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ADAPTIVE LIFE-HISTORY EVOLUTION IN THE LIVEBEARING FISH *BRACHYRHAPHIS RHABDOPHORA*: GENETIC BASIS FOR PARALLEL DIVERGENCE IN AGE AND SIZE AT MATURITY AND A TEST OF PREDATOR-INDUCED PLASTICITY

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Abstract.—I document a genetic basis for parallel evolution of life-history phenotypes in the livebearing fish *Brachyrhaphis rhabdophora* from northwestern Costa Rica. In previous work, I showed that populations of *B. rhabdophora* that co-occur with predators attain maturity at smaller sizes than populations that live in predator-free environments. I also demonstrated that this pattern of phenotypic divergence in life histories was independently repeated in at least five isolated drainages. However, life-history phenotypes measured from wild-caught fish could be attributed to environmental effects rather than to genetic differences among populations. In the present study, I reared male fish from four populations (two that co-occur with predators and two from predator-free environments) under four sets of environmental conditions. The pattern of phenotypic divergence in maturation size documented in the field between populations collected from different predation environments persisted after two generations in the laboratory. I also found a genetic basis for differences between populations in the age at which males attain maturity and in growth rates. By rearing fish in four different common environments, I tested for phenotypic plasticity in male life-history traits in response to nonlethal exposure to predators. There was a significant delay in the onset of sexual maturity in fish exposed to predators relative to those in the control, but no differences among treatments in size at maturity or growth rates. These results, coupled with previous work on *B. rhabdophora*, demonstrate a repeated pattern of parallel evolutionary divergence among genetically isolated populations that is strongly associated with predation.

Key words.—Chemical cue, common garden, convergent evolution, delayed maturity, growth rate, phenotypic plasticity, predator-induced.

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Parallel evolution of homologous traits in populations that experience similar environments can provide compelling evidence for natural selection (Jones et al. 1992; Reznick et al. 1996; Rundle et al. 2000). Demonstrating parallel evolution in natural systems requires three kinds of evidence. First, multiple populations exposed to similar selective environments should express similar phenotypes—that is, there should be a strong association between selective agents and selected traits (Endler 1986). Second, similar traits must be shown to have evolved independently among genetically distinct populations and across geographically isolated regions, as opposed to being inherited from a common ancestor (Harvey and Pagel 1991). Third, there should be evidence that phenotypic similarities among populations reflect genetic responses to similar kinds of selection pressures (Endler 1986).

The Costa Rican livebearing fish *Brachyrhaphis rhabdophora* provides a model system to test for parallel life-history evolution in response to predator-mediated mortality. I have previously shown that populations of *B. rhabdophora* that co-occurred with piscine predators attained maturity at a smaller size and produced more, smaller offspring relative to populations from predator-free environments. These differences persisted over three years and between wet and dry seasons (Johnson and Belk 2001). This pattern of phenotypic divergence is independently repeated in at least five isolated drainage basins: Populations from shared drainages with divergent life histories are genetically more similar to each other than

to populations from different drainages with similar life histories (Johnson 2001). To confirm the hypothesis of parallel evolution in *B. rhabdophora*, it is necessary to establish that phenotypic life-history divergence among populations is genetically based.

Two hypotheses could explain phenotypic divergence in *B. rhabdophora*. First, differences in life histories might be a result of genetic differentiation among populations, due to differences in predator-mediated mortality. Mortality rates in *B. rhabdophora* are higher in the presence of predators than in predator-free environments (J. B. Johnson, unpubl. data), and life-history theory predicts that such environments will favor individuals that mature early and at smaller sizes (Kozlowski and Ushmanski 1987; Abrams and Rowe 1996). In addition, there is strong genetic structuring among *B. rhabdophora* populations within rivers, within shared drainages, and across geographic regions, such that populations appear to be adequately isolated for local adaptation to occur (Johnson 2001). Alternatively, differences in life histories among populations could be due to phenotypic plasticity in response to differences between predation environments. Predator-induced plasticity in reproductive timing has been documented in a variety of invertebrates (e.g., Crowell and Covich 1990; Tollrian 1995; DeWitt 1998) and more recently, in a teleost fish (Belk 1998); in each of these cases, plasticity has been invoked as an adaptation to variable predation.

To test the genetic differentiation and plasticity hypotheses, I conducted a common-environment experiment to compare males from *B. rhabdophora* populations that co-occur with predators to those from predator-free environments. In this experiment, I evaluated the genetic basis for phenotypic

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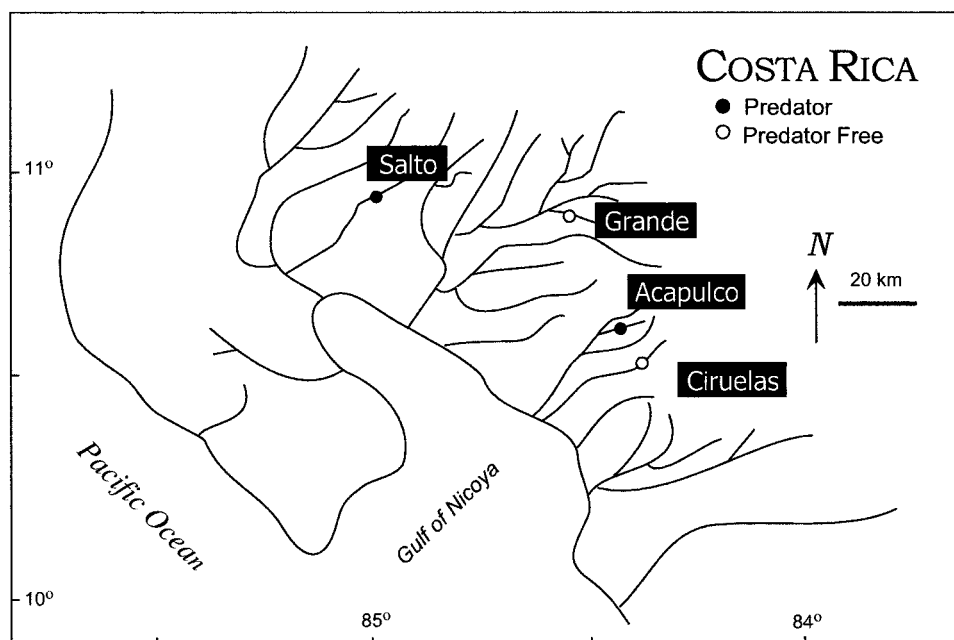


FIG. 1. Geographic locations of four populations of *Brachyrhaphis rhabdophora* evaluated in this study (open circles, predator-free sites; closed circles, predator sites). Black boxes give locality names used in the text. Specific map coordinates for each locality are available upon request.

expression of age and size at maturity under four common environments, including three treatments where fish were reared in the nonlethal presence of predators. Overall, I found that predator-associated life-history differences among populations were genetically based, although there was some indication that shifts in reproductive timing could be induced by direct exposure to a predator.

MATERIALS AND METHODS

Laboratory Stocks

In April 1998, I established four laboratory breeding stocks (each composed of 50 wild-caught fish) representing pairs of populations from environments where predators were either present or absent (Fig. 1). In predator locales, the dominant fish predator was a piscivorous cichlid, *Cichlasoma dovii* (synonymous with *Parachromis dovii*), a species that is known to prey extensively upon *B. rhabdophora* (Bussing

1998; J. B. Johnson, unpubl. data). The range of life-history phenotypes among the four source populations (Table 1) is typical of that found among populations in the wild at large; populations that occur with fish predators under natural conditions mature at smaller sizes than their counterparts from predator-free environments (Johnson and Belk 2001). Predation environment was further characterized by *B. rhabdophora* density, canopy cover, and stream width (Table 1), factors that also varied across source populations. Thus, predation environment, as defined here, reflects a composite set of potential selective agents that could independently or collectively shape prey life-history evolution. At all stages of the experiment, *B. rhabdophora* were fed ad libitum on a diet of TetraMin flakes, frozen brine shrimp, and live wingless fruit flies and were maintained at 25°C under full-spectrum VitaLites (12L:12D); laboratory conditions approximated those encountered in the field. I also collected the fish predator *C. dovii* from Costa Rica and transported these fish to

TABLE 1. Life-history phenotypes of male *Brachyrhaphis rhabdophora* and habitat variables measured for four populations from northwestern Costa Rica. Life-history phenotypes were measured from wild-caught samples taken from predator and predator-free environments. All values reported are averages from collections made over multiple years (1996–1998) during the dry season; numbers in parentheses equal one standard deviation.

Population	<i>N</i> (collections)	Std. length at maturity (mm)	Density (CPUE) ¹	Canopy (% cover)	Stream width (m)
Predator:					
Salto	2	23.5 (1.9)	2.1 (0.2)	58.2 (11.6)	8.2 (1.2)
Acapulco	2	26.1 (0.3)	6.4 (0.9)	79.4 (0.8)	4.5 (0.7)
Predator-free:					
Grande	3	27.6 (2.6)	27.9 (15.3)	34.3 (6.1)	4.0 (1.4)
Ciruelas	3	28.3 (3.6)	17.2 (10.6)	11.7 (2.3)	2.2 (0.2)

¹ CPUE, number of individuals caught per unit effort of seining. This value is positively correlated with density (fish/m³, $r = 0.56$, $n = 17$, $P = 0.02$; J. B. Johnson, unpubl. data).

the laboratory (mean SL 145.4 ± 11.1 mm SD; $N = 4$); predators were fed live *B. rhabdophora* and cichlid chips, alternating every other day.

This research was designed to reveal the genetic component of *B. rhabdophora* life-history traits using a common-environment experimental approach. Recent work suggests that maternal effects can have a strong and potentially adaptive influence on progeny life histories (reviewed in Mousseau and Fox 1998); however, I designed this study to minimize these indirect genetic effects to quantify the more fundamental measure of an individual's genetic contribution to its own life-history phenotype. To do this, I derived second-generation laboratory-reared fish from wild-caught stocks following methods outlined in Reznick and Bryga (1996). In brief, 10 wild-caught pregnant females (P) from each source population were randomly assigned to a 19-L tank and allowed to give birth. I retained 12 F_1 offspring per female and after 40 days sexed each juvenile fish based on sex-specific differences in anal fin morphology (Turner 1941). I then selected and isolated a single male and female from each brood and allowed these fish to mature under common laboratory conditions. Next, I randomly paired F_1 males with F_1 females within each population with the constraint that siblings not be mated. Second-generation (F_2) fish produced from these crosses were reared at densities of less than 12 individuals per 19 L until they were 35 days old, at which time they were sexed. To minimize size differences among F_2 male siblings included in the experiment, I selected four individuals from the middle of the size distribution of F_2 males and randomly assigned each of these fish to one of four common-environment treatments (as discussed below). My focus on male life-history traits, independent of females, is appropriate given that the reproductive ontogeny of male poeciliid fishes is predominantly under sex-linked genetic control (e.g., Kallman 1989).

Experimental Tank Design

I constructed an experimental aquarium unit (Fig. 2; patterned after Belk 1998) designed to rear full-siblings from both predator and predator-free environments in four treatments: (1) visual exposure to predator; (2) chemical olfactory exposure to predator; (3) visual plus chemical exposure; and (4) control. A single predator was centrally placed in a 76-L aquarium divided into three chambers. Opaque and transparent partitions were used to create chemical and chemical plus visual treatments, respectively. Both partitions were drilled with 12 5-mm holes (covered with mesh) that allowed water exchange between the predator chamber and the treatment chambers. The visual and control treatments were housed in separate 38-L aquaria that abutted the predator chamber of the larger aquarium; neither had chemical exposure to the predator (i.e., water flow), and the control tank was wrapped in opaque paper to prevent visual exposure. All treatment chambers were divided with opaque plexiglass into four small compartments; this eliminated both visual and physical interaction between fish from different source locations. In addition, tank exteriors were covered with opaque paper to eliminate visual interactions among fish in different treatments. The entire experimental apparatus was replicated

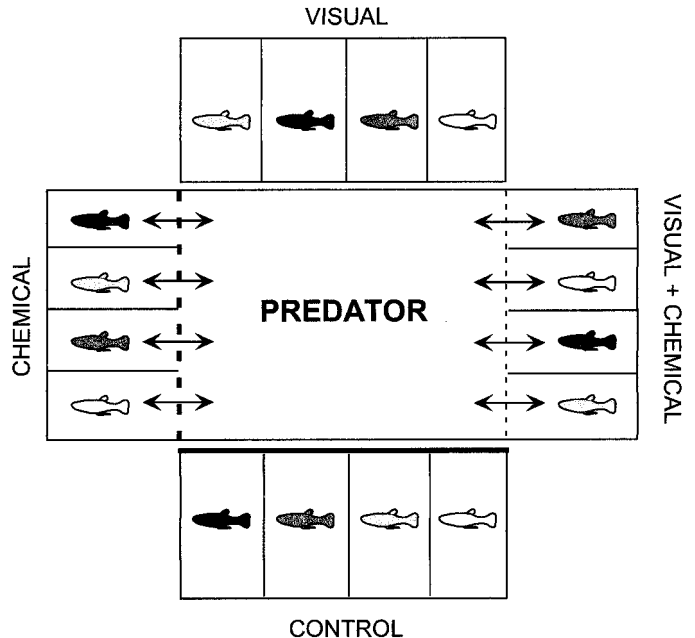


FIG. 2. Diagram of experimental aquarium set-up depicting the relative positions of the predator and the four experimental treatments. Sixteen *Brachyrhaphis rhabdophora* (four from each of four populations) and one cichlid predator (*Cichlasoma dovii*) were housed in each experimental set-up, resulting in 16 unique population-by-treatment combinations. The position of populations in treatments and the placement of treatments relative to the predator were random (with the constraint that chemical exposure to the predator had to be within the large aquarium). In the diagram, shaded-coded fish symbols demonstrate the placement of single males from four source populations into predation treatments; fish symbols do not depict scale of fish size relative to the experimental set-up. Arrows depict water flow between chambers; thick and thin dashed lines represent opaque and transparent barriers, respectively, between the predator and the treatment cells.

four times, with each unit evaluated as a block as described in the analyses below. The tank design allowed me in a single experiment to evaluate the genetic basis for predator-associated life-history differences observed in the field and to test whether nonlethal predator effects can induce ontogenetic shifts in *B. rhabdophora* life histories.

Dependent Variables

I estimated age and standard length at maturity of adult males based on the morphogenesis of the anal fin (Turner 1941). Males were scored as mature when the apical hook of the gonopodium had completely formed. Males were measured and introduced to predator treatments at approximately age 35 days. No males had initiated anal fin development prior to the beginning of the experiment. Every 10 days following introduction to the experimental treatments, fish were temporarily removed, anaesthetized in MS-222, measured, and scored for gonopodial development. As individuals neared maturity, gonopodium morphology was evaluated every 2 days. Growth rates were calculated for each individual as the difference between size at maturity and size at introduction divided by the number of days from introduction to maturity.

TABLE 2. Analyses of variance of age at maturity, size at maturity, and growth rates among male *Brachyrhaphis rhabdophora* comparing second generation laboratory fish from four populations (two naturally co-occur with predators; two are from predator-free environments) reared under four types of exposure to the natural predator *Cichlasoma dovii*: VC, visual plus chemical; C, chemical only; V, visual only; and control, no exposure to visual or chemical cues.

Source	df	Age at maturity (<i>F</i>)	Std. length at maturity (<i>F</i>)	Growth rate (<i>F</i>)
Populations	3	25.9**	16.8**	2.6†
Planned contrasts:				
Predator vs. predator-free	1	72.6**	48.4**	2.6
Within predator	1	5.5*	1.6	4.2*
Within predator-free	1	0.5	0.8	1.0
Common-environment treatments	3	1.9	1.2	1.8
Planned contrasts:				
C + V + VC vs. control	1	5.0*	2.1	2.6
C vs. V	1	0.4	0.1	0.1
C + V vs. VC	1	0.6	1.4	2.5
Block	3	12.9**	5.5**	13.4**
Error	52			

** $P < 0.01$; * $0.01 < P < 0.05$; † $0.05 < P < 0.07$.

Statistical Design and Analyses

The experiment was designed as a fully crossed factorial repeated over four experimental blocks. Four populations were crossed with four common-environment treatments resulting in 16 unique population-by-treatment combinations per block (Fig. 2). Results of the experiment for each dependent variable were evaluated as a two-way ANOVA with population and treatment as independent variables. The statistical interaction between population and treatment effects was not significant for any of the life-history traits evaluated, and was therefore not included in the final analyses. Using planned contrasts, I tested for differences between populations derived from predator environments (Salto and Acapulco) versus populations derived from predator-free environments (Grande and Ciruelas) and for differences between populations within predation categories. I also used planned contrasts to test for differences between the combined effects of treatments versus the control (chemical [C] + visual [V] + visual and chemical [VC] vs. control), between chemical versus visual treatments (C vs. V), and between chemical and

visual treatments versus chemical plus visual combined (C + V vs. CV); the latter test explored if visual and chemical effects are additive. All analyses were executing using the GLM procedure in SYSTAT 9.0 (SPSS, Chicago, IL).

RESULTS

Genetic Differences among Populations

The size and the age at which F_2 males attained sexual maturity differed among populations reared under common environmental conditions (Table 2). Planned contrasts revealed that individuals from populations derived from predator environments matured at younger ages (92 days vs. 120 days) and at smaller sizes (20.5 mm vs. 23.7 mm) than their counterparts derived from predator-free environments (Table 3). In addition, there was a significant difference in age at maturity between the two populations from the predator environment: Acapulco males matured more than 10 days earlier than Salto males (Table 3). I found a marginally significant difference ($P = 0.06$) in individual growth rates among populations (Table 2). Planned contrasts, and an evaluation of the least-square means for each population (Table 3), revealed that this difference was due to a high growth rate in Rio Acapulco relative to the other three populations.

Predator-Induced Phenotypic Plasticity

Nonlethal exposure to the predator *C. dovii* in the common-environment experiment had little effect on life-history expression in *B. rhabdophora*, with one exception. There was a significant delay of approximately eight days in the onset of sexual maturity in males exposed to the predator relative to those found in the control (Table 2). However, there was no statistical support for an overall treatment effect on age at maturity outside of this planned contrast. I also found no statistical differences in size at maturity or growth rates across common-environment treatments or for any of the planned contrasts for these traits. The trend, however, was for fish in predator-exposed treatments to mature at slightly larger sizes and to exhibit marginally higher growth rates.

TABLE 3. Least-square means of life-history traits for male *Brachyrhaphis rhabdophora* for four populations (P, predator environment; PF, predator-free environment) and four common-environment predation treatments (described in text). Values reported are least-square means (\pm SE) generated from ANOVA models presented in Table 2.

	<i>N</i>	Age at maturity (days)	Std. length at maturity (mm)	Growth rate (mm/day)
Population:				
Salto (P)	16	97.8 (4.3)	20.9 (0.6)	0.138 (0.01)
Acapulco (P)	15	87.0 (4.3)	20.1 (0.6)	0.164 (0.01)
Grande (PF)	15	118.6 (4.3)	23.4 (0.6)	0.130 (0.01)
Ciruelas (PF)	15	122.0 (4.3)	24.0 (0.6)	0.143 (0.01)
Common garden treatment:				
Control	16	100.1 (4.2)	21.5 (0.6)	0.131 (0.01)
Visual	16	105.8 (4.2)	22.5 (0.6)	0.155 (0.01)
Chemical	16	108.8 (4.2)	22.6 (0.6)	0.153 (0.01)
Visual + chemical	13	110.7 (4.4)	21.8 (0.6)	0.136 (0.01)

DISCUSSION

Predation Environment

Males derived from predator environments matured earlier and at smaller sizes than did males from predator-free environments (Table 2). These differences were evident across experimental treatments and demonstrate a genetic basis for phenotypic life-history divergence found among *B. rhabdophora* populations in the wild. Is such life-history variation among populations adaptive? Life-history theory predicts that high adult mortality rate relative to juvenile mortality rate, or higher overall mortality rates, will favor the evolution of decreased size and age at maturity (Kozłowski and Ushanski 1987; Abrams and Rowe 1996). There are no fish predators at predator-free sites, and highly piscivorous fishes at predator sites; preliminary mark-recapture experiments and tank experiments both indicate higher mortality rates for *B. rhabdophora* that live with predators relative to those that do not (J. B. Johnson, unpubl. data). Thus, given these mortality regimes, the results of this study are consistent with life-history theory and suggest adaptive evolution has occurred in *B. rhabdophora* in response to direct differences in predator-mediated mortality. However, predator-mediated mortality could also have indirect effects on life histories by reducing *B. rhabdophora* densities (Table 1) and by potentially increasing per capita resource availability. Understanding the complexity of possible interactions among such putative selective agents is an active area of poeciliid research (e.g., Trexler et al. 1992; Reznick et al. 1996). In the *B. rhabdophora* system, decomposing predation environment into its constituent (potentially confounded) parts, including an examination of direct and indirect predation effects, should provide additional insight into the underlying causes for evolutionary differences documented here.

Predator-Induced Phenotypic Plasticity

I found little evidence that nonlethal exposure to predators caused phenotypic shifts in male life-history traits. The only evidence for predator-mediated plasticity was a delay in maturation age in fish exposed to predators relative to those in an unexposed control (Table 2; planned contrast). Predator-induced delayed maturity has been described as an adaptation in a variety of organisms where prey presumably shunt resources from reproduction to growth to minimize the deleterious effects of size-selective predators (e.g., Crowl and Covich 1990; Tollrian 1995; Belk 1998; DeWitt 1998). However, in *B. rhabdophora*, delaying maturity runs counter to the fixed genetic effect of predator-mediated mortality, and thus appears to be maladaptive, because *B. rhabdophora* never grow sufficiently large to escape predation. This begs the general question as to when predator-induced delayed maturity is actually an adaptation, as opposed to being a nonadaptive byproduct of chronic exposure to a predator.

Laboratory-reared males matured at a smaller size (Table 3) than wild-caught males from the same source locations (Table 1). This phenotypic shift demonstrates that rearing environment can modify male life-history traits. However, the degree of phenotypic divergence in maturation size observed in the field between predator and predator-free sites

was still maintained in the laboratory. What could explain the uniform decrease in maturation size in my experiment relative to natural conditions? Two environmental factors that are known to induce plastic shifts in maturation size and reproductive timing in other livebearing fishes could be operating here. First, increased resource availability generally accelerates reproductive ontogeny and growth such that fish mature earlier but at larger sizes (Trexler 1989; Reznick 1990). Fish in this study were fed ad libitum, which could account for earlier age at maturity in experimental fish, but not for the observed decrease in size at maturity. Second, male-male social interactions have been shown to induce delayed maturity to larger sizes for subordinate males thereby increasing average size at maturity (Snelson 1989). I raised fish singly, thus eliminating such social interactions; this too could account for the experimental decline in maturation size.

Parallel and Convergent Evolution

Demonstrating parallel evolution in natural systems requires evidence that similar selective environments have resulted in the evolution of similar phenotypes (Endler 1986) and that such traits have evolved independently, multiple times, and in distinct geographic areas (Harvey and Pagel 1991). There was a strong association between predation environment and life-history phenotypes among populations distributed throughout northwestern Costa Rica; populations that co-occur with predators attained maturity at smaller sizes, and produced more and smaller offspring relative to populations from predator-free environments (Johnson and Belk 2001). Using allozyme and mitochondrial DNA markers, I demonstrated that populations from shared drainages that have divergent life histories are genetically more similar to each other than to populations from different drainages but with similar life histories (Johnson 2001). Thus, phenotypic divergence has occurred independently in at least five distinct drainage systems. Here, I document a genetic basis for divergent life-history phenotypes among populations. Combined, these results demonstrate parallel evolutionary divergence among genetically distinct populations of *B. rhabdophora* that is strongly associated with predation environment.

The pattern of life-history divergence documented in *B. rhabdophora* is identical to that found in the Trinidadian guppy (*Poecilia reticulata*). Guppies from populations that experience high levels of predation mature earlier and at smaller sizes than guppies from populations that experience lower levels of predation (Reznick et al. 1990). Moreover, evolutionary divergence in guppies also appears to have evolved independently, both among drainages and in response to distinct sets of predators in the northern versus southern slopes of the Northern Range of Trinidad (Reznick et al. 1996). Guppies and *B. rhabdophora* are taxonomically distinct members of the family Poeciliidae (Parenti and Rauchenberger 1989). Thus, my study demonstrates a remarkable pattern of evolutionary convergence between two phylogenetically distinct species that live with different sets of predators in different parts of the world. How could such similarities in life histories arise between *B. rhabdophora* and guppies?

Wake (1991) discussed two phenomena that could lead to

evolutionary convergence between species or evolutionary parallelisms within a species: natural selection and design constraints. These factors are not mutually exclusive. Similar forms of natural selection could be operating in both *B. rhabdophora* and guppies—selection by predation accurately predicts divergent life-history strategies in both species (Reznick et al. 1996; Johnson and Belk 2001). However, in contrast to guppies, *B. rhabdophora* populations in the upper reaches of streams live in predator-free environments, yet have still evolved delayed age and size at maturity relative to high predation environments. Moreover, genetic data indicate that colonization of predator-free environments in *B. rhabdophora* has most likely occurred from predator environments via the Gulf of Nicoya, as opposed to colonization via stream capture (Johnson 2001). This suggests that the derived life-history strategy of maturing later at a larger size has evolved repeatedly in the absence of predators. If this is true, then attention should focus on additional factors, including constraints, trade-offs, and possibly other selective agents (sensu Endler 1995), to understand how life histories evolve when populations are released from high levels of predator-mediated mortality.

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