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## Predation environment predicts divergent life-history phenotypes among populations of the livebearing fish *Brachyrhaphis rhabdophora*

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**Abstract** We document a strong association between predation environment and life-history phenotypes in the Costa Rican livebearing fish *Brachyrhaphis rhabdophora*. Populations 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 3 years and between wet and dry seasons within a year. Reproductive allotment did not differ between predation environments, but was greater in the wet season than in the dry season. We also examined the phenotypic covariance structure among life-history traits and found traits to be highly correlated. Based on life-history differences, discriminant analyses showed that populations could be neatly classified by predation category, and could be reasonably classified into wet and dry season categories. Finally, we found that the pattern of predator-associated life-history divergence in *B. rhabdophora* is remarkably similar to that of the taxonomically distinct Trinidadian guppy (*Poecilia reticulata*), possibly pointing to an evolutionary convergence between these two systems.

**Keywords** Convergent evolution · Trinidadian guppy · Life-history phenotype · Predator-mediated mortality · Wet season

### Introduction

An organism's life-history strategy is defined by ontogenetic and reproductive traits that determine individual lifetime reproductive success (Roff 1992; Stearns 1992). Such traits are typically under strong selection and are expected to produce reproductive schedules that optimize fitness in the face of age-specific mortality risk (Roff 1992). Although many factors might limit or constrain local adaptation – including gene flow, insufficient heritable genetic variation, or genetic tradeoffs – differing selective environments are often our first best predictor of divergent life-history strategies (*sensu* Endler 1986).

The relationship between age-specific mortality and reproduction is fundamental to life-history theory. Early models demonstrated that differences between populations in adult versus juvenile mortality rates, or differences in the distribution of age-specific mortality rates, could result in evolutionary divergence in age and size at maturity, reproductive effort, and number and size of offspring (Gadgil and Bossert 1970; Schaffer 1974; Law 1979; Michod 1979). More recent models have shown that predation need not be selective, but only needs to differ in intensity, to achieve the same evolutionary shifts (Kozłowski and Uchmanski 1987; Abrams and Rowe 1996). Hence, theory predicts that predator-mediated mortality should shape prey life-history evolution.

Predation in natural systems can have direct, selective effects on prey life histories, a point illustrated by evolutionary shifts in life-history traits in Trinidadian guppies (*Poecilia reticulata*; Reznick and Endler 1982; Reznick et al. 1990). However, the repeatability of predator-mediated life-history divergence across independent predator-prey systems remains uncertain. Unlike other prey taxa, guppies show a high degree of local adaptation for almost all traits examined but are resistant to speciation, resulting in an unusual accumulation of intraspecific evolutionary divergence (Magurran 1999). Hence, to conclude that phenotypic life-history divergence among prey populations is a general adaptation to predation requires independent confirmation in a phylogenetically

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distinct predator-prey system. If found, parallel life-history divergence between *Brachyrhaphis rhabdophora* and guppies in response to similar selective pressures would provide strong evidence that differential predation is responsible in both systems.

In this study, we test whether predation environment can predict phenotypic life-history divergence observed in the Costa Rican livebearing fish *B. rhabdophora*. We compare life-history traits from 15 populations of *B. rhabdophora* that co-occur with fish predators to life-history traits from 12 populations of *B. rhabdophora* that are predator-free. By evaluating populations over 3 years and in both wet and dry seasons, we test whether life-history differences persist through time and across seasons. We also examine the phenotypic covariance structure among life-history traits and employ a discriminant function analysis to see if populations can be correctly classified into predation categories based on life-history differences. Overall, we find that predation environment accurately predicts *B. rhabdophora* life histories and that the pattern of life-history divergence in *B. rhabdophora* is remarkably similar to that of the taxonomically distinct Trinidadian guppy (Reznick et al. 1990), possibly pointing to an evolutionary convergence between these two systems.

## Methods

### Study system

*B. rhabdophora* is endemic to continental northwestern Costa Rica and is widely distributed throughout a variety of freshwater stream habitats (Bussing 1987). Populations exist under a broad range of differing environmental conditions, the most notable being site-specific differences in fish community structure. In this study, we selected and compared two kinds of *B. rhabdophora* populations that differ with respect to their natural predation environment: (1)

“predator” sites are those where *B. rhabdophora* was found with the piscivorous cichlid fish *Cichlasoma dovii* and sometimes with the piscivorous catfish *Rhamdia guatemalensis*; (2) “predator-free” sites are those where *B. rhabdophora* was the only fish species present, or was found only with non-piscivorous fishes (complete fish community assemblages are available upon request). Predator and predator-free sites were often found within the same drainage with predators generally occurring in the lower reaches of streams (Fig. 1). However, there was considerable overlap in the types of environments represented by the two predation categories (J.B. Johnson, unpublished work), thus minimizing the potential for confounding environmental effects.

Marked life-history variation has been documented among *B. rhabdophora* populations (Reznick et al. 1993). Reproduction is accomplished by internal fertilization and females give birth to fully developed live young approximately every 4 weeks throughout the year. Within these constraints, populations show differences in offspring size, fecundity, reproductive allocation, size at maturity of females, and size at maturity of males (Reznick et al. 1993). This variation is widespread throughout the range of the species, a pattern well suited for testing for differences between predation environments (Endler 1986).

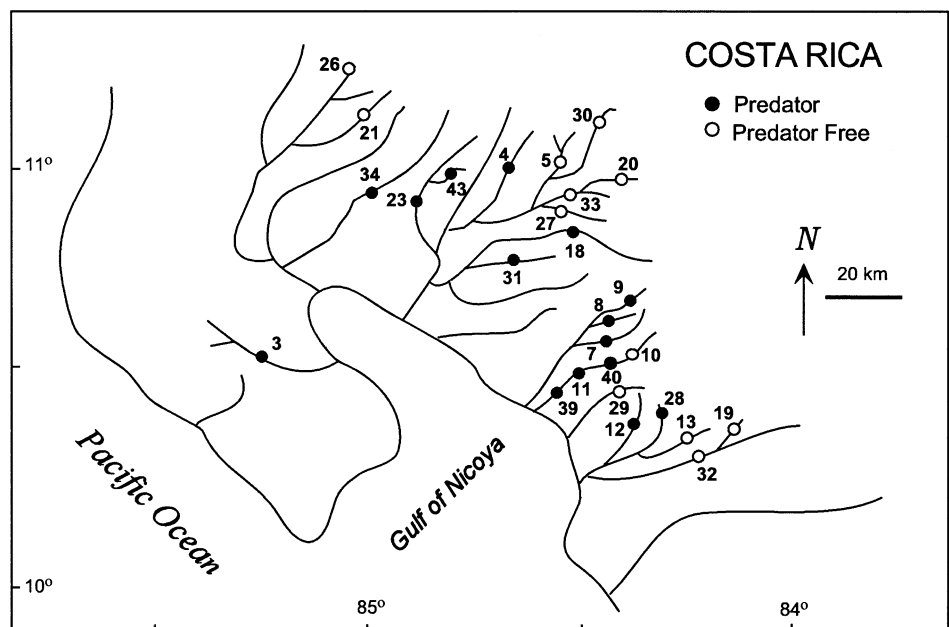
### Collections

We sampled *Brachyrhaphis rhabdophora* in three successive years (1996–1998) at the end of the dry season (April/May) and for the third year we also sampled at the end of the wet season (January 1999). In total, we collected from 27 different sites throughout northwestern Costa Rica (Fig. 1), with six or seven populations sampled during each collecting period (Table 1). Fish were collected with a hand-held seine (1.3 m×5 m; 8 mm mesh size). Approximately 200 individuals were taken from each site, a sample size that ensured adequate representation of both mature and immature males and females, but was only a small fraction of the local population. All fish were humanely killed and preserved in ethyl alcohol in the field and were transported to the laboratory for further analysis.

### Quantifying life-history traits

We measured five life-history traits for each population: (1) male size at maturity; (2) female size at maturity; (3) reproductive allot-

**Fig. 1** Geographic locations of 27 populations of *Brachyrhaphis rhabdophora* evaluated in this study. Numbers identify populations and coincide with those presented in Table 1. Specific map coordinates for each locality are available upon request



**Table 1** Descriptive statistics for life-history traits of *Brachyrhaphis rhabdophora* from 27 populations. Values for brood mass, number of offspring, and offspring size are adjusted least square

means from ANCOVA models reported in text. Population ID numbers correspond to those in Fig. 1

Predation environment	Year and season	Population ID	<i>n</i> males	Mean length of adult males (mm)	Size range of adult males (min–max)	CV for adult male length	<i>n</i> females <sup>a</sup>	Minimum size of gravid females (mm)	Brood mass (log <sub>10</sub> mg)	Number of offspring (square root count)	Offspring size (log <sub>10</sub> mg)	
Predator	1996 Dry	3	54	23.8	17.6–33.1	0.18	32/117	26	1.21	3.3	0.19	
		4	30	23.8	13.7–32.2	0.19	37/99	30	1.34	4.1	0.12	
		9	42	26.2	19.7–34.6	0.16	34/112	32	1.27	3.4	0.17	
	1997 Dry	11	32	18.9	15.2–26.2	0.14	37/69	24	1.19	3.5	0.14	
		8	48	26.3	19.5–34.5	0.14	38/54	30	1.35	3.8	0.19	
		12	30	23.7	18.9–30.4	0.13	59/89	26	0.97	2.1	0.30	
	1998 Dry	23	30	22.2	16.7–27.3	0.13	29/37	24	1.29	3.4	0.25	
		31	38	24.0	16.4–31.4	0.15	23/96	32	0.90	2.1	0.32	
		18	24	24.2	19.5–32.9	0.17	8/25	30	1.46	4.5	0.24	
	1999 Wet	28	12	20.7	17.4–25.1	0.09	16/27	22	1.28	3.6	0.17	
		34	38	24.9	18.1–35.0	0.19	64/82	24	1.27	3.4	0.21	
		7	47	25.6	20.4–34.2	0.14	28/76	30	1.39	4.3	0.15	
	1999 Wet	39	29	19.7	16.3–27.4	0.17	37/51	20	1.50	4.3	0.24	
		40	38	23.6	17.9–29.8	0.15	40/128	26	1.54	4.4	0.29	
43		39	21.9	18.0–28.4	0.12	52/76	22	1.46	3.8	0.29		
19		60	27.5	20.6–34.9	0.11	64/84	32	0.95	1.8	0.23		
Predator-free	1996 Dry	20	31	30.3	21.6–40.2	0.15	22/113	36	1.29	2.7	0.42	
		26	25	28.0	20.2–34.8	0.15	32/122	34	1.03	2.0	0.35	
		5	12	29.3	21.6–37.7	0.17	23/117	32	1.23	2.5	0.56	
	1997 Dry	32	28	25.0	19.5–35.3	0.18	45/69	28	1.07	2.9	0.26	
		33	30	25.5	20.5–33.8	0.14	29/73	36	1.22	2.6	0.34	
	1998 Dry	13	27	26.7	19.9–35.8	0.15	43/80	30	1.13	2.7	0.27	
		21	20	23.3	16.7–31.1	0.19	62/81	24	1.28	2.6	0.50	
	1999 Wet	27	24	31.7	24.6–42.1	0.16	29/58	38	1.16	2.1	0.49	
		10	18	29.5	23.7–33.8	0.10	29/72	32	1.54	3.8	0.35	
		29	16	28.6	26.4–33.2	0.07	32/62	30	1.19	2.8	0.34	
			30	40	26.3	19.4–34.3	0.17	9/37	30	1.63	4.0	0.44

<sup>a</sup>Sample sizes indicate the number of mature females observed out of the total number of females dissected

ment by females; (4) number of offspring; and (5) size of offspring. All life-history data were collected in the laboratory from the alcohol-preserved specimens using methods described in Reznick et al. (1993). In brief, because males cease to grow upon maturation (J.B. Johnson, unpublished work), we estimated size at maturity as the average standard length of adult males; mature males were distinguished by complete development of the modified anal fin (gonopodium), a structure used in sperm transfer (Turner 1941; Constanz 1989). Females were divided into 2-mm size classes. The minimum size of reproducing females, an estimate of the age at which females first reproduce, was then scored as the size class in which at least half of the individuals contained developing embryos (defined here as stage 3 or greater following Haynes 1995). Reproductive allotment was calculated as the lean dry mass of a single brood of offspring; preservation resulted in the extraction of fat prior to drying. Number of offspring equaled the total number of individuals in the developing brood. Offspring size equaled the average per capita dry weight of developing offspring. Only females with developing embryos were included in the estimates of reproductive allotment, number of offspring, and offspring size. Dry masses were measured for both embryos and adult females (digestive tract removed) after 24 h in a 55°C desiccating oven.

To generate comparable estimates among populations for reproductive allotment, number of offspring, and size of offspring, we adjusted these life-history traits by analysis of covariance (ANCOVA) using locality as a main effect and the following covariates: reproductive allotment (brood dry mass) and offspring size were adjusted for the covariates maternal dry mass and brood developmental stage; and number of offspring was adjusted only for maternal dry mass. The covariates were statistically significant in

all ANCOVA models ( $P < 0.05$ ). For each of the three reproductive life-history traits evaluated, we found a significant interaction between locality and the covariate maternal dry mass. However, we justified the inclusion of maternal dry mass in the models for three reasons (*sensu* Reznick 1989): (1) the interaction was always caused by one or two populations whose removal did not qualitatively affect the dependent variable outcome—by random chance alone we would expect one or two slopes out of 27 to differ; (2) the crossing points were typically below the biologically meaningful minimum female reproductive size; and (3) the covariates always explained a large portion of the total variance in the traits being evaluated. Our comparisons between populations for reproductive allotment, number of offspring, and size of offspring were thus based on adjusted least square means from the ANCOVA models assuming parallel slopes. All analyses were executed using the GLM procedure in SYSTAT 9.0 (SPSS, Chicago, 1999). To satisfy assumptions of the ANCOVA, all size measurements were log<sub>10</sub>-transformed and counts were square-root transformed.

#### Statistical methods

##### *Univariate analyses*

For each of the five life-history traits, we used a two-way analysis of variance (ANOVA) to test for differences between predation environments (predator versus predator-free) and to evaluate life-history variation over time (1996–1999). Using planned orthogonal contrasts, we tested for differences between wet and dry seasons within a year (dry 1998 versus wet 1999) and for differences among dry seasons between years (dry 1996 versus dry 1997).

Predation level and season were treated as fixed effects and year of collection was treated as a random effect – hence, predation and year were tested for significance against the predation×year interaction and the term predation×year was tested against the residual mean squares in the error term (Sokal and Rohlf 1995).

#### Multivariate analyses

We assessed the phenotypic correlation structure among the five life-history traits for the 27 populations by principal components analysis (PCA). Principal components (PCs) were extracted from correlation matrices because the variables were measured in non-equivalent units. We examined the position of each population in the two-dimensional PC space (PC1 versus PC2) and delineated samples by year and season of collection. We also employed linear discriminant analysis to evaluate how well populations could be distinguished by the five life-history traits using predation environment and season as grouping variables. Significance of a discriminant function was evaluated by pairwise comparison between the centroids for the classification group using the between-group *F*-matrix (SYSTAT 9.0, SPSS, Chicago, 1999).

## Results

### Quantifying life-history traits

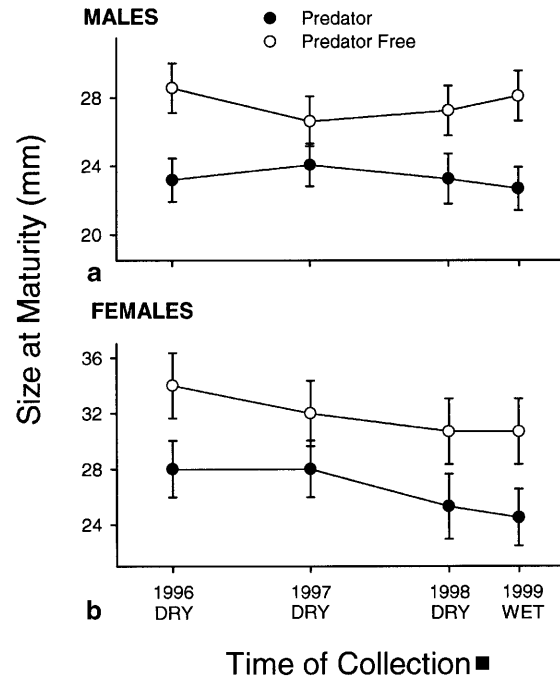
Estimates of life-history traits for each of the 27 samples are presented in Table 1. In addition to the five life-history parameters defined above, the range and coefficient of variation in adult male body size is also reported for each locality.

#### Male life history

Adult males mature across a wide range of body sizes both within and among populations. We found considerable overlap in body size distributions within populations between mature and immature males, indicating minimal post-maturation growth (a finding we have confirmed under both field and laboratory conditions). However, we found no evidence at any site for a bimodal size distribution of adult males.

#### Female life history

The onset of female maturity in each population typically occurred within a distinct 2-mm size class. Females below this size usually contained immature oocysts (stage 1 and 2; Haynes 1995), whereas most larger females contained yolking ova or developing embryos (stages 3–11). Brood mass of adult females increased with female body size (ANCOVA,  $F=32.5$ ,  $df=1,26$ ,  $P<0.01$ , mean slope=1.18) but decreased with brood developmental stage ( $F=6.05$ ,  $df=1,26$ ,  $P<0.025$ , mean slope=-0.002). Fecundity also increased with female body size ( $F=127.9$ ,  $df=1,26$ ,  $P<0.01$ , mean slope=3.84). Average embryo size was slightly larger in larger females ( $F=41.6$ ,  $df=1,26$ ,  $P<0.01$ , mean slope=0.034) and decreased considerably as embryo development progressed ( $F=16.5$ ,  $df=1,26$ ,



**Fig. 2** Estimates of size at maturity for **a** males and **b** females, comparing populations that co-occur with predators to those that do not. Plotted values are least square means ( $\pm 1$  SE) from ANOVA models reported in Table 2

$P<0.01$ , mean slope=-0.013) resulting in a mean decline of 31% in embryo mass across populations (from developmental stage 3 to stage 11).

### Effects of predation and season on life-history traits: univariate analyses

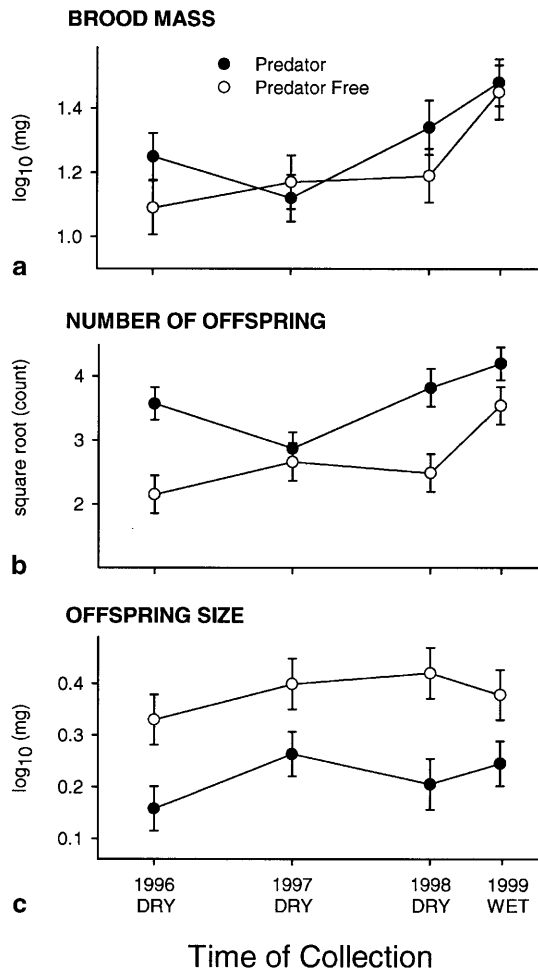
*Brachyrhaphis rhabdophora* populations that co-occurred with predators matured at smaller sizes (Fig. 2) and had more offspring and smaller offspring (Fig. 3) than did populations from predator-free environments. The association between predation and these traits persisted across years and between wet and dry seasons (Table 2). However, we found no relationship between brood mass and predation environment (Table 2).

Male size at maturity did not differ across years or between wet and dry seasons. In contrast, female size at maturity declined slightly over time (Fig. 2) resulting in a significant year effect; yet, this pattern could not be attributed strictly to differences between dry season collections or between wet and dry season collections (as evaluated by the planned contrasts). We found a marginally significant increase in brood mass during the wet season relative to the dry season (Table 2). Increased brood mass appears to be positively related to increased offspring production during the wet season among predator-free sites (Fig. 2); however, there was no significant year effect in the univariate analysis for number of offspring (Table 2).

Effects of predation and season on life-history traits: multivariate analyses

Principal components analysis revealed that the five life-history traits behaved as a highly correlated suite of traits with the first two principal components explaining 84% of the total variation. Factor loadings showed that the first component (PC1) largely described variation in size at maturity for both males and females and offspring size

while PC2 primarily described variation in brood mass and number of offspring (Table 3). Moreover, we found that PC1 clearly distinguished predator and predator-free populations while PC2 largely separated populations by season (Fig. 4). The discriminant analyses supported these findings (Table 3). Populations could be clearly discriminated by predation environment ( $F=7.93$ ,  $df=6,20$ ,  $P<0.01$ ), and to a lesser extent, could be discriminated by season ( $F=3.59$ ,  $df=5,21$ ,  $P<0.02$ ).

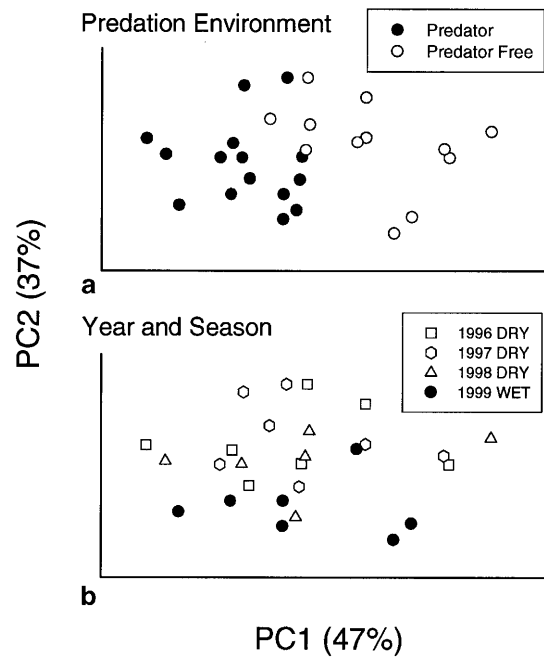


**Fig. 3** Estimates of **a** brood mass, **b** number of offspring, and **c** size of offspring, comparing populations that co-occur with predators to those that do not. *Plotted values* are least square means ( $\pm 1$  SE) from ANOVA models reported in Table 2

**Discussion**

Predation environment and season

This study reveals a clear association between predation environment and life-history phenotypes among *B. rhabdophora* populations. Populations that co-occurred



**Fig. 4a, b** Principal components (PCs) analysis of life-history traits showing the first two principal components. *Positions* of populations within the PC space are based on standardized factor scores and indicate the loadings (correlations) of populations on the PC axes. Populations are distinguished by **a** predation environment and **b** season of collection

**Table 2** Analysis of variance (ANOVA) results for five life-history traits from 27 populations evaluating the effects of predation environment and year of collection on life history. Values are *F*-ratios from two-way ANOVAs

Source	<i>df</i>	Male size at maturity	Female size at maturity	Brood mass	Number of offspring	Offspring size
<b>Main effects</b>						
Predation	1	39.6**	115.0**	1.8 <sup>ns</sup>	9.9*	64.1**
Year	3	0.2 <sup>ns</sup>	10.6*	8.4 <sup>a</sup>	3.1 <sup>ns</sup>	4.1 <sup>ns</sup>
Predation×Year	3	0.5 <sup>ns</sup>	1.6 <sup>ns</sup>	0.8 <sup>ns</sup>	2.1 <sup>ns</sup>	0.4 <sup>ns</sup>
Error	20					
<b>Planned contrasts</b>						
1996 Dry vs. 1997 Dry	1	–	2.1 <sup>ns</sup>	0.9 <sup>ns</sup>	–	–
1999 Wet vs. 1998 Dry	1	–	0.3 <sup>ns</sup>	7.7 <sup>a</sup>	–	–

\*\* $P<0.01$ , \* $0.01<P<0.05$ , <sup>a</sup> $0.05<P<0.07$ , <sup>ns</sup> not significant

**Table 3** Results of multivariate analyses for five life-history traits. Principal components analysis (PCA): component loadings are the coefficients for the standardized factor scores for each life-history trait on the first two principal components (PCs). Discriminant function analyses (DFA) with predation environment and season as class variables; results show the discriminant function (DF) (standardized canonical) coefficients and the number of populations correctly classified by each DF

Life-history trait	PCA		DFA	
	Loading PC1	Loading PC2	Predation DF1	Season DF2
Male size at maturity	0.43	-0.09	0.40	0.71
Female size at maturity	0.37	-0.01	0.09	-0.72
Brood mass	0.19	-0.60	1.70	0.83
Number of offspring	-0.02	-0.46	-1.94	0.12
Size of offspring	0.36	-0.11	0.08	0.09
Variance percent:	47%	37%	Misclassified/Total:	1/27
Cumulative:	47%	84%	Correctly classified:	96.2%
				5/27
				81.5

**Table 4** Discriminant analyses using five life-history traits<sup>a</sup> to predict predation environment among 16 populations of the Trinidadian guppy, *Poecilia reticulata*. Results show the number of guppy populations correctly classified into predation categories using *B. rhabdophora* data (this study) and the original guppy data (Reznick and Endler 1982)

	High predation <i>Crenicichla</i> site	Low predation <i>Rivulus</i> <sup>b</sup> site	Correctly classified <sup>c</sup>
Observed	7	9	—
Predicted from <i>B. rhabdophora</i> data	7	9	100%
Predicted from guppy data	7	9	100%

<sup>a</sup> To make trait values equivalent between studies, we  $\log_{10}$ -transformed embryo mass and square root transformed number of offspring in the guppy data set (Table 2 of Reznick and Endler 1982) and we recalculated reproductive allotment as a ratio in *B. rhabdophora* following methods described in Reznick and Endler (1982)

<sup>b</sup> *Rivulus* and *Aequidens* localities were combined following Strauss (1990)

<sup>c</sup> Significance assessed using a likelihood ratio test ( $-\log$  likelihood score=10.96;  $P<0.001$ ;  $df=1,14$ )

with fish predators matured at smaller sizes and had more and smaller offspring than populations from predator-free environments. These differences persisted over 3 years and between wet and dry seasons. We also found that brood mass increased during the wet season relative to the dry season, but showed no association at any time with predation environment. What do these patterns reveal about the effects of predation and season on life-history divergence within this species?

Predator-mediated mortality has long been recognized as an important selective agent of life-history evolution (Roff 1992). 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 at maturity, increased reproductive effort, more offspring, and smaller offspring (reviewed in Roff 1992). Because there are no fish predators at our predator-free sites, and highly piscivorous fishes at our predator sites, we assume higher mortality rates for *B. rhabdophora* that occur with predators relative to those that do not. Mark-recapture experiments and tank experiments are underway to test this assumption and preliminary data confirm its validity (J.B. Johnson, unpublished work). Given these mortality regimes, the results of this study are consistent with life-history theory and suggest that differential predation has primacy as a potential selective agent to explain intraspecific divergence in *B. rhabdophora* life histories. However, predation might also have indirect effects on the selective environment by altering conspecific density or by changing per capita resource

availability. In addition, abiotic factors that covary with predation environment might also influence the life history. Hence, examining the genetic basis of life-history phenotypes under common environmental conditions, and exploring the mechanisms by which predator-mediated selection could operate, will be important next steps in testing these hypotheses.

We found a significant increase in brood mass among populations in the wet season relative to the dry season, and a trend toward increased fecundity in the wet season. Increased food availability has been shown in the laboratory to elicit similar life-history shifts in other poeciliid species (Meffe 1987; Reznick and Yang 1993). Wet season flooding could increase resource availability for *B. rhabdophora* by expanding available habitat (Chapman and Kramer 1991) and by providing additional drifting insects and ants, a major component of the *B. rhabdophora* diet (J.B. Johnson, unpublished work). Unlike other life-history traits we examined, reproductive allotment appears to be highly plastic across seasons but phenotypically invariant with respect to predation environment.

#### Male life history

Reznick et al. (1993) suggested that an underlying genetic polymorphism might exist for male maturation size in *B. rhabdophora*, citing a bimodal size distribution in a single population as evidence. However, at none of our sites did we observe a deviation from unimodality, sug-

gesting that male size at maturity is not determined solely by a single locus (as occurs in some *Xiphophorus* fish species; Travis 1989). Still, polygenic control of maturation size remains plausible (Kolluru and Reznick 1996).

Mean size at maturity for males is clearly predicted by predation environment, however, the large variance around these means is not (Table 1). If predation is a selective agent that favors some optimal size at maturity (as our data suggest), we would expect to see less variation in male size within sites that have predators compared to those that do not. Instead, we find a uniformly wide range of maturation sizes within all populations (generally a two-fold difference in length) irrespective of predation environment. What factors could maintain such variation?

Sexual selection is a likely candidate. Males from both predator and predator-free environments engage in alternative male mating strategies (Mojica 1996): large males primarily court females by visual displays and small males tend to attempt forced copulations by thrusting. Hence, negative frequency dependent selection on these strategies could explain variance in male size (*sensu* Gross 1984). In dichotomous choice experiments, females spend more time with large males than with small males (J.B. Johnson, unpublished work). However, small males could counterbalance female choice with more mating opportunities and higher pre-reproductive survival by maturing earlier at a smaller size. Small males could also achieve higher fitness under some environmental conditions. Scharl et al. (1993) found that in the related livebearing fish *Limia perugiae*, small male mating success increased as the density of males increased, a result apparently caused by a tradeoff in large males between mate defense and courting effort. Luyten and Liley (1985) suggested that sneaking males could have an advantage in turbid water (such as during the wet season) when visual courting cues cannot be easily perceived. Given the evolutionary persistence of alternative mating strategies, and the strong differences among populations in selective environments, *B. rhabdophora* may be an ideal species to evaluate how natural selection and sexual selection interact to maintain variation in size at maturity.

### Phenotypic convergence with guppies

The pattern of life-history divergence documented here for *B. rhabdophora* is almost identical to that found in the Trinidadian guppy. Guppies from populations that experience high levels of predation (*Crenicichla* sites) mature at smaller sizes, have higher reproductive allotment, and produce more and smaller offspring than guppies from populations that experience lower levels of predation (*Rivulus* sites) (reviewed in Reznick et al. 1996). Only a difference in phenotypic divergence for reproductive allotment in guppies distinguishes it from *B. rhabdophora*. To illustrate the extent to which these two systems have converged, we used a discriminant analysis generated from the *B. rhabdophora* life-history data to classify guppies into predation categories (guppy data were taken from

Table 2 in Reznick and Endler 1982). The discriminant function generated from *B. rhabdophora* data predicted guppy predation regimes with complete accuracy, a result equivalent to that achieved using a discriminant function generated directly from the guppy life-history data (Table 4). Hence, we document phenotypic convergence between two phylogenetically distinct species (Parenti and Rauchenberger 1989) that occur with different predators in different parts of the world. Such evidence strongly supports the argument that similar predation environments favor similar life histories.

Comparative life-history research between *B. rhabdophora* and guppies could provide insight into questions not readily addressed in either system alone. Consider two examples. First, Farr (1989) concluded that in livebearing fishes, female choice for male courting behavior might be responsible for the evolution of sexual dimorphism. *Brachyrhaphis rhabdophora* and guppy males both court females, but only guppies show marked intersexual differences in coloration. Thus, comparing these species could clarify the role of female choice in the evolution of male size and male secondary sexual characters. Second, unlike the relatively deep phylogenetic divergence found among Trinidadian guppy populations (Fajen and Breden 1992), *B. rhabdophora* populations share very recent common ancestry (J.B. Johnson, unpublished work), yet still show comparable levels of life-history divergence to guppies. This is consistent with experimental evidence showing that life-history evolution in livebearing fishes can occur very rapidly (Stearns 1983; Reznick et al. 1997). If a genetic basis for *B. rhabdophora* life histories is found, it also suggests that life-history divergence is ultimately not limited by time, but more likely by intrinsic tradeoffs and constraints (Arnold 1992). Hence, the emergence of *B. rhabdophora* as a new model system could provide additional insight into processes that affect the mode and tempo of life-history evolution in natural systems.

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