in theoretical models for the evolution of phenotypic plasticity. This theory has demonstrated that for adaptive plasticity to evolve there must be phenotypic trade-offs (such that no single phenotype is optimal in all environments) and there must be reliable environmental cues that inform an organism of the current state of its environment (Via & Lande 1985; Moran 1992).

During the past several decades, there has been a great deal of empirical interest in predator-induced plasticity. Most of this research has focused on the adaptive value of predator-induced plasticity. In general, researchers have found that predator-induced prey experience a reduced susceptibility to predation (Karban & Baldwin 1997; Tollrian & Harvell 1999). Moreover, the benefits of most

predator-induced defences (i.e. how particular defences cause reduced predation rates) have been understood from a mechanistic perspective. Typically, the predator-induced traits make prey less susceptible to predation because the prey become harder to detect, capture, or consume.

As expected from the adaptive plasticity hypothesis (Dudley & Schmitt 1996), predator-induced traits also have associated costs in predator-free environments. In the vast majority of cases, this cost appears as a reduction in growth and development (Tollrian & Harvell 1999). For strictly behavioural defences (e.g. a reduction in foraging activity), the mechanism underlying the cost is likely a simple reduction in energy intake. However, we lack a mechanistic explanation of why a reduction in growth is such a common cost of morphological defences across a wide variety of predator-induced taxa. A possible explanation for this common growth cost lies in the field of optimal digestion theory. Optimal digestion theory predicts that animals consuming low food quantity or quality should have longer digestive systems (Sibly 1981). Longer digestive systems allow for longer transit times and improved digestive efficiency while larger diameter guts increase food processing per unit body weight (Savory & Gentle 1976; Sibly 1981; Yang & Joern 1994). There is ample support of these theoretical predictions when one compares across species of fish (Kapoor *et al.*

1975; Hoffer 1988; Benavides *et al.* 1994), rodents (Korn 1992) and birds (Jackson 1992; Starck 1996). Gut length can also exhibit phenotypic plasticity. Several species of birds, fish, insects, mammals and reptiles can change the length of their gut in response to changes in food quality and quantity (Starck 1996; Piersma & Lindström 1997; Siems & Sikes 1998). If we combine the predictions from optimal digestion theory with theory on phenotypic plasticity, we arrive at the hypothesis that the reason many predator-induced prey suffer a growth cost may be that induced defences cause a change in intestinal morphology making the prey less efficient at foraging, therefore slowing growth.

Larval amphibians represent an excellent study system for testing this hypothesis. Amphibians are well known for their flexible life history (Wilbur & Collins 1973; Alford & Harris 1988; Warkentin 1995), behaviour (Laurila 2000; Relyea 2001) and morphology (Relyea 2002c, 2004; Van Buskirk 2002) in response to different predator and resource environments. Morphological plasticity has received a great deal of attention as biologists have discovered that a diversity of larval anuran species develop relatively large tails and small bodies with increased predation risk, but small tails and large bodies with increased competition (Smith & Van Buskirk 1995; McCollum & Leimberger 1997; Relyea 2002a). These morphological changes appear to be adaptive such that tadpoles with larger tails are better at surviving predator environments (Van Buskirk *et al.* 1997; Van Buskirk & Relyea 1998). However, when predators are absent, large-tailed tadpoles experience slower growth than small-tailed tadpoles (Relyea 2002a,b).

It has been hypothesized (Relyea 2002a) that the inferior growth abilities of the smaller-bodied, predator-induced tadpoles might arise from differences in the relative size of the alimentary tract (foregut, midgut and hindgut; hereafter termed 'gut'). Because a tadpole's body is largely composed of the gut, changes in relative body size might translate into changes in relative gut length and, therefore, translate into differences in nutrient assimilation and growth ability. Thus, it seems plausible that the difference in growth ability associated with changes in external morphological traits in predator and competitor environments might be mediated via changes in gut length. To test this idea, we exposed wood frog tadpoles (*Rana sylvatica*) to different predator and competitor environments and quantified the relative gut length of the tadpoles. We tested the following hypotheses: (1) tadpoles exposed to competitor environments will develop relatively long guts, (2) because intraspecific competition in wood frogs is typically more intense than interspecific competition, wood frog tadpoles exposed to intraspecific competitors will develop relatively longer guts than tadpoles exposed to interspecific competitors and (3) tadpoles exposed to predator environments will develop relatively short guts.

METHODS

Experiment 1: intra- vs. interspecific competition

In the first experiment, we examined how four populations of larval wood frogs altered their relative gut length in response to increasing levels of intra- and interspecific competition. This experiment was conducted at the University of Michigan's Edwin S. George Reserve (ESGR) with the original goal of understanding competition-induced changes in external morphology (for additional experimental details, Relyea 2002a). We collected wood frogs as newly-deposited eggs (≥ 10 egg masses per population) from natural wetlands on the ESGR, allowed the eggs to hatch in wading pools containing aged well water, and fed the hatchlings rabbit chow *ad libitum* until used in the experiment. The experiment used a randomized block design with a factorial combination of four populations, three competitor densities, and two competitor species (intraspecific and interspecific). Thus, there were 24 treatment combinations that were replicated twice for a total of 48 experimental units. The experimental units were 100-L mesocosms (i.e. wading pools) containing aged well water, 100 g oak leaves (*Quercus* spp.), 5 g of rabbit chow, and an aliquot of zooplankton and phytoplankton from a nearby pond. All pools were covered with 60% shade cloth to prevent other animals from colonizing.

The experiment was initiated on 8 May 1997. We began with a density of 20 wood frog tadpoles from one of four populations (Buffer Zone Marsh, Cattail Marsh, Southwest Woods Pond and Dreadful Hollow Pond). Multiple populations were used because previous work had shown that there can be population-specific responses to environmental conditions (Relyea 2002c). To this base density, we added 0, 20, or 40 additional wood frog tadpoles (from the appropriate population) or 0, 20, or 40 western chorus frog tadpoles (*Pseudacris triseriata*). The two control treatments (20 wood frog tadpoles +0 intraspecific competitors and 20 wood frog tadpoles +0 interspecific competitors) were identical treatments but were independently replicated. Wood frogs and chorus frogs were all early in their development (wood frogs = 10–16 mg, depending on population source; chorus frogs = 19 mg). The two species naturally coexist (Collins & Wilbur 1979) and the densities of tadpoles in the experiment (wood frogs = 25–75 m⁻²; chorus frogs = 0–50 m⁻²) were similar to the range of densities of tadpoles in natural ponds (wood frogs = up to 400 tadpoles m⁻²; chorus frogs = up to 40 tadpoles m⁻²; E.E. Werner, R.A. Relyea, D.K. Skelly, K.L. Yurewicz, unpublished data).

After 40 days, 10 wood frog tadpoles from each experimental unit were euthanized and preserved in 10% formalin. After measuring the external morphological dimensions in 1998 to assess their responses to competition,

we returned the animals to the preservative (Relyea 2002a). In 2002, we retrieved these animals again, weighed them, extracted their guts, and measured the length of the guts with digital calipers (to the nearest 0.1 mm).

Experiment 2: intraspecific competition vs. predation

In the second experiment, we tested how wood frog tadpoles responded to combinations of competitors and caged predators. This experiment was conducted at the University of Pittsburgh's Pymatuning Laboratory of Ecology (PLE) in 2001 with the original goal of understanding how tadpoles alter their behaviour and external morphology in response to different competitor and predator environments (for additional details, see Relyea 2004). As in the first experiment, wood frogs were collected as eggs (10 egg masses from a single population) and reared in wading pools until used in the experiment. Initial wood frog mass was 108 ± 8 mg (mean \pm 1 SE).

The experimental design was a randomized block design with a factorial combination of four densities of intraspecific competitors (20, 40, 80 and 160) and four densities of caged predators (0, 1, 2 and 4). The four levels of competition correspond to *c.* 10, 20, 40 and 80 m⁻², respectively, well within relevant natural densities (up to 400 tadpoles m⁻²). The predator used was a late instar Aeshnid dragonfly naiad, *Anax junius*, a natural predator of wood frogs. The 16 treatment combinations were each replicated four times (four spatial blocks) for a total of 64 experimental units. The experimental units were 1200-L cattle tank mesocosms containing 1000-L of well water (filled on 24–26 April), 300 g of leaves (primarily *Quercus* spp.), 25 g of rabbit chow, and an aliquot of pond water containing phytoplankton and zooplankton from 10 nearby ponds to simulate natural pond conditions. All tanks were covered with 60% shade cloth to prevent colonization by other organisms. All tanks in the experiment were equipped with four predator cages constructed of 10 × 10 cm well pipe covered with window screen at each end. The cages allowed the chemical cues emitted by predators to diffuse through the water while preventing the predators from killing our target animals (Petranka *et al.* 1987; Kats *et al.* 1988). Depending on treatment, each cage could house a single dragonfly nymph. Each dragonfly was fed *c.* 300 mg of wood frog tadpoles three times per week.

The experiment began on 5 May 2001 and was terminated on 31 May to 1 June 2001. Upon removing all animals from the tanks, 10 tadpoles were euthanized and preserved in 10% formalin. The external morphological traits were measured in 2001 and then returned to the preservative (Relyea 2004). In 2003, we extracted these tadpoles again, weighed them, removed their guts, and measured gut length as described above.

Statistical analyses

Differences in morphology can be due to differences in overall size (i.e. mass) as well as differences in shape. Therefore, to determine whether gut length changed with competition and predation, we first had to remove the effect of overall size (i.e. mass). We first tried to remove size effects by using the standard approach of regressing log-transformed gut lengths of all individuals against their log-transformed mass (log-transforming improves the linearity of the relationship). However, the regression through all data points was not parallel to the regressions for each treatment (an important assumption in size-independent analyses). Thus, we calculated a mean regression line (based on 16 separate regressions, one for each treatment) and this mean regression was superior to the original regression (i.e. parallel to the mass-gut regressions of each treatment). Based on this mean regression line, we calculated the residual values for each tadpole from this line and saved the mean residuals for each pool. This size-independent measure of 'relative intestine length' served as our primary response variable. This size-adjustment technique has proven successful in previous experiments (Relyea 2000, 2001; Relyea & Hoverman 2003). For each experiment, we analysed the data using an analysis of variance (ANOVA). When interactions were non-significant and not of interest to the hypotheses (e.g. block-by-treatment interactions and population-by-treatment interactions), we pooled the degrees of freedom with the error term. When treatments were significant, we conducted mean comparisons using Fisher's LSD test.

RESULTS

In the first experiment, we examined the impact of intraspecific and interspecific competition on the relative gut length of wood frog tadpoles (Fig. 1). There was a significant effect of spatial block ($F_{1,38} = 4.5$, $P = 0.040$), but the different wood frog populations had no effect on relative gut length ($F_{3,38} = 0.6$, $P = 0.622$). Increased density caused an increase in relative gut length ($F_{2,38} = 8.0$, $P = 0.001$), but the competitor species (intraspecific or interspecific) had no effect ($F_{1,38} = 0.1$, $P = 0.748$), nor did the interaction between density and competitor species ($F_{2,38} = 0.4$, $P = 0.705$). When we conducted mean comparisons, we found that a density of 20 tadpoles had shorter guts than densities of 40 and 60 tadpoles ($P \leq 0.002$). Tadpoles reared under the latter two densities did not differ in relative gut length ($P = 0.796$).

In the second experiment, we examined the combined impacts of competitors and caged predators on gut length (Fig. 2). The block effect was not significant ($F_{3,45} = 1.9$, $P = 0.137$). However, there were significant effects of

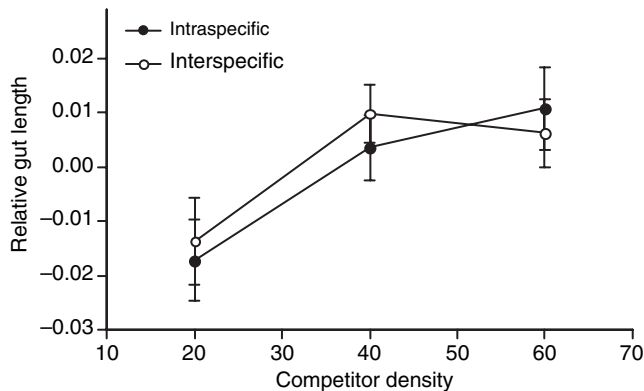


Figure 1 The change in relative gut length of wood frog tadpoles when reared under different densities of intraspecific or interspecific competitors. Gut length was made size independent by regressing log gut lengths against log tadpole mass and saving the residuals. Data are mean \pm 1 SE.

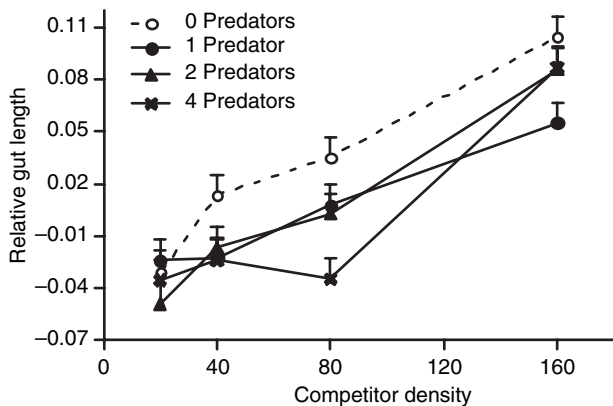


Figure 2 The change in relative gut length of wood frog tadpoles when reared under 16 combinations of competitors and caged predators. Gut length was made size independent by regressing log gut lengths against log tadpole mass and saving the residuals. Data are mean \pm 1 SE.

competitors ($F_{3,45} = 74.8$, $P < 0.001$) and predators ($F_{3,45} = 5.8$, $P = 0.002$), as well as a marginal competitor-by-predator interaction ($F_{9,45} = 2.0$, $P = 0.063$). When we conducted mean comparisons across competitor treatments, we found that tadpoles reared under the lowest competition had the shortest guts while tadpoles reared under densities of 40, 80 and 160 had longer guts ($P \leq 0.01$). Tadpoles reared at a density of 40 had marginally shorter guts than those reared at 80 ($P = 0.078$) and significantly shorter guts than those reared at 160 ($P < 0.001$). Tadpoles reared at a density of 80 had shorter guts than tadpoles reared at 160 ($P < 0.001$). When we conducted mean comparison across predator treatments, we found that tadpoles reared with no predators had relatively longer guts than tadpoles reared

with 1, 2 or 4 caged predators ($P \leq 0.005$). However, there were no differences in relative gut length among the tadpoles reared with 1, 2 or 4 predators ($P > 0.35$).

DISCUSSION

The two experiments provided substantial evidence that wood frog tadpoles are able to adjust the relative length of their gut in response to competitors and predators. In both experiments, competition induced wood frog tadpoles to develop relatively longer guts. This increase in relative gut length parallels the increase in relative body length that has been repeatedly observed in wood frogs exposed to competition (Relyea 2000, 2002a, 2004). Further, intraspecific and interspecific competition have similar impacts on relative gut length (current study) and similar impacts on relative body length (Relyea 2002a). Because guts compose a large fraction of a tadpole's body, these results suggest that changes in body size may be a reflection of changes in gut length. Interestingly, several other species of tadpoles are induced by competition to have relatively larger body dimensions including leopard frogs (*R. pipiens*) and grey tree frogs (*Hyla versicolor*; Relyea 2000, 2002d; Relyea & Hoverman 2003). This suggests that competition-induced gut plasticity may be quite common in tadpoles.

Gut plasticity has been commonly observed in other taxa but the emphasis has been on food quality and quantity rather than on competitive induction *per se*. In a variety of taxa (including several species of birds, mammals, reptiles and insects) individuals develop relatively longer guts in response to decreased food quality or quantity (Yang & Joern 1994; Starck 1996; Piersma & Lindström 1997). For example, intestine length of wild-caught starlings (*Sturnus vulgaris*) varies monthly in conjunction with changes in the proportion of consumed plant and animal material (Al-Joborae 1980). In amphibians, gut plasticity has been observed much less frequently. Tadpoles of *Rhacophorus arboreus* develop longer guts when fed lower quality plant diets compared to high quality animal diets (Horiuchi & Koshida 1989). Similarly, in larval spadefoot toads (*Scaphiopus multiplicatus*), tadpoles that switch from an omnivorous phenotype to a carnivorous phenotype develop relatively shorter guts (Pfennig 1992). As in other taxa, the shorter guts would be an appropriate response to the higher quality (i.e. high protein) diet of a carnivorous phenotype compared to a lower quality (i.e. low protein) omnivorous diet.

Based on optimal digestion theory (Sibly 1981), the competition-induced increase in wood frog gut length appears to be an adaptive response. Longer guts extend the time it takes for food to pass through the alimentary tract and increase the efficiency of nutrient extraction from food (Savory & Gentle 1976; Sibly 1981; Yang & Joern

1994). Thus, competition-induced tadpoles, which have relatively longer guts, should grow more efficiently. This prediction is supported in previous studies of wood frog tadpoles (Relyea 2002a). In that study, we initially exposed wood frog tadpoles to high or low competition environments, removed the tadpoles, and then placed them into new mesocosms containing competitors to test the growth performance of the high-competition-induced and low-competition-induced wood frog phenotypes. After 1 week, the two wood frog phenotypes did not differ in their impact on the new competitor, implying that there were no differences in the amount of periphyton that each phenotype consumed (R.A. Relyea, unpublished data). However, the high competition-induced phenotype had a faster growth rate than the low competition-induced phenotype, implying that the high competition-induced phenotype (which we now know had relatively longer guts) was more efficient in extracting energy from the periphyton (Relyea 2002a).

There are a number of possible environmental cues that could be responsible for inducing the competition-induced changes in gut length. Early laboratory experiments have hypothesized that tadpoles compete via growth inhibitors associated with yeast (*Prototheca richardsi*) that can accumulate in tadpole guts (see reviews by Beebee 1995; Griffiths 1995; Petranka 1995). However, field studies have found little evidence for this mechanism (Petranka 1995). Other potential cues include food cues, visual cues between competing individuals, and tactile cues between competing individuals (e.g. bumping into each other at high density). We have investigated competition cues in wood frog tadpoles to understand the cues that induce changes in tadpole behaviour and external morphology. We reared wood frogs either at a single density with different food rations or at a single food ration with different densities to disentangle the impact of density and per-capita food level. We found that while cues associated with density are responsible for inducing some traits (e.g. activity level), per-capita food ration is the primary cue responsible for inducing larger bodies (Relyea 2002a). Thus, it is likely that per-capita food ration is the primary cue responsible for other competition-induced morphological shifts including increases in relative gut length.

While relative gut length was increased with competitors, it was decreased with predators. The predators could not directly consume any of the target tadpoles; the gut length changes were induced via water-borne chemical cues that were emitted by the caged predators. The reduction in gut length in predator environments is parallel to the reduction in body length that typically occurs in predator environments with wood frogs (Relyea 2001, 2003a, 2004). Moreover the predator-induced reduction in body size observed in wood frogs is also observed in numerous other

species of tadpoles (Lardner 2000; Van Buskirk 2002; Relyea 2003b), suggesting that the predator-induced reduction in relative gut length may be a common phenomenon in tadpoles.

Based on optimal digestion theory, the shortening of relative gut length with predators should cause less efficient digestion and consequently slower growth (Sibly 1981). The reduction in gut length with predators appears to be an indirect impact of a phenotypic trade-off. Predators induce tadpoles to develop relatively large tails which allow improved escape from predators either via improved acceleration from predators or by improved escape ability after being attacked (McCollum & Leimberger 1997; Van Buskirk *et al.* 1997; Van Buskirk & Relyea 1998). However, because growth is constrained by energy intake, tadpoles can either build a large tail or a large body, but not both. Thus, tadpoles build large tails to escape predators, but this comes at the cost of slower growth (i.e. reduced fitness in a no-predator environment). Based on optimal digestion theory, we now know that the mechanism underlying this slower growth appears to be the induction of a shorter, less efficient digestive system. That is not to say that other phenotypic changes play no role in reducing tadpole growth (e.g. behavioural and physiological changes such as varying retention time and digestive enzyme concentration), but it does indicate that internal morphological changes appear to play a major role in the costs of the external morphological defences. Given that a wide diversity of prey taxa with inducible morphological defences suffer a common cost of slower growth (e.g. fish, salamanders, snails and *Daphnia*; Tollrian & Harvell 1999), the impact of predator environments on gut length and digestive efficiency may very well be a unifying mechanism for this ubiquitous growth cost.

Conclusions

The evolution of phenotypic plasticity relies on the existence of phenotypic tradeoffs such that no single phenotype can be optimal in all environments (Via & Lande 1985; Moran 1992). For many environmentally-induced organisms, we can frequently identify the benefits of being induced. However, identifying the costs of being induced and the mechanisms underlying these costs can be more elusive (Pigliucci 2001). Larval amphibians express dramatic plasticity in response to competitor and predator environments. While the benefits of exhibiting predator-induced morphological traits have been apparent for some time in larval amphibians (Van Buskirk *et al.* 1997; Van Buskirk & Relyea 1998), only recently have we documented the costs of being predator-induced (reduced growth). The underlying mechanisms explaining this reduced growth in tadpoles and perhaps many other predator-induced taxa can be

understood by adding optimal digestion theory to our framework of phenotypic plasticity theory. Simply stated, the induction of external morphological defences simultaneously induces other traits that cause a reduction in growth and, thus, pose a cost of induction. While our focus has been on documenting changes in external morphological traits, it is now clear that by examining internal morphological traits (e.g. gut length) we can arrive at a much better understanding of *why* inducible defences incur a growth cost. If this mechanism is generalizable to other taxa, then it suggests a unifying explanation for the widespread costs of slower growth in predator-induced prey.

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