

Predator-induced plasticity in guppy (*Poecilia reticulata*) life history traits

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Abstract A number of invertebrates show predator-induced plasticity in life-history and morphological traits that are considered adaptive. Evidence is accumulating that vertebrates may also adjust their life-history traits in response to predators; however, some of the patterns of plasticity, which appear to be an adaptive response specifically to the risk of size-selective predation, may instead result from reduced foraging in response to predator presence. Here, we describe a study of predator-induced plasticity in guppies (*Poecilia reticulata*). We have predicted that the plastic response to cues from a small, gape-limited, natural predator of guppies, the killifish (*Rivulus hartii*), would be the opposite of that caused by reduced food intake. We have found that male guppies increased their size at maturity, both length and mass, in response to the non-lethal presence of this predator. This pattern of plasticity is the opposite of that observed in response to reduced food intake, where male guppies reduce size at maturity. The increase in size at maturity that we observed would likely reduce predation on adult male guppies by this native predator because it is gape-limited and can only eat juvenile and small adult guppies. This size advantage would be important especially because male guppies grow very little after maturity.

Therefore, the pattern of plasticity that we observed is likely adaptive. In contrast, female guppies showed no significant response in size at first parturition to the experimental manipulation; however, we did find evidence suggesting that females may produce more, smaller offspring in response to cues from this predator.

Keywords Size at maturity · Age at maturity · Offspring size · Offspring number · Non-lethal effect

Introduction

Life-history traits, such as age and size at maturity, because of their close association with fitness, can rapidly evolve to new optima in response to directional selection (e.g., Reznick et al. 1997). However, there are systems in which selective pressures vary considerably through space or time; for example, where predator presence varies between seasons or microhabitats. In such environments, plasticity in life-history traits may be favored (Via and Lande 1985).

Some of the best examples of predator-induced phenotypic plasticity in life-history traits are for *Daphnia* species. *Daphnia* are eaten by a wide variety of predators including fish and *Chaoborus* (phantom midge) larvae. These two predator types exert opposing selective forces on life-history traits; fish

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predators hunt visually and prey primarily on larger, mature individuals (O'Brien et al. 1980), while *Chaoborus* is gape-limited and preys mainly on smaller, immature *Daphnia* (Pastorak 1981). *Daphnia* clones exposed to dissolved chemicals excreted by vertebrate predators (kairomones) mature earlier and at a smaller size, produce more, smaller offspring, and invest more in reproduction than individuals without kairomone exposure (e.g., Taylor and Gabriel 1993; Weber and Declerk 1997; Spaak et al. 2000; Boersma et al. 1998); these inducible shifts are considered adaptive for co-existence with the high mortality rates and selective predation on large size classes associated with vertebrate predators (e.g., Law 1979; Michod 1979). In contrast, in response to *Chaoborus* kairomones, *Daphnia* mature at a later age, larger size, and produce fewer offspring (Brett 1992; Riessen 1999); this pattern is also considered adaptive. Therefore, *Daphnia* can detect the type of predator that is present and make the appropriate life-history trait shifts. In addition, *Daphnia* were more responsive to predator kairomones than to crushed conspecifics (Pijankowska and Kowalczewski 1997). *Daphnia* are thus explicitly responding to specific predator signals and not just conspecific death or alarm signals.

There is increasing evidence for predator-induced phenotypic plasticity of life-history traits in vertebrates. Anurans have been shown to adjust the timing of hatching (e.g., Warkentin 1995; Chivers et al. 2001) and metamorphosis (e.g., Lardner 2000) to cues of predation risk such as kairomones and, as predicted by optimality models of phenotypic plasticity (Roff 1992), these responses were greatest in species exposed to highly variable predation rates (Lardner 2000). The bank vole (*Clethrionomys glareolus*) suppressed reproduction via extended estrus cycles when exposed to its weasel predator (Koskela et al. 1996). Populations of bluegill sunfish that had co-existed with largemouth bass (size-selective predators) for 30–40 years significantly delayed maturity when visually and chemically exposed to this predator; populations with a history of low predation showed no response to bass (Belk 1998). A significant delay in the age at maturity was also documented for *Brachyrhaphis rhabdophora*, a Costa Rican live-bearing fish, when visually and chemically exposed to a natural predator (Johnson 2001). It is possible that these predator-induced life-

history responses have been a direct response to the risk of predation. However, it is also possible that some of the observed patterns resulted from reduced activity and foraging in the presence of the predator/predator cue (Johnson 2001). Reduced foraging can be an adaptive behavioral response, as it reduces the risk of predation (e.g., Blanckenhorn 2000; Mangel and Stamps 2001) and the changes in life-history traits could simply be the result of this reduced food intake (e.g., Skelly and Werner 1990). Indeed, Belk (1998) and Lardner (2000) did find reduced growth in their predator treatments (but see, for example, Chivers et al. (1999)).

We conducted an experiment, where the predicted (i.e., adaptive) plastic response to predation risk was opposite to that expected in response to reduced food intake. In order to do this, it was important to use a species with a well-characterized response to food limitation and, also, well-characterized population differentiation in life history traits in response to size-selective predators. The guppy (*Poecilia reticulata*), a small, freshwater, livebearing fish, and meets these criteria. Guppies living with different predator assemblages exhibit strong inter-population differences in life-history strategies. Guppies co-occurring with the small, gape-limited killifish, *Rivulus hartii*, mature later and at a larger size, and have fewer, larger, offspring than guppies co-occurring with a larger predatory cichlid, *Crenicichla alta* (e.g. Reznick 1982, 1989; Reznick and Endler 1982). The evidence suggests that these differences have evolved in response to differences in the predation regimes that is well documented (e.g., Reznick et al. 1990, 1996a, 1997). However, although these differences have a genetic basis (Reznick 1982), some of the inter-population differences are greater in field-caught than in lab-reared individuals; for example, mass of individual offspring differs among populations in wild-caught fish by 100%, but this difference is reduced to 10–20% in the laboratory (Reznick 1982). Some proportion of the life-history differences between field and laboratory likely result from plasticity in response to resource level (Reznick and Yang 1993; Reznick et al. 2001; Bashey 2006) and social environment (Rodd et al. 1997); however, it is possible that predator-induced plasticity is also contributing to the population differences. Dzikowski et al. (2004) found that female guppies exposed to a large, cichlid predator had larger brood sizes and

shorter brood intervals, both predicted to be adaptive, and neither explained by a reduced food intake (Reznick and Yang 1993).

Our study was designed to test the plastic nature of guppy life-history traits in response to the presence of a natural predator, and the small, gape-limited predator, and *Rivulus hartii*. *Rivulus* can only eat immature guppies and small size classes of mature guppies; adult female guppies are less vulnerable than adult males because the latter grow little after maturity (Seghers 1973; Reznick et al. 1996b). The presence of *Rivulus* that are large enough to eat mature male guppies is patchy in space and time (Seghers 1973; Gilliam et al. 1993), suggesting that plasticity should be selected for. If guppies can adaptively adjust their life-history traits in response to the threat of predation by *Rivulus*, we predicted that the guppies would respond with an increase in offspring size and, especially for males, with a larger size at maturity. To test this, immature guppies derived from *Rivulus* sites were raised in the presence or absence of *Rivulus hartii* in divided tanks that allowed both chemical and visual predator cues. This experiment tests the prediction that non-lethal exposure to this species of predator can induce life-history shifts in guppies that are independent of reduced growth in response to predation risk.

Material and methods

Source populations

Guppies were collected in the fall of 2001 from two localities in northern Trinidad. Both the Paria Tributary (UTM coordinates: 689584 1188585) and Quare 7 Tributary (697407 1179935) are characterized as low-predation, where adult guppy mortality rates are relatively low, and where guppies co-occur with the omnivorous, gape-limited killifish, *Rivulus hartii* (Reznick et al. 1996b; H. Rodd personal observation); however, there is no barrier between the Quare 7 site and the main Quare River (which has been a high predation site, with large predators of guppies like the pike cichlid (*Crenicichla alta*), for at least the last 26 years), so gene flow between them is possible. All fish used were the first generation offspring of wild-caught dams. The source population of *Rivulus hartii* was Ramdeen stream, also in northern Trinidad.

Experiment 1: females

Experiment 1 was run from January 2002 to April 2002. 19 1 tanks were partitioned by installing a clear Lexan divider down the center. The dividers were drilled with 50 1/16" holes thus allowing for both visual and chemical contact between the two sides of the tank. Lexan lids were placed on all tanks to prevent *Rivulus* from jumping over the dividers. Air stones increased oxygen supply and water circulation. Black cardboard was inserted between each tank to assure that guppies did not have any visual stimulus from adjacent predators or guppies, which could affect results (Nishibori and Kawata 1993). Predators were given aquatic plants and plastic tubes in which to hide. Guppies were also provided with plants to provide adequate cover for newborn offspring.

Four immature guppies were selected at random from one of the source populations and added to one side of each tank. This guppy density was considered low enough to prevent any confounding factors of high density environments (Rodd et al. 1997; Nishibori and Kawata 1993). Experimental tanks had a single *Rivulus* predator living on the opposite side of the divider, while control tanks were empty on that side. There were a total of 18 tanks, nine treatment, and nine controls.

Guppies were allowed to mature in the treatment tanks under standard conditions of temperature (25°C) and light:dark schedule (12:12), reflecting their natural habitat. Limited (debris from the bottom of the tank was vacuumed up) partial water changes were done every 4–6 weeks. The fish were fed daily to satiation with brine shrimp and flake food in order to ensure non-limiting resource levels, which can affect life histories (Reznick and Yang 1993). *Rivulus* were fed identical flake food daily and two immature guppies once a week. Feeding with guppies was particularly important to ensure strong predatory cues. Chemical cues from conspecific's skin and predator faeces have been shown to help aquatic prey species recognize potential predators and assess predation risk (Smith 1992; Mathis et al. 1996). These cues are highly diffusible through aquatic systems and guppies could have either received alarm cues from conspecifics attempting to escape predation or from predator excretions. Guppies from high predation populations show strong behavioral responses to chemical cues from cichlids, *Crenicichla*

alta, that have eaten guppies (T. Michalak et al. unpublished ms). As the smallest ‘prey’ guppies were able to swim through the holes in the divider, a solid plexiglass sheet was inserted when feeding *Rivulus*.

When one or two males in a tank matured, all but a single male and female per tank were randomly selected and removed from the tank. These pairs were allowed to mate and remained in the tanks until their first brood was collected. Two tanks (one treatment and one control) contained only male fish and these tanks were eliminated from the analyses.

Effects of the experimental treatment were assessed for females for the following traits: size at parturition and offspring mass and number. Females show no outward indication of maturity so females’ length and mass were measured at first parturition. Offspring were killed with an overdose of anaesthetic, frozen, later dried overnight at 55°C, and weighed. Sample sizes for males that did not mature soon after being placed in this experiment were small; since the results for these males were similar to those in Experiment 2, they are not presented here.

Differences due to treatment were tested using analysis of variance (ANOVA). As reproductive output is often highly correlated with maternal size, female length was tested as a covariate in the analyses of individual offspring mass and offspring number, but was removed from both analyses as it was not significant. Offspring mass and number were transformed using natural log to meet the assumptions of the test.

Experiment 2: males

A second, male-only experiment was done May–August 2002, using broods of known age derived solely from the Paria population. At 2 weeks of age, three broods of immature guppies were sexed using criteria described by Reznick (1990). Thirteen males were then individually housed in 19 l tanks divided into two sections. Dividers were made of lexan with 8-cm high, fine-mesh windows at the bottom, allowing both visual and chemical cues to cross among sections.

Males approaching maturity were visually monitored for gonopodial development every 1–3 days until they were considered mature (when the hood on the gonopodium was even with the hook (Houde 1997)). At this point they were removed from the

tank, anaesthetized, and maturation was verified using a microscope before being weighed and their standard length measured. Age of maturity was also recorded for each male.

For Experiment 2, we used untransformed values for all three variables because they met the assumptions of ANOVA. Since males from each brood were raised in each treatment, the data were analyzed as a mixed-model ANOVA using SAS PROC MIXED (version 8.02 for Windows). We have used the Keward-Rogers method of computing degrees of freedom for fixed effects tests (option: ddfm = KR) (see Bauer et al. 2006). Brood and brood-by-treatment were treated as random effects; treatment was a fixed effect.

Results

Experiment 1: females

There was not a statistically significant effect of predator exposure on any female life-history trait (Table 1). However, females in the Predator treatment tended to have more (least squares mean of ln(offspring number): 1.66 (SE = 0.29)) and smaller (LS Mean of ln(mass): -7.06 (0.08)) offspring than those in the Control treatment (number: 0.92 (0.25), mass: -6.83 (0.07)). It is possible that a few of the offspring in the Predator treatment swam through to the *Rivulus* and were eaten; this would make the observed difference between the treatments conservative. Since the sample sizes were so small in this experiment, we ran a power analyses (JMP version 3.1.5) that showed that a sample size of 16 for each offspring trait should yield a significant difference. Female sizes at the production of their first broods were as follows (least squares means and (SE)): standard length (mm): Predator: 24.13 (0.88), Control:

Table 1 Life history traits for female guppies in Experiment 1. (Predator treatment: $n = 6$; Control: $n = 8$)

Female trait	MS	MS error	F	P	R ²
Length at parturition	8.46	4.60	1.84	0.20	.13
Mass at parturition	1.64E-02	1.207E-02	1.37	0.27	.11
Ln(Offspring number)	1.92	0.49	3.88	0.07	.24
Ln(Offspring mass)	0.17	0.04	4.04	0.07	.25

22.56 (0.76); Ln(mass) (g): Predator: 0.38 (0.04), Control: 0.30 (0.04)). Since we later found that males delayed maturity in the presence of predators, females in the predator treatment may not have been inseminated until several days after they had matured.

Experiment 2: males

For all three male life-history traits measured in this study, we found a significant effect of the predator treatment. Males exposed to the predator delayed maturity ($F_{1,9.07} = 11.86$, $P < 0.001$), attained a larger length ($F_{1,11} = 8.18$, $P < 0.02$) and a larger mass at maturity ($F_{1,9.3} = 10.43$, $P < 0.01$) than the control males (Fig. 1).

Discussion

Male guppies, in response to non-lethal predator presence, increased both length and mass at maturity. This increase in size could reduce adult mortality from their native predator, *Rivulus hartii*, because it is gape-limited and are only able to eat juvenile and small adult guppies (Seghers 1973; Reznick et al. 1996b; Mattingly and Butler 1994). In fact, gut contents of wild-caught *Rivulus* show that there is a strong positive relationship between the size of *Rivulus* and the largest guppies they had consumed (Seghers 1973), meaning that a small increase in size at maturity for male guppies should reduce their vulnerability to predation. Therefore, the pattern of plasticity that we observed in this study, with an increase in size at maturity after predator exposure, is likely adaptive, especially given that male guppies grow little after maturity. However, this increase in size did come at a cost; the treatment males took 8.6 days longer to reach maturity (an increase of 14%) than the controls. However, since guppies in low predation sites can live for several months after maturity (Bryant and Reznick 2004), the increase in size and reduction in risk of mortality may outweigh the cost of delayed maturity. In addition, in populations where larger males have an advantage through female choice (females from this population actually prefer smaller males (Endler and Houde 1995)) or male-male competition (Gorlick 1976, but see Kodrick-Brown 1992; 1993), the cost of delaying

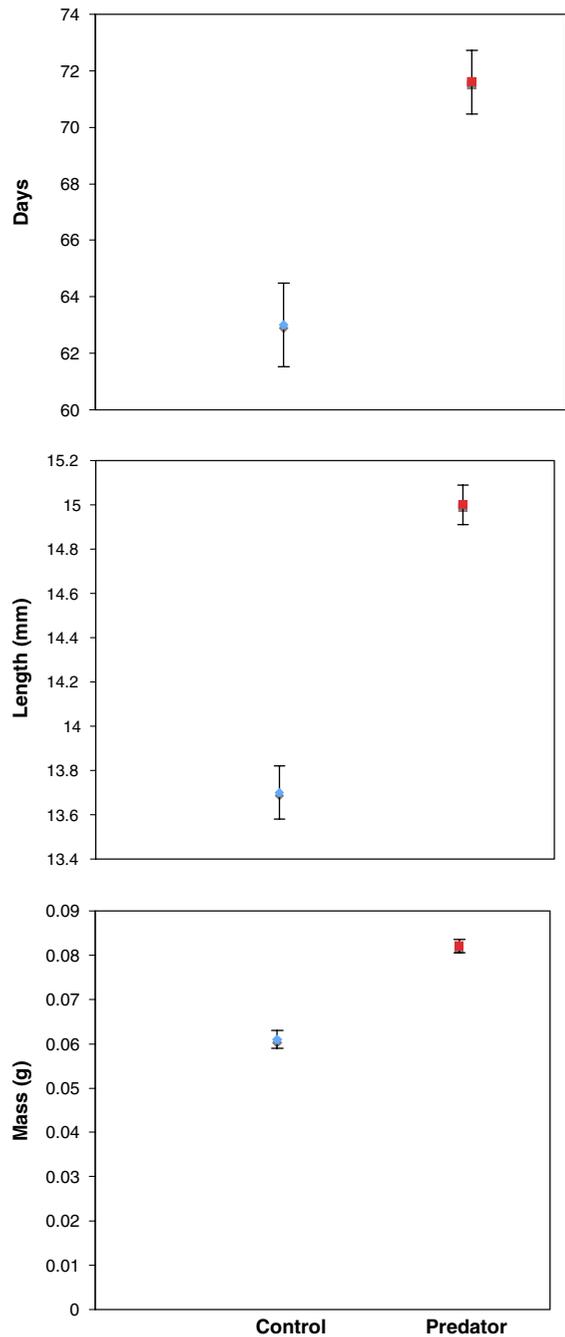


Fig. 1 Effect of predator presence on life history traits of male guppies. Upper panel: age at maturity; middle panel: standard length at maturity; bottom panel: mass at maturity

maturity would be reduced. The pattern of plasticity that we observed is the opposite of that observed in response to reduced food intake, where male guppies reduce their size at maturity (Reznick 1990).

Unlike the males in this study, female guppies showed no significant change in size at first parturition. It is possible that female guppies do not show a response in size/age at maturity to cues from small gape-limited predators like *Rivulus* because females continue to grow after they reach maturity and are much less susceptible to mortality by *Rivulus* than adult males, even when both sexes are similar in size (Reznick et al. 1996b).

Given that females guppies in *Rivulus* (i.e. low predation) sites produce fewer, larger offspring than females in high predation sites (Reznick 1982; Reznick et al. 1990), and given that *Rivulus* prey selectively on small juvenile guppies (Mattingly and Butler 1994; Bashey 2002; in preparation (a)), we predicted that the females in our predator treatment would respond to *Rivulus* cues by producing larger offspring. Yet, in this study, females exposed to predators showed the opposite pattern and tended to produce more, smaller offspring than their control counterparts. Evidence from *Daphnia* experiments also shows highly variable responses to predators with respect to the number and size of offspring; while some studies support the predictions, others showed no response or responses counter to that predicted (as reviewed in Reissen 1999). Dzikowski et al. (2004) did find that female guppies increased offspring number, in response to cues from a large predator (offspring size was not measured). It is possible that females in our study showed a trend towards increased offspring number, with a corresponding reduction in offspring size, in order to cope with increased risk of juvenile mortality. Interestingly, field patterns of juvenile survival suggest that size-selective predation by *Rivulus* may not be the distinguishing selective force for increased offspring size at these sites as juveniles have a greater increase in survival with increasing size at *Crenicichla* sites than at *Rivulus* sites (F. Bashey in preparation (b)). Instead, intraspecific competition may be selecting for large offspring at *Rivulus* sites because larger newborn size results in a growth advantage at *Rivulus* sites (F. Bashey in preparation (b)) and can affect growth and maturity in competitive environments (Bashey 2002 in preparation (a)). Furthermore, the responses to the presence of predators (this study, Dzikowski et al. (2004)) is opposite to the ones guppies show to reduced food levels; there, females produced fewer, larger offspring (Reznick and Yang 1993; Bashey 2006).

Male guppies responded to the experimental treatment, as predicted, in a fashion that is likely to reduce adult mortality by a gape-limited predator such as *Rivulus hartii*. This plasticity would enhance the genetically-based, between-population differences in the sizes of adult males co-occurring in Trinidad with *Rivulus* versus those cohabiting with larger predators (Reznick 1982, 1989; Reznick and Endler 1982; Reznick et al. 1996a).

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