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PHENOTYPIC PLASTICITY IN THE LIFE HISTORY TRAITS OF GUPPIES: RESPONSES TO SOCIAL ENVIRONMENT

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Abstract. Guppies (*Poecilia reticulata*) living in the streams and rivers of Trinidad show significant interpopulation variation in life history traits. Some of the greatest divergence is among guppies that co-occur with different assemblages of predators. Reznick has demonstrated that there is a genetic basis for some, but not all, of these differences. Several features of guppies' biology co-vary with the predatornities including their social and sexual behaviors and the demography of their populations. Here, we test the hypothesis that some of the observed phenotypic variation in life history traits is induced by differences in the social environment of guppies. We tested this by rearing focal individuals in the laboratory in experimental populations composed of wild-caught guppies. The experimental populations were designed to represent two types of guppy communities: (1) *Rivulus* communities, where guppies co-occur only with a small killifish, *Rivulus hartii,* that preys on small guppies, and (2) *Crenicichla* communities, where they co-occur with several larger species of predator including *Crenicichla alta,* a cichlid that prefers to prey on large guppies. We manipulated both the demography and the origin (predator community) of the guppies comprising the experimental populations. The focal guppies were offspring of guppies from one of the two predator localities. We found that guppies responded to both the demography and origin of the conspecifics with which they were reared. Therefore, phenotypic plasticity in response to social environment is probably contributing to the variation in life history traits that has been observed in the field. Our discovery that there are differences in the responsiveness of guppies from *Rivulus* and *Crenicichla* localities to our manipulations of social environment suggests that the patterns of plasticity have themselves evolved.

Key words: age at maturity; behavioral interactions; fecundity; interpopulation variation; life history traits; offspring size; phenotypic plasticity; Poecilia reticulata; *population demography; size at maturity.*

Introduction

A geographic pattern in the distribution of an organism with a variable trait often provides the first clue that the trait is an adaptation (Endler 1986). Such a pattern may have evolved directly in response to a feature of the environment, i.e., there is a genetic basis for the observed variation (e.g., Endler 1978, 1980). Alternatively, or additionally, such a pattern may represent a plastic response to the environment, such as the induction of defensive morphologies in response to the presence of predators (see Spitze and Sadler 1996). A third possibility is that the pattern is an indirect response to some aspect of the environment. For example, aquatic predators can cause reduced fecundities in insects with terrestrial adults and aquatic larvae; the presence of predators causes the immature stages to reduce feeding rates and this ultimately results in reduced fecundities of the adults (Feltmate and Williams 1991, Peckarsky et al. 1993). In this paper, we evaluate the indirect effects of predators on the life history traits of a small freshwater fish, the guppy (*Poecilia reticulata*).

Reznick and Endler (1982, Reznick 1989) have shown that there are substantial interpopulation differences in the life history traits of guppies that live with different assemblages of predators in natural populations in Trinidad. Guppies in one type of population co-occur with a small killifish, *Rivulus hartii,* that preys on small guppies (Seghers 1973, 1974, Liley and Seghers 1975, Mattingly and Butler 1994). Guppies in the other type of population co-occur with a number of predators, the most important of which is a large cichlid, *Crenicichla alta,* that prefers to prey on larger guppies (Seghers 1973, Liley and Seghers 1975, Mattingly and Butler 1994). Laboratory studies have shown that there is a genetic basis for the interpopulation differences in the life histories of guppies (Reznick 1982). However, the magnitudes of the differences are reduced when the guppies are reared in the laboratory. For example, offspring size of guppies from the two predator localities differs by 10–20% in the laboratory but by 100% in field samples (Reznick 1982). Therefore, some

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of the observed phenotypic variation among wild guppies must be environmentally induced. What characteristic of the environment is contributing to the variation in life history traits? Although guppies living with *Rivulus* tend to live in smaller, higher elevation streams than those living with *Crenicichla*, Strauss (1990) showed that 83% of the variation in life history traits was associated with the major species of predator at a site; only an additional 10% could be accounted for by geographic patterns, such as stream size. This suggests that differences in the physical environment make only a minor contribution to observed life history patterns.

We propose that variation in the social environment of guppies, including variation in their population demography (Haskins et al. 1961, Seghers 1973, Reznick and Endler 1982, Rodd and Reznick 1997) and social behavior (see Endler 1995 for a review), is contributing to the observed patterns. Total densities of guppies are higher at *Rivulus* sites than at *Crenicichla* sites (Reznick and Endler 1982). Populations at *Rivulus* sites have lower proportions of immature guppies than those at *Crenicichla* sites (Rodd and Reznick 1997). The sex ratios of adults tend to be more female biased at *Rivulus* sites than at *Crenicichla* sites (Haskins et al. 1961, Seghers 1973, Rodd and Reznick 1997). All of these aspects of population demography could influence the number and types of interactions a guppy would experience. Guppies from *Rivulus* and *Crenicichla* sites also differ behaviorally. *Crenicichla* locality guppies school more readily, are less aggressive, and engage more frequently in sexual behavior (Seghers 1973, 1974, Farr 1975, Liley and Seghers 1975, Magurran and Seghers 1990, 1991, 1994; see Endler 1995 for a review). These differences in behavior could also influence the ways in which guppies interact with conspecifics.

Previous studies have shown that conspecific interactions can have a profound influence on an individual's fitness (e.g., Itzkowitz 1990, McLain 1992, Madsen and Shine 1993). The advantages of an ability to assess current and future reproductive prospects, which often depend on conspecific interactions, and to adjust life history traits accordingly have been described (Williams 1966, Schultz and Warner 1989). Indeed, poeciliids, including guppies, are known to vary their life history traits with social conditions (e.g., Borowsky 1973, Warren 1973, Sohn 1977*a*, *b*, Dahlgren 1979, 1985). Hence, we hypothesized that some of the observed interpopulation variation in guppy life history traits is a phenotypic response induced by differences in social interactions.

To test this, we reared offspring of guppies from both *Rivulus* and *Crenicichla* localities in the laboratory in social conditions that were designed to represent those experienced in the field. We reared juvenile guppies either in a demographic environment representative of conditions in a *Rivulus* locality (high density, female-biased sex ratio, low proportion of juveniles) or in a *Crenicichla* locality (low density, even sex ratio, high proportion of juveniles) (Haskins et al. 1961, Seghers 1973, Reznick and Endler 1982, Rodd and Reznick 1997). The juvenile guppies were reared with wild-caught adults and lab-born subadults from *Rivulus* or *Crenicichla* localities. Since the behavior of guppies from different localities varies, using guppies from the two localities should manipulate the types of interactions to which the juveniles were exposed. The juveniles were reared to maturity and their life history traits measured.

If social environment is indeed responsible for inducing some of the interpopulation variation in life history traits, we should be able to reproduce some of the variation that has been observed in the field. For example, size at maturity is larger and guppy population densities are higher in *Rivulus* localities. If population density is responsible for some of the variation in size at maturity, guppies reared at high densities should be larger than those reared at lower densities.

MATERIALS AND METHODS

Methods used to conduct this experiment are fully detailed in Rodd and Sokolowski (1995) and are briefly described here. Both studies consider the response of juvenile guppies to the social environment they encounter while maturing. The previous study considered the effects of social environment on male sexual behavior. This study considers the effects of social environment on life history traits. The females in this study were siblings of the males described in both studies.

Juvenile guppies, the test individuals, were reared to sexual maturity under one of four social conditions (*Rivulus*-type demography + *Rivulus* locality conspecifics; *Rivulus*-type demography + *Crenicichla* locality conspecifics; *Crenicichla*-type demography + *Rivulus* locality conspecifics; *Crenicichla*-type demography + *Crenicichla* locality conspecifics). Test individuals were offspring of guppies from either *Rivulus* or *Crenicichla* localities. All combinations of social environment and origin of test individuals were evaluated for a total of eight treatments. Therefore, the three independent variables considered here are: the origin of the test individual's parents, labeled ''Parents''; the origin of the guppies with whom the test individuals were reared (''Residents''); and population demography, the type of demography in which the test individuals were reared (''Demography''). Parents presumably influenced the genetic background of the guppies. Given the differences in the behavior of guppies from the two predator localities, Residents presumably varied the interactions between the test individuals and the residents. Other characteristics of guppies from the two localities also differ, including male coloration (Endler 1978, 1980) and possibly pheromones (Snyder 1978 cited in Luyten and Liley 1991) (see Endler 1995 for a review), and may also have had an influence on the test individual's development. Demography assessed the effects of density, age structure, and sex ratio. Two replicates of six of the eight treatments were run at a time; 17 sets of replicates were done over 32 mo to accumulate sufficient sample sizes.

Origin of test guppies

Test individuals were born in the lab to wild-caught females from either *Crenicichla* or *Rivulus* localities in the Northern Range in Trinidad. Dams were isolated before parturition so that we could collect complete broods of known age. The young were reared with no more than twelve (usually 6–8) of their broodmates in a 35.5 × 20.2 cm aquarium until they were introduced into the treatment tanks.

Origin and demography of the residents

Populations of guppies from *Rivulus* or *Crenicichla* localities were established in large aquaria in the laboratory; these were the Residents. Adult residents were captured, as adults, in Trinidad. They were collected in September 1988, March 1989, February-March 1990, and March-April 1991 from four *Rivulus* sites and four *Crenicichla* sites. Subadult residents were lab-born offspring of guppies from either *Crenicichla* or *Rivulus* localities. Subadults were marked, to distinguish them from test individuals, by the injection of a tiny drop of acrylic paint solution into their caudal peduncle (Rodd and Reznick 1991). Residents were chosen randomly from among the collections from the appropriate predator locality.

The sex ratios, densities, and age structures of the populations of residents were designed to represent natural populations of guppies in those localities (*Crenicichla*-type demography: two adult females : two adult males : two juveniles; *Rivulus*-type demography: five adult females : two adult males : two juveniles) (Haskins et al. 1961, Seghers 1973, Rodd and Reznick 1997). The treatment tanks were large (31.6 × 76 cm filled to a depth of ≈31.5 cm) and the densities of guppies ranged from the maximum observed in the field (25/m^2) (Reznick and Endler 1982) to twice that number. However, guppies exhibit schooling behavior and that can increase the density they experience in the field (Seghers 1974, Farr 1975). The demography of the populations was maintained throughout the experiment by replacing the few individuals that died with similar-sized animals, by replacing subadult residents as they matured, and by removing newborn individuals.

Test procedures

The test individuals were introduced into the treatment tanks when they were 5–6 wk old; at this age they were large enough that they were no longer at risk of being eaten by the residents. Males had not initiated the maturation process (i.e., they showed no development of their anal fin [Reznick 1990]) when they were introduced. One week after being introduced, most individuals were 10–14 mm (standard length) (range: 9.5–15.7 mm). Introductions of test individuals from *Rivulus* and *Crenicichla* localities were paired so that a male and/or a female (depending on the size of the brood) were added to each treatment tank within a 1-wk period. We used the presence of melanophores in the region of females' brood spot to distinguish males from females. All test individuals from one locality in one introduction period were from the same brood. Subsequent introductions were made as previously added test individuals reached maturity. Most test individuals were exposed to the experimental treatments for at least 4 wk before they reached sexual maturity.

The fish were fed liver paste or brine shrimp nauplii once or twice a day. The food was dispersed so that all individuals would have access to it. High-density treatment tanks received twice the ration that low-density tanks did so that the availability of food per fish was similar.

Measurement of female life history traits

We evaluated the influence of the experimental treatments on age and size at first parturition, number of offspring per brood, size of offspring (total and lean [fat-extracted] mass), interbrood interval, reproductive allocation (percentage of dry mass allocated to their last brood), and growth rate. Females were weighed and their standard lengths measured 1 wk after they were first introduced into the treatment tank. They were then weighed and measured every other week until they were placed in an isolation tank. Females provide no external cues to their reproductive status so we assumed that they would mature at about the same time as their male sibs and give birth 25–30 d later (Reznick 1982). Therefore, females were placed in an isolation tank (4L) 7–14 d after their most rapidly developing male sib attained maturity. They were held there with two mature males, of the same origin as the residents in the treatment tank, until they produced their first brood. Males were added to the isolation tank to ensure that she had an adequate sperm supply. Floating plants were placed in the tank to provide cover for newborn young. Isolation tanks were checked twice daily for the presence of babies. Young were removed immediately, killed with an overdose of anesthetic, and preserved in formalin. Later they were dried overnight at 55°C, weighed, then placed in ether to extract their fat until there was no further change in their dry mass, then reweighed. After the females produced their first brood, they were weighed, measured, marked with an injection of latex paint and returned to their treatment tank. After 16 d (minimum length of time between broods), they were returned to the isolation tank until they had a second brood. Interbrood interval was the time duration between broods. We kept females until they produced two broods for replicates nos. 1–6 and three broods for replicates nos. 7–17. Females were euthanized in anesthetic after they produced their last litter, then frozen.

TABLE 1. Analyses of variance on female life history traits.

	Characteristics of the female when she produced her first brood				Duration of the interbrood intervals (d)	
	i) Length (mm)		ii) Age (d)		iii) First interval (covariate = Length 2†)	
Source	MS	*F*	MS	*F*	MS	*F*
Covariate†					319.47§	29.90***
Parents‡	12.02§	1.60	185.14§	4.40*	9.44	0.88
Residents	11.42	1.52	36.59	0.87	33.22	3.11‖
Demography	0.80	0.11	21.78	0.52	8.62	0.81
Parents × Residents	4.57	0.61	5.36	0.13	5.17	0.48
Parents × Demography	20.08	2.68‖	11.86	0.28	2.49	0.23
Residents × Demography	4.02	0.54	145.87	3.47‖	1.26	0.12
Parents × Residents × Demography	0.00	0.00	2.81	0.07	17.59	1.65
Error	7.49		42.08		10.68	
Error df	80		88		66	
R^2	0.080		0.110		0.374	

Notes: Influences of the three experimental factors: origin of the female's parents (Parents), origin of the residents (Residents), and demography of the population (Demography) on female traits. Degrees of freedom = 1 in each case except for the error term; the degrees of freedom for the error term are shown after the error mean square.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

† Covariate used in the ANOVA. Covariates were the length, mass, or age of the female when she produced the indicated brood. All covariates were transformed using natural logarithms.

‡ Parents = origin of the test male's parents (*Rivulus* or *Crenicichla* locality). Residents = source of the tank residents (*Rivulus* or *Crenicichla* locality). Demography = population demography.

§ MS × 1000.

‖ $0.05 < P < 0.10$.

Later, they were dried and weighed so that reproductive allotment (dry mass of embryos)/(dry mass of embryos + somatic dry mass of female) could be calculated (see Reznick and Endler 1982 for details).

Measurement of male life history traits

We evaluated the growth and development rates of the test males as well as their final ages and sizes at maturity. Males were weighed and their standard length measured the 1st wk after they were introduced into the treatment tanks, then every other week until the process of maturation was initiated, on the day they initiated the maturation process (when the number of segments on the third ray on the anal fin increased from 9 to 10 [Reznick 1990]), and then weekly until they reached maturity. If males had more than 10 segments when initiation was first observed, we back-calculated the age and size at initiation based on the subsequent relationship between age and segment number (Reznick 1990). During the final phase of maturation, individuals were checked daily to determine the age and size at maturation. Maturation was scored as in Reznick (1990). The duration of the maturation interval was the number of days between initiation and maturation.

Statistical analyses

The experiment was designed for a three-way analysis of variance (Sokal and Rohlf 1981, SAS Institute 1989). The three independent variables were parents, residents, and demography. Each independent variable was represented by two levels, either *Rivulus* or *Crenicichla* localities. Type III sums of squares were used since sample sizes were unequal among cells (SAS Institute 1989). Where necessary, data were transformed to meet the assumptions of the analyses (Sokal and Rohlf 1981, Zar 1984). For males, the following variables were transformed using natural logarithms: mass at initiation of maturation, duration of the maturation interval, growth rate during the maturation interval, and length and mass at maturity. Length at initiation was transformed by taking the square root. The reciprocal of ages at initiation and maturation were used. For females, all length and mass measurements, age at maturity, durations of interbrood intervals, growth rate during the first interbrood interval, and numbers of offspring per brood were transformed using natural logarithms. Least squares means by treatment for all traits are provided in Rodd (1994).

Several variables (length, mass, and age at the time of the production of current and previous broods) were evaluated as potential covariates for female traits following Reznick (1989). All covariates that satisfied the assumptions of ANCOVA (homogeneity of slopes and variances) and that accounted for significant variation were included in the reported analyses (Table 1).

Where none of the main effects nor interactions in a particular ANOVA were, nor approached ($0.05 < P < 0.10$), statistical significance, the ANOVA is not presented here. This was true for the following variables: female mass for the first brood, female mass and length for the second and third broods, fecundity in the first brood, offspring mass (dry mass and lean dry mass) for the first and second broods, and female growth rates during the first and second interbrood in-

TABLE 1. Continued.

Duration of the interbrood intervals (d)		Fecundity (number)				Mass of the offspring in the third brood (mg)	
iv) Second interval (covariate = Length 3)		v) Second brood (covariate = Age 1†)		vi) Third brood (covariate = Length 3†)		vii) Mean dry mass (covariate = Length 1†)	
MS	*F*	MS	*F*	MS	*F*	MS	*F*
102.42§	15.53***	1.41	5.76*	1.10	4.66*	29.95	4.48*
10.55	1.60	0.23	0.93	1.52	6.43**	26.87	4.02*
1.76	0.27	0.10	0.43	1.83	7.75**	19.33	2.89‖
29.84	4.53*	0.60	2.45	0.78	3.29‖	5.05	0.76
4.75	0.72	0.00	0.01	1.09	4.61*	15.68	2.35
2.97	0.45	0.02	0.07	0.09	0.39	1.17	0.18
11.10	1.68	1.34	5.45*	0.06	0.24	0.40	0.06
1.47	0.22	1.04	4.25*	0.01	0.04	1.60	0.24
6.59		0.24		0.24		6.68	
34		72		38		36	
0.452		0.225		0.330		0.246	

tervals. The results of those ANOVAs are presented in Rodd (1994).

Interpopulation differences in reaction norms may not be detected if only analyses of variance are used (Sultan 1987). Therefore, we used regression analyses to examine the responses of test males to a range of demographic conditions. It was possible to do these analyses because of short-term deviations from the original experimental design caused by the presence of other test individuals in the tanks. For example, adult female numbers increased when adult test females were still in the treatment tanks, waiting to produce their second and third broods. Adult male numbers increased when older test males were awaiting tests of their sexual behavior. Even with such variations, the total densities in aquaria with a *Crenicichla*-type demography were always lower than those in *Rivulus*-type demographies (see Rodd and Sokolowski 1995 for more details).

We performed multiple regressions for each male dependent variable with the numbers of mature females, mature males, and immature animals in the test individual's tank as the independent variables (PROC GLM, SAS Institute 1989). For each test male, we counted the numbers of guppies in each category in his tank 1 wk before he initiated the maturation process. We used this date as a rough estimate of the time when young males would be sensitive to interactions with conspecifics. The numbers of individuals in each category ranged from: immatures: 2–5, mature males: 2–7, mature females: 2–7. To ensure that the assumptions of this test were met, we checked residuals and tolerances and verified that correlations among the numbers of guppies in each category were not significant (Sokal and Rohlf 1981, Zar 1984). We also checked for interactions among the independent variables; interactions that were not significant were excluded from the regressions.

We further examined the influences of conspecifics on male traits by doing analyses of covariance with the

TABLE 1. Continued.

	Mass of the offspring in the third brood (mg)				Reproductive allotment	
	viii) Mean dry mass (covariate = Age 1†)		ix) Mean, lean, dry mass (covariate = Age 1†)		x) Reproductive allotment for females that produced a third brood (covariate = Length 3†)	
Source	MS	*F*	MS	*F*	MS	*F*
Covariate	34.60	5.41*	14.49	5.63*	4.29§	3.50‖
Parents	9.30	1.45	10.61	4.12*	1.97	1.61
Residents	13.55	2.12	9.50	3.69‖	9.08	7.42**
Demography	14.25	2.23	5.51	2.14	5.16	4.22*
Parents × Residents	44.36	6.93**	14.69	5.71*	2.74	2.24
Parents × Demography	16.59	2.59	2.87	1.12	0.03	0.02
Residents × Demography	1.62	0.25	1.57	0.61	0.46	0.38
Parents × Residents × Demography	1.48	0.23	3.16	1.23	0.08	0.07
Error	6.40		2.57		1.22	
Error df	39		39		34	
R^2	0.262		0.286		0.362	

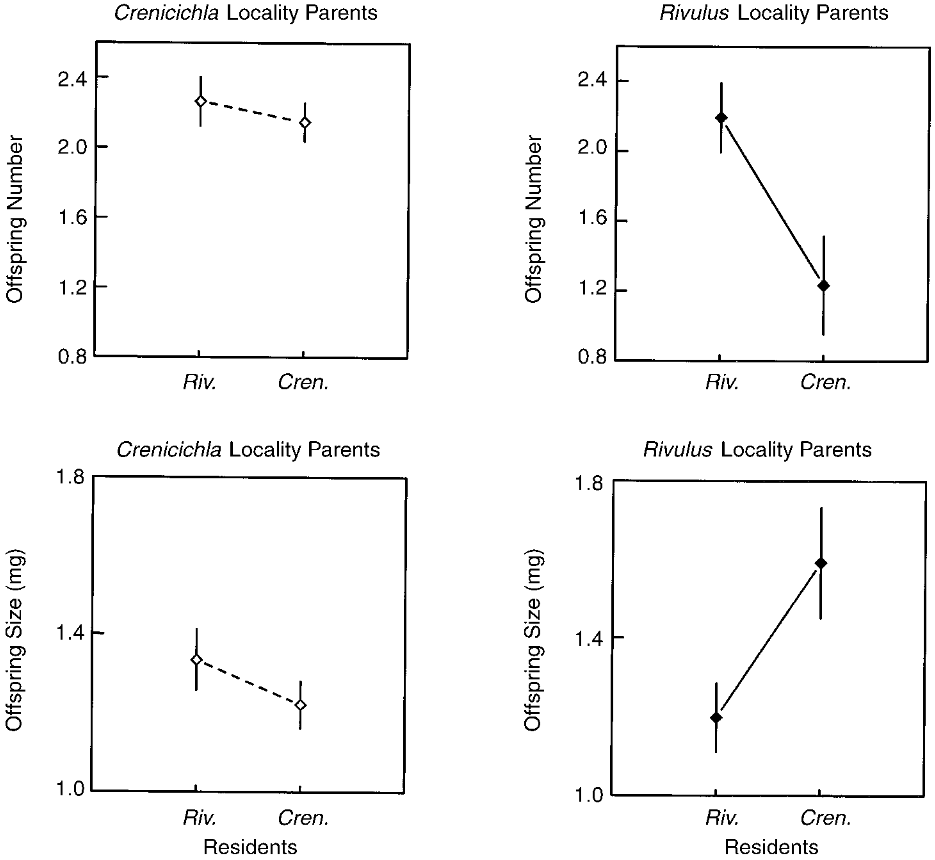

FIG. 1. Mean number and size (dry mass) (±1 SE) of offspring produced in the third brood by females from *Rivulus* and *Crenicichla* localities when they were reared with residents from those localities. Demography did not have a significant influence on fecundity (i.e., these results were obtained irrespective of the density at which females were reared). Fecundity data were transformed using natural logarithms.

numbers of immature and/or mature male residents as the covariate (mature females were not used as a covariate since the multiple regressions indicated that they did not contribute to the variation in male traits). Again, we used Type III sums of squares. Where appropriate, data were transformed to comply with the assumptions of the analysis.

RESULTS

Females

Influence of parental origin.—Daughters of *Crenicichla* locality guppies were younger at first parturition (least squares mean: 122 d) than those from *Rivulus* localities (134 d) (Table 1:ii). There was no influence of any of the three main factors (parents, residents, nor demography) on female size at first parturition and they had little influence on offspring size and number in the first two broods (Table 1:i–v). Number of offspring in the second brood was the only exception: there was a significant interaction among all three experimental factors but there was no clear pattern to their effects. For characteristics of the third brood, there were significant interactions between the origin of the parents and the origin of conspecific residents.

Interlocality variation in plasticity and the influence of the origin of the residents.—Daughters of *Rivulus* locality guppies had fewer, larger offspring in their third broods when they were reared with guppies from *Crenicichla* localities than when they were reared with guppies from *Rivulus* localities (least squares means comparisons: offspring number: $P = 0.009$; total offspring mass: $P = 0.023$; lean offspring mass: $P = 0.017$ [SAS Institute 1989]) (Figs. 1 and 2, Table 1:vi,–ix). Daughters of *Crenicichla* locality guppies did not respond differently to residents from different localities (offspring number: $P = 0.51$; total offspring dry mass: $P = 0.26$; lean offspring mass: $P = 0.65$).

One possible explanation for this response of *Rivulus* females to the origin of the residents is that the intensity of competition for food was greater for females living with *Crenicichla* locality residents and hence less food was available to them. A decrease in food availability will cause a decrease in female growth rates and fecundity and an increase in offspring size (Reznick and Yang 1993). To examine this possibility, we looked at

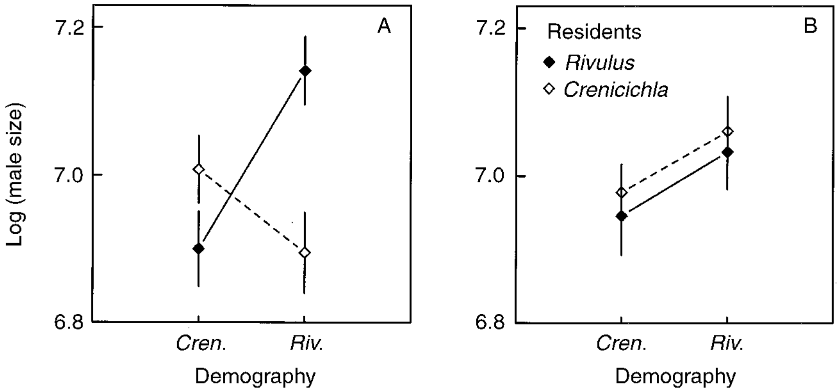

FIG. 2. Natural log of mean mass at sexual maturity (±1 SE) of male Trinidadian guppies reared under different demographic conditions with resident guppies from different predator localities. (A) = sons of guppies from *Rivulus* localities. (B) = sons of guppies from *Crenicichla* localities. The original data for male size (mg) were multiplied by 10 prior to log-transformation.

the daily growth rates of *Rivulus* locality females. Growth rates were not significantly different between those females when they were reared with *Rivulus* locality residents vs. with *Crenicichla* locality residents (least squares means comparisons: growth rate during the first interbrood interval: $P = 0.60$; growth rate during the second interbrood interval: $P = 0.92$). This suggests that competition for food is not responsible for the differences in offspring size and number.

The reproductive allotment (RA) of all guppies, regardless of locality of origin, was greater when they were reared with *Rivulus* residents (least squares mean ± 1 SE: 11.6 ± 0.9%) than when they were reared with *Crenicichla* residents (7.5 ± 1.1%) (Table 1:x).

Influence of population demography.—The second interbrood interval (mean ± 1 SE) was significantly shorter (31.1 ± 0.7 d) when females were reared in a *Crenicichla*-type demography (low density) than for those in a *Rivulus*-type demography (high density) (33.2 ± 0.8 d) (Table 1:iv). RA was significantly greater for females reared in a *Crenicichla*-like demography (11.0 ± 0.9%) than for those in a *Rivulus*-type demography (8.0 ± 1.0%) (Table 1:x). These results are consistent with the pattern expected if guppies in the *Crenicichla*-type demography had more energy at their disposal than those in the *Rivulus*-like demography (Reznick and Yang 1993). However, growth rates did not differ between females from the two types of demography. We also compared a subset of test females from both demographic treatments so that only those with similar growth rates were considered. In this analysis, the influence of differences in growth rates (energy availability) on the life history traits of interest should be eliminated. There were still differences between females reared in the two demographic conditions (duration of the second interbrood interval: $F_{1,33} = 4.37$, $P = 0.044$, $n = 42$; RA: $F_{1,33} = 4.12$, $P = 0.048$, $n = 42$). Therefore, the differences in interbrood interval and RA do not seem to be attributable to differences among females in resource acquisition.

Males

Influence of parental origin.—Males (mean ± 1 SE) from *Crenicichla* localities were younger (61.4 ± 2.7 d) and smaller (71.53 ± 1.88 mg, 14.74 ± 0.13 mm) when they initiated the maturation process than males from *Rivulus* localities (68.6 ± 2.9 d, 80.73 ± 1.91 mg, 15.38 ± 0.13 mm) (Table 2). When all males were considered, the duration of the maturation interval (age at maturity minus age at initiation of maturity) was similar for *Crenicichla* and *Rivulus* locality males; when only those individuals with similar growth rates before initiation were considered, the interval was shorter for *Crenicichla* locality guppies than *Rivulus* locality guppies (i.e., they developed at a faster rate) ($F_{1,76} = 4.04$, $n = 84$, $P = 0.048$). *Crenicichla* locality males were younger at maturity (85.6 ± 3.0 d) than *Rivulus* locality males (94.1 ± 3.2 d) (Table 2); this result should be considered with caution given that the assumption of homogeneity of variances was not met for this variable, despite the use of several transformations (Sokal and Rohlf 1981, Zar 1984). Therefore, the rate of development was accelerated in *Crenicichla* locality fish compared with *Rivulus* locality fish. These results are consistent with earlier studies (Reznick and Endler 1982, Reznick and Bryga 1987, Reznick 1989).

For growth rates during the maturation interval, there was an interaction among all three factors examined in this study but the most obvious pattern among them is that males from *Crenicichla* localities tended to grow faster (1.69 ± 0.07 mg/d) than those from *Rivulus* localities (1.20 ± 0.07 mg/d). Finally, for the mass at sexual maturity and the duration of the maturation interval, there was an interaction among all three factors.

Interlocality variation in plasticity.—For mass at maturity, only males from *Rivulus* localities responded

TABLE 2. Analyses of variance on male life history traits.

Source	Maximum growth rate before the initiation of the maturation process (mg/d)		Characteristics at the initiation of maturation	
			Length (mm)	
	MS	F	MS	F
Parents†	14.56	0.51	2001.98‡	11.91***
Demography	166.03	5.77*	18.50	0.11
Residents	140.55	4.88*	0.28	0.00
Parents × Demography	31.13	1.08	76.98	0.46
Parents × Residents	0.11	0.00	289.51	1.72
Residents × Demography	112.18	3.90*	475.92	2.83‖
Parents × Residents × Demography	10.40	0.36	63.12	0.38
Error	28.78		168.05	
Error df	97		118	
R^2	0.146		0.127	

Note: Influences of the three experimental factors: origin of the male's parents (Parents), origin of the residents (Residents), and demography of the population (Demography) on male traits. Degrees of freedom = 1 in each case except for the error term; the degrees of freedom for the error term are shown after the error mean square.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

† Parents = origin of the test male's parents (*Rivulus* or *Crenicichla* locality). Residents = source of the tank residents (*Rivulus* or *Crenicichla* locality). Demography = population demography.

‡ MS × 1000.

§ MS × 100 000.

‖ $0.05 < P < 0.10$.

to the treatments (Table 2, Fig. 2A). Residents from *Rivulus* localities exerted a greater influence on them than residents from *Crenicichla* localities and *Rivulus* locality residents were most influential when they were at high densities (least squares means comparisons: $P < 0.0077$, this is significant when compared with the Bonferroni-corrected P value of 0.0083 [Milliken and Johnson 1984, SAS Institute 1989]). On the other hand, males from *Crenicichla* localities did not show a significant response to the manipulations ($P > 0.014$ for all comparisons, this is not significant when compared with the corrected P value of 0.0083; Fig. 2B). The results for the duration of the maturation interval also suggest that males from *Rivulus* localities were more sensitive to our manipulations than those from *Crenicichla* localities for this trait.

Influences of population demography and origin of the residents.—The duration (mean ± 1 SE) of the maturation interval was significantly shorter for males reared in the *Crenicichla* locality-type demography (24.4 ± 0.6 d) than for those reared in the *Rivulus* locality-type demography (27.0 ± 0.7 d). This difference remained significant even when we only examined individuals with similar growth rates ($F_{1,82} = 5.85$, $n = 84$, $P = 0.018$). For the rest of the traits that were influenced by demography (mass at the initiation of maturation, length at maturation, and the maximum growth rate attained before the initiation of maturation), there was an interaction between demography and the origin of the tank residents. If males were reared with residents from *Crenicichla* localities, population demography had no influence on these traits (least squares means comparisons: mass at initiation: $P = 0.65$ [77.14 ± 2.51 mg]; length at maturity: $P = 0.35$ [17.05 ± 0.19 mm]; maximum growth rate: $P = 0.75$ [1.69 ± 0.10 mg/d]). However, if males were reared with residents from *Rivulus* localities, population demography had a significant influence (least squares means comparisons: mass at initiation: $P = 0.0049$; length at maturity: $P = 0.0038$; maximum growth rate: $P = 0.0037$). Males reared at high densities (*Rivulus* demography) grew more quickly before initiation (2.16 ± 0.10 mg/d), were larger at the onset of maturation (80.54 ± 2.69 mg), and were longer at the completion of maturation (17.69 ± 0.20 mm) than males reared at low densities (*Crenicichla* demography) (1.69 ± 0.12 mg/d, 69.69 ± 2.90 mg, 16.84 ± 0.21 mm). When we considered a subset of juveniles reared with *Rivulus* locality residents, those with similar maximum growth rates before initiation, the significance level for mass at initiation fell just below the critical value ($F_{1,35} = 3.53$, $n = 37$, $P = 0.069$) while length at maturity was still significant ($F_{1,36} = 5.00$, $n = 38$, $P = 0.032$). Given that the decline in samples sizes in these analyses is expected to reduce significance levels, they suggest that food consumption did not play a large role in these differences.

To determine what aspect of population demography was influencing the size at maturity of males reared with *Rivulus* locality residents, we first used multiple regression analyses (see *Methods*) (Table 3) and then analyses of covariance (Table 4). Both analyses indicated that the length at maturity of guppies from both localities increased as the density of mature males increased when they were reared with residents from *Rivulus* localities; when they were reared with residents from *Crenicichla* localities, there was no such response. All males, including those reared with *Creni-*

TABLE 2. Continued.

Characteristics at the initiation of maturation				Characteristics of the maturation interval (initiation to completion of maturation)			
Mass (mg)		Age (d)		Duration (d)		Growth rate (mg/d)	
MS	*F*	MS	*F*	MS	*F*	MS	*F*
421.44‡	10.98**	0.12‡	6.53**	69.56‡	2.49	3.66	24.70***
125.65	3.27‖	0.00	0.00	238.92	8.56**	0.06	0.43
16.16	0.42	0.04	1.98	31.51	1.13	0.37	2.47
4.41	0.11	0.03	1.40	0.18	0.01	0.01	0.07
52.84	1.38	0.04	2.06	7.89	0.28	0.03	0.18
224.04	5.84*	0.00	0.02	9.22	0.33	0.38	2.55
14.95	0.39	0.01	0.61	101.05	3.62‖	0.87	5.86*
38.38		0.02		27.90		0.15	
118		106		106		105	
0.153		0.098		0.143		0.225	

cichla locality residents, increased their length at maturity in response to an increase in the number of immature males. We could not interpret a similar analysis of male mass at maturity because of interactions among the independent variables.

In a multiple regression on the maximum growth rate attained before initiation, for males reared with *Rivulus* locality residents, growth rates increased with the number of mature male residents. This increase was associated with larger sizes before the initiation of maturation as the density of mature males increased. Mature females and immature individuals had no influence on test males' growth rates. For males reared with *Crenicichla* locality residents, the residents had no influence on growth rates.

We found no effect of the manipulations of social conditions (demography and residents) on the ages of males at the initiation or completion of maturation.

DISCUSSION

Plasticity as an explanation for phenotypic variation in the field

Our results suggest that phenotypic variation induced by population demography contributes to the life history differences between guppies in *Rivulus* and *Crenicichla* localities. Reznick and Endler found that *Rivulus* locality males were larger at maturity than *Crenicichla* locality males but that the difference was greater for guppies collected in the field than for those maintained in the laboratory for two generations (Reznick 1982, Reznick and Endler 1982; D. N. Reznick, *unpublished data*). We found that the size at maturity of males from *Rivulus* localities increased with density. Since guppy densities tend to be higher in *Rivulus* localities than in *Crenicichla* localities (Reznick and Endler 1982), the genetically based difference in size between guppies from the two localities would be enhanced by the effects of the differences in demography. For two other traits, reproductive allotment (RA) and interbrood interval, the plastic responses to differences in demography would also augment the genetic differences.

Previous studies also found greater differences between *Rivulus* and *Crenicichla* locality guppies in the field than in the laboratory for female size at maturity and for offspring size (Reznick 1982, Reznick and Endler 1982). We did not detect an influence of our manipulations on female size at maturity. We did detect an effect of conspecifics' origins on offspring size for daughters of *Rivulus* locality guppies and on repro-

TABLE 2. Continued.

	Characteristics at maturity					
	Length (mm)		Mass (mg)		Age (d)	
Source	MS	*F*	MS	*F*	MS	*F*
Parents†	0.74‡	0.18	10.39‡	0.29	5.25§	9.81**
Demography	9.30	2.27	170.50	4.73*	0.18	0.34
Residents	3.70	0.90	12.02	0.33	0.95	1.77
Parents × Demography	1.42	0.35	3.33	0.09	0.85	1.60
Parents × Residents	5.86	1.43	75.82	2.10	1.03	1.93
Residents × Demography	32.07	7.83**	247.32	6.86**	0.02	0.04
Parents × Residents × Demography	10.04	2.45	237.29	6.58**	0.10	0.18
Error	4.10		36.07		0.54	
Error df	120		120		111	
R^2	0.112		0.147		0.115	

TABLE 3. Multiple regression analyses with tank residents (by sex and age category) as the independent variables and the life history trait as the dependent variable.

Source	df	MS	F	P	Slope
A) Dependent variable = male length at maturity					
i) *Crenicichla* locality residents					
Mature females	1	4.31†	0.10	0.757	−0.0023
Mature males	1	1.30	0.03	0.865	−0.0014
Immature	1	239.03	5.35	0.024	0.0218
Error	66	44.71			
$R^2 = 0.084$, intercept = 5.088					
ii) *Rivulus* locality residents					
Mature females	1	92.53†	3.09	0.085	0.0094
Mature males	1	118.52	3.95	0.052	0.0145
Immature	1	175.02	5.84	0.019	0.0282
Error	54	29.99			
$R^2 = 0.286$, intercept = 4.977					
B) Dependent variable = maximum growth rate before initiation of maturation					
i) *Crenicichla* locality residents					
Mature females	1	0.02†	0.00	0.997	−0.0002
Mature males	1	531.76	0.56	0.459	0.0326
Immature	1	1410.77	1.47	0.230	0.0544
Error	54	957.16			
$R^2 = 0.040$, intercept = 2.499					
ii) *Rivulus* locality residents					
Mature females	1	108.00†	0.09	0.763	0.0114
Mature males	1	7868.72	6.69	0.013	0.1325
Immature	1	1202.39	1.02	0.318	0.0778
Error	43	1176.99			
$R^2 = 0.226$, intercept = 2.114					

Note: Analyses were run separately for males reared with *Crenicichla* locality residents and those reared with *Rivulus* locality residents.

† MS × 10 000.

ductive allotment; however, the effect we observed would appear to reduce the difference between *Rivulus* and *Crenicichla* locality guppies for these traits.

Interpopulation variation in plasticity

For several traits, guppies from *Rivulus* localities expressed plasticity in response to our manipulations but those from *Crenicichla* localities did not. For example, females from *Rivulus* sites varied the number and size of their offspring in response to the type of residents with which they were reared. Females from *Crenicichla* sites showed no such response. However, females from *Crenicichla* localities modify the size of their offspring when reared in isolation on different levels of food availability, so they are capable of varying this trait (Reznick 1983, Reznick and Yang 1993). Males from *Rivulus* localities showed plasticity in two life history traits, mass at maturity and duration of the maturation interval, for which males from *Crenicichla* localities did not. This is in contrast to identical patterns of plasticity in size at maturity in males from both localities in response to varying food supply (Reznick 1990; D. N. Reznick, *unpublished data*). Rodd and Sokolowski (1995) also showed that males from *Rivulus* localities were more likely to express flexibility in courtship behavior than those from *Crenicichla* localities.

Why did *Rivulus* locality guppies show greater flexibility than *Crenicichla* locality guppies in response to the conditions tested here? We offer several possible explanations. First, environmental heterogeneity can select for phenotypic plasticity (Levins 1968, Via 1993). We have found that there is greater temporal and spatial variation in the sex ratios of adults in *Rivulus* localities than there is in *Crenicichla* localities (Rodd and Reznick 1997). Since sex ratio can influence the degree of competition for mates (e.g., Itzkowitz 1990, Madsen and Shine 1993), young males may use their social environment as an indicator of the degree of competition they will face when they mature and hence adjust their reproductive strategy (e.g., adult body size) accordingly (Schultz and Warner 1989). Greater variation in sex ratio among populations of guppies in *Rivulus* localities may thus select for increased plasticity in response to social environment. Another possibility is that the costs of plasticity (Johnston 1982, Alcock 1989, Lott 1991, Newman 1992) are higher for guppies living in *Crenicichla* localities. For example, high mortality rates combined with the delay in maturation necessary to attain a larger body size could offset the benefits of a larger size. Male mortality rates are substantially higher in *Crenicichla* localities than in *Rivulus* localities (Reznick et al. 1996). A third possibility is that there are reduced benefits of plasticity

TABLE 4. Analyses of covariance to compare the responses of males from different treatments to varying numbers of conspecifics.

Source of variation	df	MS	*F*	*P*
A) Dependent variable = male length at sexual maturity				
i) *Four treatment groups according to source of parents and source of tank residents*				
Immature (I)†	1	1099.64	8.92	0.003
Treatment (T)	3	57.83	0.47	0.704
I × T	3	68.40	0.55	0.646
Error	120	123.27		
Slope = 4.20, intercept = 159.45				
Mature males (M)‡	1	459.06	3.70	0.057
Treatment (T)	3	278.58	2.25	0.086
M × T	3	389.12	3.14	0.028
Error	120	124.01		
ii) *Separate analyses for different sources of tank residents*				
a) *Rivulus* locality residents				
Mature males (M)	1	1229.30	12.31	0.0009
Origin of parents (O)§	1	9.18	0.09	0.763
M × O	1	5.36	0.05	0.818
Error	54	99.82		
Slope = 3.72, intercept = 159.00				
b) *Crenicichla* locality residents				
Mature males	1	98.27	0.68	0.411
Origin of parents	1	1.44	0.01	0.921
M × O	1	0.02	0.00	0.990
Error	66	143.80		
Slope = −0.86, intercept = 174.32				
B) Dependent variable = maximum growth rate before maturation				
i) *Four treatment groups according to source of parents and source of tank residents*				
Mature males	1	408.55	16.30	0.0001
Treatment	3	57.14	2.28	0.084
M × T	3	105.81	4.22	0.008
Error	97	25.07		
R^2 = 0.256				
ii) *Separate analyses for different sources of tank residents*				
a) *Crenicichla* locality residents				
Mature males	1	13.20	0.66	0.421
Origin of parents	1	6.08	0.30	0.585
M × O	1	12.31	0.61	0.437
Error	54	20.09		
R^2 = 0.023				
b) *Rivulus* locality residents				
Mature males	1	544.07	17.37	0.0001
Origin of parents	1	63.63	2.03	0.161
M × O	1	87.08	2.78	0.103
Error	43	31.32		
R^2 = 0.272				

† The number of immature conspecifics present in the male's tank one week before he initiated the maturation process.

‡ The number of mature male conspecifics present in the male's tank one week before he initiated the maturation process.

§ *Rivulus* or *Crenicichla* locality.

in *Crenicichla* localities. Females in *Crenicichla* localities are less likely to base their mate choice decisions on male size than those in *Rivulus* localities (Houde 1988, Reynolds and Gross 1992, Endler and Houde 1995) so the advantages of maturing at a larger size are reduced in *Crenicichla* localities. Also, there may be less male–male competition for mates in *Crenicichla* localities (Farr 1980). A fourth possibility, at least for male size at maturity, is that plasticity is well developed in guppies from *Rivulus* localities because the phenotypic response to increased density, an increased size at maturity, enhances the genetic response to predators, an increased size at maturity. However, in *Crenicichla* localities, if the risk of mortality via predation increases with size, the genetic and plastic responses would conflict. Therefore, this may be a case where selection for plasticity by one factor may be counteracted by selection on the mean of the trait by a different factor.

Plasticity in male life history traits

We found that male development and size at maturity were influenced by interactions with conspecifics. These effects were not a result of competition for food because variation in growth rates did not explain the patterns of results. Also, our observations are very different from the effects of food availability on the maturation of males reared in isolation (Reznick 1990). Reznick found that the duration of the maturation interval was fixed, even at a wide range of food availabilities; here, we found that the duration varied with population demography.

Previous studies have shown that large male guppies sire more offspring than smaller ones both because females tend to prefer them and because they have an advantage when competing with other males for access to females (Gandolfi 1971, Gorlick 1976, Houde 1988, Magurran and Seghers 1991, Kodric-Brown 1992, Reynolds and Gross 1992). Since male guppies grow little after they mature, body size during their reproductive life-span is essentially their size at maturity (Reynolds et al. 1993, F. H. Rodd, *personal observation*). In this study, males adjusted their size at maturity in response to the density, reproductive status, and origin of potential competitors. These cues should be reliable indicators of the degree of competition a male can expect to face because there was a short delay (3–5 wk) between the time when we detected males' sensitivity to cues from conspecifics (1 wk before the initiation of maturation) and the time when the newly matured males faced those male competitors and choosy females. If it looks as though there will be little competition, they mature early and small; if there will be a lot, they delay maturation and mature at a larger size. This pattern suggests that this plasticity is adaptive.

Other poeciliid species also show an effect of agonistic interactions with male conspecifics on male age and size at maturity (Borowsky 1973, 1978, Sohn 1977*a*, *b*, Farr 1980, Hughes 1985, Campton and Gall 1988, Campton 1992). The general pattern is that inhibited males delay maturation and hence mature at a larger size than they would have otherwise (Borowsky 1973, 1987, Sohn 1977*a*, *b*, Farr 1980, Campton and Gall 1988, Campton 1992). As in this study, Campton (1992) also found increased growth rates of group-reared fish.

Hormones, especially androgens, appear to be the mediator between agonistic male–male interactions and delayed sexual development in male poeciliids. Androgens are required to stimulate the initiation of the maturation process (Grobstein 1948) and increasing levels are needed to successfully complete maturation (Turner 1942, Kallman and Schreibman 1973). At higher concentrations, maturation is accelerated (Grobstein 1948). Androgens also retard growth in poeciliids (Pickford and Atz 1957, Clemens et al. 1966). For *Xiphophorus helleri*, androgen levels are reduced for ≈24 h in mature males that lose a bout with another mature male (Hannes et al. 1984). Therefore, after every agonistic interaction, androgen levels are probably depressed in immature males and, as a result, maturation is delayed but growth rates remain high. As density increases, agonistic interactions per individual increase (Magurran and Seghers 1991) and androgen levels are likely reduced for longer and/or to lower levels. In this study, the responses of two traits were consistent with the ''androgen'' hypothesis: the duration of the maturation interval was longer and growth rates were higher at increased densities. Therefore, these results provide further evidence that hormones may be involved in the life history responses of male guppies to interactions with conspecifics. However, we found no evidence that the initiation of the maturation process was delayed at increased densities. This may have been due to the relatively short duration between the introduction of the test males to the treatments and the initiation of maturation.

The size at maturity of focal males increased with the density of resident males when they were reared with *Rivulus* residents, but not when they were reared with *Crenicichla* residents. Because aggressive interactions among guppies are reduced in *Crenicichla* localities (Magurran and Seghers 1991), adult males from these sites may not suppress hormone production in immature males. Alternatively, there may be reduced benefits of an increased size in *Crenicichla* locality populations (see previous section).

Plasticity in female life history traits

All females reduced RA in response to being reared with *Crenicichla* locality residents. Females from *Rivulus* localities increased offspring size and reduced fecundity in response to *Crenicichla* locality residents. The observed patterns are similar to the ones expressed by guppies in response to variation in food availability (Reznick and Yang 1993). It is possible that females reared with *Crenicichla* locality residents acquire less food or expend more energy than those reared with *Rivulus* locality residents. The increase in interbrood interval and decline in RA in response to *Rivulus*-type demography were also consistent with variation in energy intake or expenditure (Reznick and Yang 1993). It is possible that energy intake varied with the manipulations because the feeding rates of small guppies were inhibited by larger ones (Nagoshi 1967). It is also possible that energy expenditure increased with density because of an increase in aggressive acts per guppy (Warren 1973, Magurran and Seghers 1991). However, if the plasticity we observed was simply a result of differences in energy budgets, we would expect to find differences in the growth rates of females living with the two types of residents or living in different densities. We found no such differences. This suggests that energy budgets are not involved directly. However, it is possible that as resource availability declines, the reduction may first appear as decreased allocation to reproduction (Reznick 1983) and only later as a reduction in growth.

Alternatively, the observed patterns of plasticity in female life history traits may represent adaptations. For example, it is possible that females reared with *Crenicichla* locality residents and those reared at high densities reduce their RA because they are withholding resources for future survival and/or reproduction (Williams 1966, Warner 1984). This did not appear to be the case since we detected no differences in growth rates; however, it is possible that females were storing energy as fat (Reznick 1983), a parameter not measured in this study. Variation in offspring size is another example where plasticity may be an adaptation. Females from *Rivulus* localities may modify the size of their offspring in response to the behavior of residents when larger offspring would have a significant advantage over smaller ones (e.g., larger offspring may be produced in response to competitive conspecifics) (Brockelman 1975, Lloyd 1987, Hutchings 1991, Gliwicz and Guisande 1992).

As in an earlier study (Reznick 1982), we found that daughters of *Crenicichla* locality guppies matured earlier than those of *Rivulus* locality guppies. However, we found no evidence of effects of residents nor of demography on female age and size at maturity nor on the first two broods produced by females. This may have been because some females were isolated well in advance of maturation and hence they were not exposed to the experimental manipulations during the period when they were maturing, producing their first brood, and initiating the allocation of resources for their second brood (Reznick and Yang 1993).

Conclusions

Our results suggest that the guppies' phenotypically based responses to population demography are contributing to the observed association between predator community and guppy life history traits. Therefore, the predators are contributing to the patterns in guppy life history traits both indirectly and directly. Predators are indirectly responsible for the patterns because much of the variation in population demography, to which the guppies are responding, is caused by differences in predation pressure among localities (Rodd and Reznick 1997). Predators are also directly responsible for the patterns because some of the life history trait differences have evolved in response to the differences in predation pressure (Reznick 1982, Reznick and Bryga 1987, Reznick et al. 1990).

The guppies' phenotypic responses to differences in population demography would augment the genetic differences between guppies from *Rivulus* and *Crenicichla* localities. However, this plasticity may not have evolved directly to enhance fitness in the face of predation pressure. Rather, it has probably evolved to improve an individual's reproductive success under varying social conditions. For example, when competition for mates is low, males mature early at a small size; when competition is stiff, males delay maturity, mature at a larger size, and possibly enhance their ability to procur mates.

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LITERATURE CITED

Alcock, J. 1989. Animal behavior. An evolutionary approach. Fourth edition. Sinauer, Sunderland, Massachusetts, USA.

Borowsky, R. L. 1973. Social control of adult size in males of *Xiphophorus variatus.* Nature **245**:332–335.

———. 1978. Social inhibition of maturation in natural populations of *Xiphophorus variatus* (Pisces: Poeciliidae). Science **201**:933–935.

———. 1987. Genetic polymorphism in adult male size in *Xiphophorus variatus* (Atheriniformes: Poeciliidae). Copeia **1987**:782–787.

Brockelman, W. Y. 1975. Competition, the fitness of offspring, and optimal clutch size. American Naturalist **109**: 677–699.

Campton, D. E. 1992. Heritability of body size of green swordtails, *Xiphophorus helleri*: I. Sib analyses of males reared individually and in groups. Journal of Heredity **83**: 43–48.

Campton, D. E., and G. A. E. Gall. 1988. Effect of individual and group rearing on age and size at maturity of male mosquitofish, *Gambusia affinis.* Journal of Fish Biology **33**: 203–212.

Clemens, H. P., C. McDermitt, and T. Inslee. 1966. The effects of feeding methyl testosterone to guppies for sixty days after birth. Copeia **1966**:280–284.

Dahlgren, B. T. 1979. The effects of population density on fecundity and fertility in the guppy, *Poecilia reticulata* (Peters). Journal of Fish Biology **15**:71–91.

———. 1985. Relationships between population density and reproductive success in the female guppy, *Poecilia reticulata* (Peters). Ekologia Polska **33**:677–703.

Endler, J. A. 1978. A predator's view of animal color patterns. Evolutionary Biology **11**:319–364.

———. 1980. Natural selection on color patterns in *Poecilia reticulata.* Evolution **34**:76–91.

———. 1986. Natural selection in the wild. Princeton University Press, Princeton, New Jersey, USA.

———. 1995. Multiple-trait coevolution and environmental gradients in guppies. Trends in Ecology and Evolution **10**: 22–29.

Endler, J. A., and A. E. Houde. 1995. Geographic variation in female preferences for male traits in *Poecilia reticulata.* Evolution **49**:456–468.

Farr, J. A. 1975. The role of predation in the evolution of social behavior of natural populations of the guppy *Poecilia reticulata* (Pisces: Poeciliidae). Evolution **29**:151–158.

———. 1980. The effects of juvenile social interaction on growth rate, size and age at maturity, and adult social behavior in *Girardinus metallicus* Poey (Pisces: Poeciliidae). Zeitschrift fur Tierpsychologie **52**:247–268.

Feltmate, B. W., and D. D. Williams. 1991. Evaluation of predator-induced stress on field populations of stoneflies (Plecoptera). Ecology **72**:1800–1806.

Gandolfi, G. 1971. Sexual selection in relation to the social status of males in *Poecilia reticulata* (Teleostei: Poeciliidae). Bollettino di Zoologia **38**:35–48.

Gliwicz, Z. M., and C. Guisande. 1992. Family planning in *Daphnia*: resistance to starvation in offspring born to mothers grown at different food levels. Oecologia **91**:463–467.

Gorlick, D. L. 1976. Dominance hierarchies and factors influencing dominance in the guppy *Poecilia reticulata* (Peters). Animal Behaviour **24**:336–346.

Grobstein, D. 1948. Optimum gonopodial morphogenesis in *Platypoecilus maculatus* with constant dosage of methyl testosterone. Journal of Experimental Zoology **109**:215–237.

Hannes, R. P., D. Franck, and F. Liemann. 1984. Effects of rank-order fights on whole-body and blood concentrations of androgens and corticosteroids in the male swordtail (*Xiphophorus helleri*). Zeitschrift fur Tierpsychologie **65**: 53–65.

Haskins, C. P., E. F. Haskins, J. J. A. McLaughlin, and R. E. Hewitt. 1961. Polymorphism and population structure io *Lebistes reticulatus*, a population study. Pages 320–395 *in* W. F. Blair, editor. Vertebrate speciation. University of Texas Press, Austin, Texas, USA.

Houde, A. E. 1988. The effects of female choice and male–male competition on the mating success of male guppies. Animal Behaviour **36**:888–896.

Hughes, A. L. 1985. Male size, mating success, and mating strategy in the mosquitofish *Gambusia affinis* (Poeciliidae). Behavioral Ecology and Sociobiology **17**:271–278.

Hutchings, J. A. 1991. Fitness consequences of variation in egg size and food abundance in brook trout *Salvelinus fontinalis.* Evolution **45**:1162–1168.

Itzkowitz, M. 1990. Sex-ratio biasing and male reproductive variation in a coral-reef fish. American Naturalist **136**:557–559.

Johnston, T. D. 1982. Selective costs and benefits in the evolution of learning. Advances in the Study of Behavior **12**: 65–106.

Kallman, K. D., and M. P. Schreibman. 1973. A sex-linked gene controlling gonadotrop differentiation and its significance in determining the age of sexual maturation and size of the platyfish, *Xiphophorus maculatus.* General and Comparative Endocrinology **21**:287–304.

Kodric-Brown, A. 1992. Male dominance can enhance mating success in guppies. Animal Behaviour **44**:165–167.

Levins, R. 1968. Evolution in changing environments. Some theoretical explorations. Princeton University Press, Princeton, New Jersey, USA.

Liley, N. R., and B. H. Seghers. 1975. Factors affecting the morphology and behaviour of guppies in Trinidad. Pages 92–118 *in* G. P. Baerends, C. Beer, and A. Manning, editors. Function and evolution in behaviour. Oxford University Press, Oxford, UK.

Lloyd, D. G. 1987. Selection of offspring size at independence and other size-versus-number strategies. American Naturalist **129**:800–817.

Lott, D. F. 1991. Intraspecific variation in the social systems of wild vertebrates. Cambridge University Press, Cambridge, UK.

Luyten, P. H., and N. R. Liley. 1991. Sexual selection and competitive mating success of male guppies (*Poecilia reticulata*) from four Trinidad populations. Behavioral Ecology and Sociobiology **28**:329–336.

Madsen, T., and R. Shine. 1993. Phenotypic plasticity in body sizes and sexual size dimorphism in European grass snakes. Evolution **47**:321–325.

Magurran, A. E., and B. H. Seghers. 1990. Risk sensitive courtship in the guppy (*Poecilia reticulata*). Behaviour **112**: 194–210.

Magurran, A. E., and B. H. Seghers. 1991. Variation in schooling and aggression amongst guppy (*Poecilia reticulata*) populations in Trinidad. Behaviour **118**:214–234.

Magurran, A. E., and B. H. Seghers. 1994. Sexual conflict as a consequence of ecology: evidence from guppy, *Poecilia reticulata*, populations in Trinidad. Proceedings of the Royal Society of London **B 255**:31–36.

Mattingly, H. T., and M. J. Butler, IV. 1994. Laboratory predation on the Trinidadian guppy: implications for the size-selective predation hypothesis and guppy life history evolution. Oikos **69**:54–64.

McLain, D. K. 1992. Population density and the intensity of sexual selection on body length in spatially or temporally restricted natural populations of a seed bug. Behavioral Ecology and Sociobiology **30**:347–356.

Milliken, G. A., and D. E. Johnson. 1984. Analysis of messy data. Lifetime Learning, Belmont, California, USA.

Nagoshi, M. 1967. Experiments on the effects of size hierarchy upon the growth of guppy (*Lebistes reticulata*). Journal of the Faculty of Fisheries Prefectural University of Mie **7**:167–189.

Newman, R. A. 1992. Adaptive plasticity in amphibian metamorphosis. BioScience **42**:671–678.

Peckarsky, B. L., C. A. Cowan, M. A. Penton, and C. Anderson. 1993. Sublethal consequences of stream-dwelling predatory stoneflies on mayfly growth and fecundity. Ecology **74**:1836–1846.

Pickford, G., and J. W. Atz. 1957. The physiology of the pituitary gland of fishes. New York Zoological Society, New York, New York, USA.

Reynolds, J. D., and M. R. Gross. 1992. Female mate preference enhances offspring growth and reproduction in a fish, *Poecilia reticulata.* Proceedings of the Royal Society of London **B 250**:57–62.

Reynolds, J. D., M. R. Gross, and M. J. Coombs. 1993. Environmental conditions and male morphology determine alternative mating behaviour in Trinidadian guppies. Animal Behaviour **45**:145–152.

Reznick, D. N. 1982. The impact of predation on life history evolution in Trinidadian guppies: Genetic basis of observed life history patterns. Evolution **36**:1236–1250.

———. 1983. The structure of guppy life histories: the tradeoff between growth and reproduction. Ecology **64**:862–873.

———. 1989. Life-history evolution in guppies: 2. Repeatability of field observations and the effects of season on life histories. Evolution **43**:1285–1297.

———. 1990. Plasticity in age and size at maturity in male guppies (*Poecilia reticulata*): an experimental evaluation of alternative models of development. Journal of Evolutionary Biology **3**:185–203.

Reznick, D. N., and H. Bryga. 1987. Life-history evolution in guppies (*Poecilia reticulata*): 1. Phenotypic and genetic changes in an introduction experiment. Evolution **41**:1370–1385.

Reznick, D. N., H. Bryga, and J. A. Endler. 1990. Experimentally induced life-history evolution in a natural population. Nature **346**:357–359.

Reznick, D. N., M. J. Butler IV, F. H. Rodd, and P. N. Ross. 1996. Life history evolution in guppies (*Poecilia reticulata*): 6. Differential mortality as a mechanism for natural selection. Evolution **50**:1651–1660.

Reznick, D. N., and J. A. Endler. 1982. The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). Evolution **36**:160–177.

Reznick, D. N., and A. P. Yang. 1993. The influence of fluctuating resources on life history: patterns of allocation and plasticity in female guppies. Ecology **74**:2011–2019.

Rodd, F. H. 1994. Phenotypic plasticity in the life history traits and sexual behaviour of Trinidadian guppies (*Poecilia reticulata*) in response to their social environment. Dissertation. York University, Toronto, Canada.

Rodd, F. H., and D. N. Reznick. 1991. Life history evolution in guppies: III. The impact of prawn predation on guppy life histories. Oikos **62**:13–19.

Rodd, F. H., and D. N. Reznick. 1997. Variation in the demography of guppy populations: the importance of predation and life histories. Ecology **78**:405–418.

Rodd, F. H., and M. B. Sokolowski. 1995. Complex origins of variation in the sexual behaviour of male Trinidadian guppies, *Poecilia reticulata*: interactions between social environment, heredity, body size and age. Animal Behaviour **49**:1139–1159.

SAS Institute. 1989. SAS/STAT user's guide, version 6. Fourth edition. SAS Institute, Cary, North Carolina, USA.

Schultz, E. T., and R. R. Warner. 1989. Phenotypic plasticity in life-history traits of female *Thalassoma bifasciatum* (Pisces: Labridae). 1. Manipulations of social structure in tests for adaptive shifts of life-history allocations. Evolution **43**: 1497–1506.

Seghers, B. H. 1973. An analysis of geographic variation in the anti predator adaptations of the guppy, *Poecilia reticulata.* Dissertation. University of British Columbia, Vancouver, Canada.

———. 1974. Schooling behavior in the guppy (*Poecilia reticulata*): An evolutionary response to predation. Evolution **28**:486–489.

Sohn, J. J. 1977*a.* Socially induced inhibition of genetically determined maturation in the platyfish, *Xiphophorus maculatus.* Science **195**:199–201.

———. 1977*b.* The consequences of predation and competition upon the demography of *Gambusia manni* (Pisces: Poeciliidae). Copeia **1977**:224–227.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. Second edition W.H. Freeman, New York, New York, USA.

Spitze, K., and T. D. Sadler. 1996. Evolution of a generalist genotype: multivariate analysis of the adaptiveness of phenotypic plasticity. American Naturalist **148**:S108–S123.

Strauss, R. E. 1990. Predation and life-history variation in *Poecilia reticulata* (Cyprinodontiformes: Poeciliidae). Environmental Biology of Fishes **27**:121–130.

Sultan, S. E. 1987. Evolutionary implications of phenotypic plasticity in plants. Evolutionary Biology **21**:127–178.

Turner, C. L. 1942. A quantitative study of the effects of different concentrations of ethynyl testosterone and methyl testosterone in the production of gonopodia in females of *Gambusia affinis.* Physiological Zoology **15**:263–281.

Via, S. 1993. Adaptive phenotypic plasticity: target or byproduct of selection in a variable environment? American Naturalist **142**:352–365.

Warner, R. R. 1984. Deferred reproduction as a response to sexual selection in a coral reef fish: a test of the life historical consequences. Evolution **38**:148–162.

Warren, E. W. 1973. The effects of relative density upon some aspects of the behaviour of the guppy—*Poecilia reticulata* (Peters). Journal of Fish Biology **5**:753–765.

Williams, G. C. 1966. Adaptation and natural selection. Princeton University Press, Princeton, New Jersey, USA.

Zar, J. H. 1984. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey, USA.