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Life-History Evolution in Guppies. VII. The Comparative Ecology of High- and Low-Predation Environments

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ABSTRACT: Prior research has demonstrated a strong association between the species of predators that co-occur with guppies and the evolution of guppy life histories. The evolution of these differences in life histories has been attributed to the higher mortality rates experienced by guppies in high-predation environments. Here, we evaluate whether there might be indirect effects of predation on the evolution of life-history patterns and whether there are environmental differences that are correlated with predation. To do so, we quantified features of the physical and chemical environment and the population biology of guppies from seven high- and low-predation localities. We found that high-predation environments tend to be larger streams with higher light levels and higher primary productivity, which should enhance food availability for guppies. We also found that guppy populations from high-predation environments have many more small individuals and fewer large individuals than those from low-predation environments, which is caused by their higher birth rates and death rates. Because of these differences in size distribution, guppies from high-predation environments have only one-fourth of the biomass per unit area, which should also enhance food availability for guppies in these localities. Guppies from high-predation sites allocate more resources to reproduction, grow faster, and attain larger asymptotic sizes, all of which are consistent with higher levels of resource availability. We conclude that guppies from high-predation environments experience higher levels of resource availability in part because of correlated differences in the environment (light levels, primary productivity) and in part as an indirect consequence of predation (death rates and biomass density). These differences in resource availability can, in turn, augment the effect of predator-induced mortality as factors that shape the evolution of guppy life-history patterns. We found no differences in the invertebrate communities from high- and low-predation localities, so we conclude that there do not appear to be multitrophic, indirect effects associated with these differences in predation.

In every well-studied example of adaptation in natural populations, a general conclusion is that adaptations represent responses to, and often compromises among, multiple agents of selection (Reznick and Travis 1996). For example, in an article entitled "Shell Color Polymorphism in *Cepea*: A Problem with Too Many Solutions," Jones et al. (1977) considered all of the factors believed to influence the distribution of color morphs in these snails. Initially, Cain and Sheppard (1950, 1952, 1954) concluded that the relative abundance of different morphs was associated with background color matching and was a trait selected for by frequency-dependent selection resulting from the formation of a search image by visually oriented predators. Many features of the system were characterized with elegant observations and experiments, resulting in an explanation that was satisfying and appeared complete. However, when other investigators evaluated shell color polymorphisms on a larger geographical scale, across Western Europe or England, morph frequencies were found to be correlated with variables like altitude or latitude, suggesting the importance of temperature and physiology as factors that influence morph fitness. Subsequent studies confirmed that shells with different colors had different thermal properties and that these factors might also play an important role in the evolution of the polymorphism (Cameron 1970). The central message from this case study, among others, is that adaptations often reflect a compromise among a multitude of selective factors, many of which vary geographically.

Here, we develop a similar argument for the evolution of life-history patterns in natural populations of guppies (*Poecilia reticulata*). Our prior work indicates that predators and predator-induced mortality has played an important role in molding the evolution of guppy life histories in streams in Trinidad, West Indies (Reznick 1982;

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Reznick and Endler 1982; Reznick et al. 1990; Reznick et al. 1996*a*, 1997). In high-predation localities, guppies co-occur with predators, like the pike cichlid *Crenicichla alta*, that frequently prey on guppies. Many other species of potential predators co-occur with *Crenicichla* in these localities. In low-predation sites, the killifish *Rivulus hartii* is the only other fish that lives with guppies. *Rivulus* is an omnivore that occasionally feeds on guppies (Liley and Seghers 1975). High- and low-predation localities are often found in the same drainage, separated by waterfalls that exclude the larger species of fish, but not guppies and *Rivulus*. This contrast between high- and low-predation localities is repeated in a large number of drainages throughout Trinidad, yielding a large number of sites and a diversity of environments in which guppies are exposed to high- and low-predation pressure.

When we compare the life histories of guppies from high- and low-predation environments, we find that guppies from high-predation environments attain maturity at an earlier age and smaller size than their counterparts from low-predation environments. In addition, they devote more of their consumed resources to reproduction and produce more young per litter, but each offspring is smaller than its counterparts from low-predation localities. These patterns agree with the predictions of life-history theory (Gadgil and Bossert 1970; Law 1979; Michod 1979; Charlesworth 1980).

The evidence in favor of predation as the cause of these life-history patterns includes the following: first, comparisons of the life histories of wild-caught guppies from a large number of high- and low-predation localities from throughout Trinidad (Reznick and Endler 1982; Reznick 1989), in combination with laboratory experiments that demonstrate that differences in wild-caught fish have a genetic basis (Reznick 1982); second, parallelism in the life histories of guppies from communities with different suites of predators, but that share the property of having either high and low predation (Reznick and Bryga 1996; Reznick et al. 1996*b*); third, analyses of the combined effects of predation and environmental factors that reveal that predation is the dominant correlate of life-history variation (Strauss 1990); fourth, evaluations of mortality rates in natural populations that reveal that guppies from high-predation environments sustain consistently higher mortality rates than their counterparts from low-predation environments (Reznick et al. 1996*a*); and finally, replicated introduction experiments (Reznick and Bryga 1987; Reznick et al. 1990, 1997) that reveal rapid evolution in response to a change in predator communities that is correlated with a change in mortality rate (Reznick et al. 1996*a*).

In spite of the strong argument in favor of predation as a dominant agent of selection, other factors may influence the evolution of guppy life histories. First, high-predation localities also tend to be higher-order streams. High-order streams are generally wider and have more open canopies, higher light levels (Reznick and Endler 1982), and often higher levels of primary productivity (Hawkins et al. 1982; Power 1984; Feminella et al. 1989; Grether et al., in press). These differences in environment can, in turn, result in higher levels of per capita resource availability for guppies. Therefore, higher rates of predation are potentially confounded with consistent differences in the environment (i.e., productivity) that can also select for changes in the life history. While life-history theory does not make consistent predictions for how resource availability will influence the evolution of life histories, resource availability has been incorporated into many models and appears to be a potential agent of selection (e.g., Charlesworth 1980; Kozlowski and Wiegert 1987; Abrams and Rowe 1996). Second, predation can cause a variety of indirect effects that may also play an important role in how predators influence their prey (see Kerfoot and Sih 1987). These effects have been studied extensively from an ecological perspective. For example, "trophic cascades" occur when the removal of a top predator results in an increase in the abundance of individuals in the next trophic level with a consequent decrease in the abundance two trophic levels down, and so on (Power 1990, 1992; Wootton and Power 1993). Predators also influence the amount of resource available to their prey. They can reduce resource availability by restricting the distribution of prey to marginal, less productive habitats (e.g., Werner et al. 1983; Power et al. 1985; Fraser and Gilliam 1992), or they can increase resource availability by reducing the abundance of a competitor (e.g., Werner et al. 1983; Wilbur 1987). In spite of the extensive work on the ecology of such indirect effects, little consideration has been given to their potential evolutionary consequences (Wootton 1994).

Our goal was to evaluate the plausibility of either environmental correlates or indirect effects of predators as agents of selection in guppy life histories. To do so, we compared a series of guppy populations subjected to either high- or low-predation risk to determine whether there are average differences among community types that define potential agents of selection other than the direct effects of predation.

Material and Methods

Study Sites

We characterized guppy populations and the environment at the same 14 pools for which we obtained estimates of guppy mortality (Reznick et al. 1996*a*). Guppy populations were characterized at all 14 pools, while environmental variables were characterized for 11 of the 14 pools. These sites included seven high- and seven low-predation pools on five different streams, all on the south slope of the Northern Range mountains in Trinidad, West Indies (table 1). All five

Table 1: Schedule of pool sampling for ecology/mortality rate studies

Year	High predation	Low predation
1988	Ceniza 1[a]	Quare Tributary 1[a]
1989	Ceniza 2, 3; El Cedro 1[b]	Quare Tributary 2; El Cedro 3, 4[b]
1990	Mausica 1, 2, 3[c]	Aripo Tributary 1, 2, 3[c]
1991	El Cedro 2; Oropuche[b]	El Cedro 5, 6

Note: Each entry represents a different sampling point. For example, "Mausica 1, 2, 3" represents three different pools sampled in the Mausica River on the same year. "El Cedro 1" and "El Cedro 2" represent two different pools sampled in the high-predation portion of the El Cedro River on two different years.

[a] Only mark-recapture data were collected at these sites.

[b] Only environmental variables were evaluated at these sites.

[c] Mark-recapture data were collected at all sites, but other variables were only collected at two of the three sites.

streams chosen for study were similar in size and riffle-pool structure, in part to facilitate the mark-recapture studies but also to minimize potential among-site differences in uncontrolled environmental variables. Guppies congregate within pools and rarely migrate among pools (Reznick et al. 1996*a*); the average rate of emigration over 12 d was <5% of the marked population. It is possible to collect all of the guppies in an individual pool (Reznick et al. 1996*a*), so we chose pools as the unit of investigation. As a consequence of the requirement for a riffle-pool structure, the variance in fish community structure and environmental parameters between high- and low-predation sites are likely to be smaller than would be seen in a random selection of high- versus low-predation sites.

When there were multiple sites in a stream, they were separated from one another by at least 200 m and sometimes by waterfalls. For example, a 5-m-high waterfall that serves as a barrier to upstream movement by large predatory fish separated the high- and low-predation sites on the El Cedro River. Sites were sampled during the dry season (February through April) over a 4-yr period (1988–1991, table 1); two to six sites were evaluated per year. Prior research (Reznick 1989) revealed that resource availability tended to decline during the wet season, as evidenced by a decline in fecundity or reproductive allocation. The proportional declines were approximately equal in both types of localities (e.g., fig. 2 of Reznick 1989), which suggests that seasonality had a similar impact on reproduction in both types of localities. All data (mortality rate, population structure, physical and chemical characteristics of the pool, and invertebrate samples) were collected during the same time period.

In addition to these 14 pools, we also collected environmental data at one high- and two low-predation sites on the El Cedro River in 1989 and on the Oropuche River (high predation) in 1991. The El Cedro sites were all different from those sampled in 1991. The Oropuche River is a more typical high-predation site because it is a larger, wider stream that lacks the riffle-pool structure of the other high-predation sites.

Characterization of Study Sites

Each study site (i.e., stream pool) was characterized in terms of its general physical, chemical, and biotic environment and in terms of the resident guppy population size structure, growth, emigration, mortality, reproduction, and habitat use. Estimates of guppy size-specific mortality and emigration are provided elsewhere (Reznick et al. 1996*a*).

We constructed a bathymetric map of each pool by first measuring its longest axis, which generally paralleled the direction of flow, and then measuring the stream width perpendicular to the main axis at regular intervals. We took depth measurements at 0.2-m intervals along each width axis. The surface area of each pool was estimated from these maps, and the volume was estimated as the surface area times the average depth.

Surface water velocity and stream depth were measured at 1-m intervals across each stream on a line perpendicular to stream flow. Water velocity was determined by measuring the time that it took for a surface float to move 1 m; three replicate readings were taken at each 1-m interval. Stream discharge (Q; units = m³/sec) was estimated with a commonly applied formula: $Q = wdla/t$, where w = stream width (m), d = mean stream depth (m), l = distance float traveled (1 m), t = time (s), and a is a constant that equals 0.8 (used for rough stream bottoms; Wetzel and Likens 1994).

Temperature, conductivity, and dissolved oxygen were measured at streamside with a Yellow Springs Instruments (YSI; Yellow Springs, Ohio) conductivity meter and YSI oxygen meter. Water samples for other analyses (i.e., nitrate-nitrogen, orthophosphate, turbidity, pH) were collected in 1-L acid-washed polyethylene bottles and kept in the dark during transport back to the laboratory. In the laboratory,

the samples were analyzed immediately with a Hach portable spectrophotometer and the standard methods and chemicals supplied for analysis by the Hach Chemical Company (Loveland, Colo.). Suspended total organic carbon (TOC) was analyzed with the presulfate-ultraviolet oxidation method on a Xertex-Dohrman (Stuttgart, Germany) DC-80 total organic carbon analyzer.

We quantified benthic macroinvertebrate abundance with a modified Hess invertebrate box sampler equipped with a 1-mm mesh collection bag. Six to eight 0.025-m^2 samples were collected at each site, three to four along the stream edge and three to four in the center of each pool. Samples were immediately preserved in 10% buffered formalin with rose bengal and later washed through a 0.5-mm sieve. Macroinvertebrates were counted, and because the larval macroinvertebrate taxonomy of this region is largely undescribed, the organisms were sorted to class or order. For each sample, we recorded the total number of macroinvertebrates, the number per taxa, and the size of taxa that were potential guppy predators (e.g., dragonflies, damselflies, and decapod crustaceans).

To estimate periphyton production at each site, we placed six unglazed ceramic tiles (5 cm × 5 cm) on the bottom along the stream edge and in the middle of the stream ($n = 12$ per site) and left them there for 21 d. In preliminary trials, we left tiles for 14, 21, and 28 d and found that 21 d was sufficient time for periphyton growth and was a time period similar to that used in other studies of tropical periphyton (Paaby 1988). After 21 d, a single tile was placed within either a light or dark Plexiglas chamber filled with stream water (0.75 L) and then incubated in situ for 3 h. The dissolved oxygen in the water within the light and dark chambers was determined before and after the incubation period with the modified-Winkler method and reagents supplied by Hach Chemical Company. Gross productivity, net productivity, and respiration of the periphyton community expressed as mg C/m^2/d was calculated with standard light-dark bottle equations (American Public Health Association 1985) assuming a 12-h-daylight photoperiod. Light intensity (lux) was also measured with a hand-held light meter positioned at the water surface near each incubation chamber at the start of the incubation period.

Guppy Measurements

We collected all of the guppies in each pool by repeated sampling with butterfly nets. Investigators held a net in each hand and removed guppies by entrapping them in one or the other net. Because guppies are attracted to the sediment that is raised by this activity, it is possible to collect every individual in the pool without further disturbing the habitat (Reznick et. al 1996a). Once collected,

guppies were placed in plastic bags filled with water and immediately transported back to the laboratory.

We measured standard length on all individuals as the distance from the lower jaw to the tip of the hypleural plate, then marked each individual by injecting a dot of red or black acrylic latex paint (Liquitex) diluted with teleost Ringer's solution (30% paint, 70% Ringer's). The mark indicated the size class (nearest millimeter) of the individual at the beginning of the study. Guppies <12 mm were marked as a cohort by immersing them in a solution of calcein (250 mg/L) for 24 h. Calcein binds to calcium bearing tissue and is visible under an epifluorescent microscope at a wavelength of 460–480 nm (Wilson et al. 1987; Rodd and Reznick 1991). All fish were held for 1 d, treated with medication as a prophylaxis, and then released. They were re-collected 12 d later. At the time of re-collection, we estimated growth as the difference between the average size of all individuals in a given millimeter size class at the beginning and the end of the interval.

The numbers and sizes of individuals at initial collection were used for subsequent estimates of population density and biomass. We estimated guppy biomass by converting length-based guppy size distributions to dry weight, using a length–dry weight regression derived from the associated dissections of these fish. We then divided the density or calculated total dry weight of the guppy population by pool surface area or volume to estimate either population density or biomass per unit surface area or per unit volume.

Life Histories

We characterized the life histories of females from nine of these localities following the methods of earlier studies (e.g., Reznick and Endler 1982; Reznick et al. 1996b). All such characterizations were based on the dissection of a subset of the marked females re-collected at the end of the mark-recapture experiment and on additional unmarked adults that had migrated into the pool during the course of the experiment or that had been collected from a neighboring pool. The dependent variables used to characterize the life history were as follows: first, fecundity, with female size as a covariate; second, mean dry mass of offspring, with their stage of development as a covariate (offspring lose weight as they develop); and finally, the percent of total dry weight that consisted of developing offspring, with stage of development as a covariate.

Habitat Utilization

At each study site, we recorded the number of guppies per unit area at the stream edge and midstream. Such observations were made during the 1989–1991 field seasons at 12 of the 14 sampling sites (six high- and six low-predation

Table 2: MANOVA results for the three analyses comparing water chemistry, stream physical characteristics, macroinvertebrate density, and macroinvertebrate size between high- and low-predation sites

Analysis	Pillai's trace approximate F	Hypothesis df	Error df	P	Power
A: Water chemistry	4.648	7	5	.055	.639
B: Physical features	.625	5	6	.689	.127
C: Macroinvertebrate density	.784	10	8	.648	.189
D: Macroinvertebrate size	2.290	3	27	.101	.228

Note: Analyses A–D correspond to panels *A–D* in figure 1.

localities). At each site, two to four observers each selected two 0.5 × 0.5-m observation quadrats within one pool, one near the pool edge and one in the center. Colored rocks marked the corners of each quadrat, and the water depth was measured in the center of each quadrat. Mean depth varied from 3.9 cm to 5.4 cm in the edge quadrats and from 8.9 cm to 9.6 cm in the midstream quadrats. After establishing and measuring the quadrats, each observer sat quietly next to the stream for 5 min. We found this to be sufficient time for the guppies to resume their normal activities of feeding and courtship. Each observer then counted the guppies within both quadrats every 2 min for 30 min, which yielded 15 observations per quadrat. We calculated the mean number of guppies per 0.25-m² quadrat by first calculating mean values for each quadrat, then calculating the means for edge versus center quadrats. The mean values for each quadrat were used in all subsequent analyses.

Statistics

While there is the potential for structure other than high- versus low-predation sites in our sampling scheme (e.g., drainage or year), the pattern of replication (table 1) does not allow us to incorporate these effects into a linear model. All variables were evaluated with pool means, yielding a potential maximum of seven data points representing high- or low-predation pools for each analysis. Environmental and invertebrate data were not collected for the Ceniza 1988 and Quare 1988 sites, one of the Aripo 1990 sites, and one of the Mausica 1990 study sites. We included data from the three El Cedro 1989 and Oropuche 1991 localities for these analyses, which balances the representation of high- and low-predation environments. The actual number of data points sometimes deviates from seven for each predation environment because not all data were collected at all study sites.

The productivity estimates and habitat utilization by guppies were expressed as the mean of the replicate readings taken in the margin and the center of each pool. Margin versus center was then added as an additional "habitat" independent variable in analyses of these results, which resulted in a split-plot ANOVA, with "predator" as the plot, stream site as the block, and habitat (margin vs. center) as the subplot, yielding estimates of "predator," "habitat," "site (predator)," and "predator × habitat." The invertebrate density data were first analyzed as a one-factor MANOVA on just the edge data, since only edge data were available for the 1988 samples. The data from 1989–1991 were also analyzed, including the "habitat" independent variable. The result reported for invertebrate density in table 2 is the "edge only" analysis that includes all 4 yr of data; both analyses yielded similar results. In all analyses except habitat utilization, neither the habitat nor the predator × habitat interaction was significant, so the analyses were simplified to one-way, nested ANOVAs with site nested within predator treatment. All of the remaining variables (e.g., growth rate or asymptotic size) were not associated with a habitat effect and, hence, were analyzed as one-way ANOVAs. All ANOVAs and associated power analyses were performed with the SPSS general linear models procedure (Norusis 1990). The effect size in the power analyses was equal to the observed effect size, or the difference between the treatment means.

We characterized the size distribution of guppy populations by dividing them into the same four size categories used to evaluate mortality rates (<12 mm, 12–14 mm, 14–18 mm, >18 mm; Reznick et al. 1996*a*). We tested for differences in size structure among stream sites and predator regimes with a logistic regression (Proc Catmod, SAS Institute 1988) and the following model: size = predation site(predation). The smallest size class was not evaluated in the Ceniza 1988, Quare 1988, and one of the Aripo Tributary 1990 samples. The data were, therefore, analyzed two ways, with all 14 localities but only including the three largest guppy size classes or with 11 localities and all four size classes. Details on additional analyses are included with the results.

Results

Life Histories

Female life histories differed between the high- and low-predation sites in a similar fashion to all earlier published
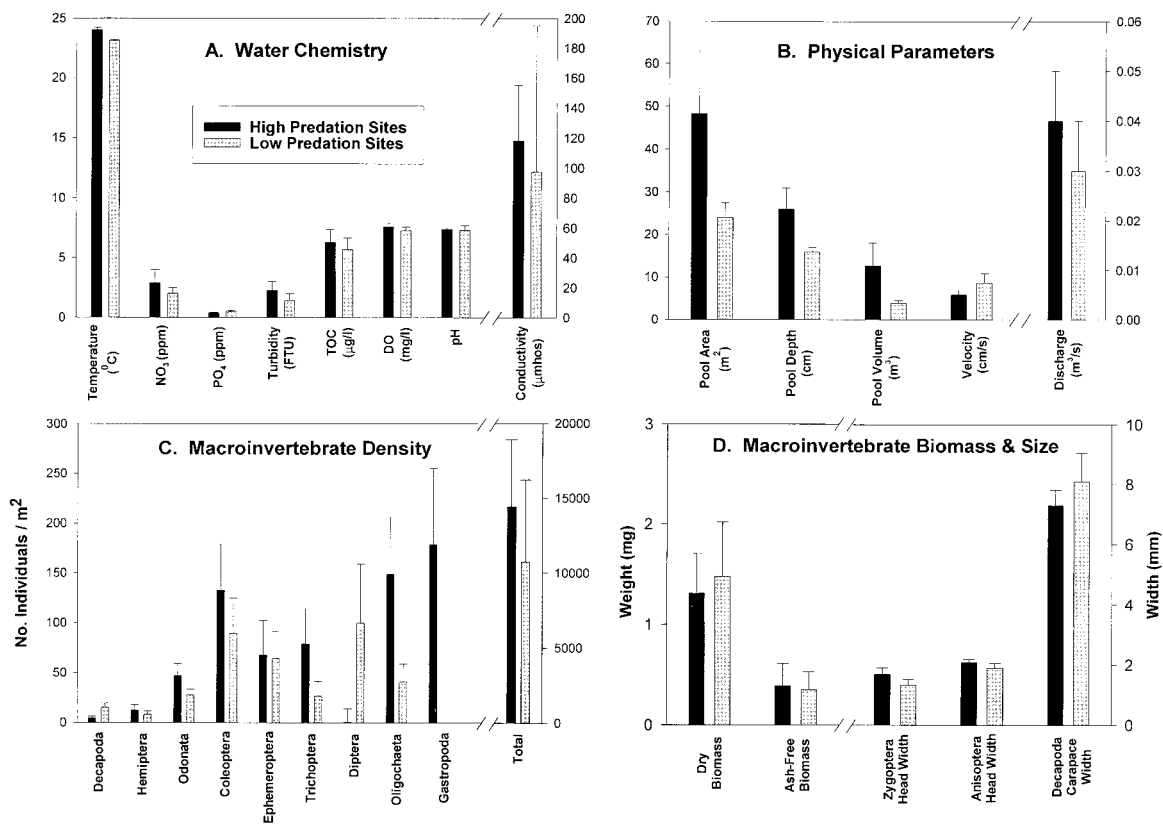
Figure 1: Mean values for high- and low-predation sites. Bars = least square means from the appropriate ANOVAs. Error lines = 1 SE. In addition to the MANOVAs reported in the text, all variables were also evaluated with univariate ANOVAs. The only significant difference ($P < .05$) between high- and low-predation sites in the univariate tests was for water temperature. *A*, Water chemistry and quality. *TOC* = total organic carbon. *DO* = dissolved oxygen. All variables and methods of estimation are described in "Material and Methods." *B*, Physical descriptions of the sampled pools. *C*, Density of individual orders of macroinvertebrates in the sampled pools. *D*, Two estimates of total invertebrate biomass as well as estimates of the sizes of individuals in three different groups of invertebrates that potentially prey on guppies.

results (e.g., Reznick and Endler 1982; Reznick 1989; Reznick et al. 1996*a*). Specifically, female guppies in high-predation localities differed from those in low-predation localities by having higher reproductive allotments (high = 16.4%, low = 13.8%; $P < .0093$), smaller offspring (high = 1.01 mg, low = 1.66 mg; $P < .0001$), and higher fecundity in females of equal size (high = 7.24 offspring, low = 3.92 offspring; $P < .0001$). All statistical comparisons were derived from one-way ANOVAs with localities as the independent variable and a planned comparison for high versus low predation. The differences in life-history patterns among guppies from high- and low-predation environments reported in earlier comparisons were, therefore, repeated in these samples.

The Chemical and Physical Environment

We analyzed these variables first with two separate MANOVAs that characterize water quality (temperature,

conductivity, pH, nitrate, phosphate, turbidity, dissolved oxygen, and total organic carbon) and the physical structure of the stream (pool area, mean depth, pool volume, velocity, and discharge volume). The predator effect was not significant in either MANOVA (table 2). The power of both comparisons was low (water chemistry = 0.187, physical characteristics = 0.172).

The differences that we observed in the mean values of several parameters characterizing the low- and high-predation sites were all statistically insignificant when evaluated with univariate tests (results not shown; means and SEs reported in fig. 1*A*, 1*B*). Because these variables differed in the degree to which they complied with the assumptions of ANOVA and in the degree to which transformations of the data alleviated this problem, they were evaluated with both parametric and nonparametric tests, with the same results in both cases. The one exception to this trend was the small but significant difference in mean

water temperature. In terms of water chemistry, the conductivity, nitrates, and turbidity were 20%, 45%, and 60% higher, respectively, in the high-predation sites. The statistical power was 0.821 for temperature and 0.434 for phosphates but was quite low for the remaining variables (0.05–0.17). The differences in the physical attributes were more impressive, with the high-predation sites having 101% greater surface areas, 63% greater depth, 226% greater volumes, and 32% slower velocities. Again, all of these comparisons had low statistical power ($P < .30$), and none of the differences was significant. However, all of these differences are consistent with the high-predation sites tending to be larger, higher-order streams.

It is important to note that these comparisons apply primarily to the five streams that were deliberately chosen for their similarity in structure. A random selection of high- versus low-predation localities would almost certainly result in larger differences in many of these parameters, with high-predation localities tending to be found in larger streams, as they were found to be by Reznick and Endler (1982).

Light Level and Productivity

Light intensities averaged considerably higher in high-predation localities (2,554 lux vs. 545 lux), but this difference was not significant ($F_{1,10} = 4.24$, $P = .073$ on log-transformed data, power = 0.442). The absence of significance is attributable to the high variance in light levels, particularly in the high-predation localities, where canopy cover and shading of the streams vary considerably. These light intensities are low by most standards. Natural light intensities can exceed 20,000 lux, and experiments on shade-adapted periphyton are often conducted at light intensities of 2,000 lux or lower (Allan 1995).

High-predation localities had significantly higher gross periphyton productivity than low-predation localities (352.3 vs. 152.1 mg C/m^2/d; $F_{1,12} = 5.93$, $P = .0315$). This difference is consistent with the trend toward higher light levels and dissolved substances (e.g., nitrates, conductivity, and oxygen) in these localities. The residuals were normally distributed in this analysis, although they also tended to be correlated with the mean. Log-transformation corrected this correlation and yielded the same statistical results. There were no significant effects for comparisons of net primary productivity, although high-predation localities still tended to have higher values (185.3 vs. 108.2; $F_{1,12} = 1.44$, $P = .25$). Our estimates of periphyton productivity fall near the upper end of the range recorded for shaded stream systems (e.g., net productivity range: <10 mg to about 100 mg C/m^2/d) but well below those recorded where the canopy is open and net productivity values often exceed 2,000 mg C/m^2/d (Allan 1995). Guppies in these types of habitats feed primarily on invertebrates and on organisms they scrape from environmental surfaces (Dussault and Kramer 1981). When scraping, guppies feed indiscriminately on all organisms present, so gross primary productivity is the best indicator of the relative resource availability in these two types of localities.

Invertebrates

Differences in predator communities were not associated with significant differences in the invertebrate community (table 2 for MANOVA results; fig. 1C). None of the corresponding univariate tests was significant (not reported), although all of these tests had low power (range: 0.013–0.106). Seven of the nine invertebrate categories were more abundant in high- than low-predation sites (fig. 1C), which is consistent with the higher productivity in these localities.

We also evaluated other variables that characterize predator sizes and invertebrate community biomass. These additional variables include the mean size of predatory invertebrate taxa, estimated as width of the head capsule for odonates and carapace width for crabs. We estimated size variables because a between-site difference in the size distribution of potential guppy predators, even in the absence of an overall difference in abundance, could be biologically significant. For example, only large odonate (families: Zygoptera and Anisoptera) larvae and large juvenile crabs (Pseudothelphusidae) are likely to prey on guppies. Thus, a consistent difference among community types in the size of the invertebrate predators could translate into a difference in predation on guppies. There were no significant differences among stream types for any of these variables, either when evaluated with a MANOVA (table 2) or with separate univariate ANOVAs (Zygoptera head width, $P = .10$; Anisoptera head width, $P = .40$; crab carapace width, $P = .73$), although both the Anisoptera and Zygoptera tended to be larger in the high-predation localities (fig. 1D). Finally, we also analyzed the total biomass of invertebrates per sample, evaluated as the dry weight and ash-free dry weight; neither variable differed significantly between the high- and low-predation sites (invertebrate dry weight, $P = .87$; invertebrate ash weight, $P = .91$).

In summary, we found little in the way of significant differences in the physical habitat or invertebrate communities of high- versus low-predation localities. The most impressive result was the higher light levels and primary productivity in high-predation localities. Such differences tend to arise because they are higher-order streams and, hence, tend to be wider and to have more open canopies. Other trends in the results for water chemistry, physical characteristics of the pools, and invertebrate abundance

are all consistent with the high-predation sites being larger streams with higher productivity.

Comparisons of Guppy Populations

Size Structure. The guppy size distribution differed significantly between high- and low-predation communities ($\chi^2 = 57.6$, $P < .0001$) and among localities within a predator community ($\chi^2 = 136.8$, $P < .0001$). The predator effect is primarily attributable to a much larger number of small guppies (<12-mm size category) in the high-predation localities and the larger number of large guppies (>18-mm size category) in the low-predation localities (fig. 2). The <12-mm and 12–14-mm fish are almost exclusively immature. The 14–18-mm fish include almost all mature males and smaller mature females. The >18-mm category is exclusively adult females.

Habitat Use and Density. Our visual censuses revealed no differences between high- and low-predation pools or edge versus center in the average number of guppies seen per census period (predator: $F_{1,9} = 0.28$, $P = .61$; habitat: $F_{1,21} = 1.96$, $P = .20$). However, there was a significant interaction between stream type and habitat ($F_{1,21} = 17.06$, $P = .0026$; table 3). This interaction occurred because guppies were found at higher densities on the margins of high-predation streams and at higher densities in the center of low-predation streams.

We also evaluated density as the total number of guppies found in pools, in terms of either the number per unit area or the unit volume (table 4). We did these calculations for fish ≥12 mm or for all fish. The former analysis includes
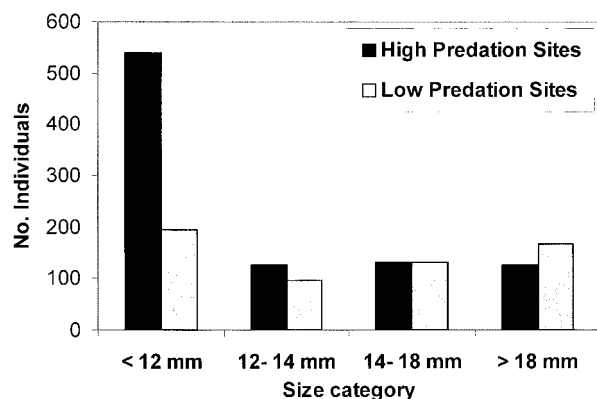
Table 3: Least squares means (1 SE) for the number of guppies recorded in visual censuses of quadrats in the margin versus the center of the stream

Least squares means	Margin	Center
High predation	3.21 (.57)	1.23 (.57)
Low predation	1.49 (.61)	2.34 (.61)

all sampling points, while the latter includes only the 11 sites for which the <12-mm fish were also enumerated. In all cases, the differences in guppy density between stream types were not significant (F-values ranged from 0.00 to 0.72, depending on the analysis, with $P > .5$ in all cases). This result differs from that of Reznick and Endler (1982), who found that guppies were found at lower population densities in high-predation localities. The earlier investigation included larger streams in the high-predation localities, rather than being restricted to small streams with riffle-pool structures. These larger streams have lower population densities of guppies, so including them reduced the estimated density for guppies in high-predation localities.

If we view this result, instead, in terms of the biomass of guppies per unit area or volume, then the difference between stream type is much more dramatic and statistically significant. Low-predation sites contain a fourfold higher guppy biomass per unit area or volume (high-predation mean = 126 mg/m^3, mean rank = 3.2; low-predation mean = 530 mg/m^3, mean rank = 7.8; $P = .0216$). The reason for the more dramatic difference when stream types are compared in this fashion is that biomass incorporates the effect of differences in size distribution, and mass increases exponentially with size. High-predation localities are dominated numerically by fish of <12 mm standard length, which results in far lower biomasses per unit volume. While the fourfold difference in density will not translate into a fourfold difference in the demand for resource availability because of differences in the size-specific metabolic rate, this result indicates that there will be a higher demand for resources in the low-predation environments.

Growth Rate. A logical consequence of the higher primary productivity and lower guppy biomass per unit volume in high-predation localities is that food availability and growth rates should be higher. To compare growth rates, we restricted our comparison to immature fish because these fish allocate assimilated resources only to growth, rather than dividing them between growth and reproduction, thus making growth a more reliable indicator of food availability. We determined the mean growth increment for fish in the 12–13-, 13–14-, and 14–15-mm size classes for each locality, and then we compared high- and low-predation localities. Males that matured during the experiment were excluded

Figure 2: Size distribution of guppies from high- and low-predation environments. The <12-mm and 12–14-mm size classes are immature fish. The 14–18-mm size class includes mature males and females giving birth for the first time. The >18-mm size category is exclusively adult females, most of which are giving birth to their second and subsequent litters.

from these analyses because growth virtually ceases at maturity. Each locality was, thus, represented by three dependent variables (i.e., size-class growth increments), each of which is dependent on the others because the subjects experienced a common environment. We analyzed these data with a repeated-measures, one-way ANOVA.

Guppies from the high-predation localities grew approximately 45% faster than those from low-predation localities (fig. 3), although the difference was not significant in the multivariate (repeated measures) comparison of high- versus low-predation sites ($F_{1,11} = 3.65$, $P = .0827$). This trend toward higher growth rate is consistent with the hypothesized higher resource availability in these localities. The analysis also revealed that there was a significant effect of initial size ($F_{2,10} = 6.09$, $P = .0186$), because larger fish tended to grow more slowly, but not a significant interaction between growth and stream type ($F_{2,10} = 1.63$, $P = .2448$).

A second way to evaluate growth is to use the growth increments from the mark-recapture study for all size classes of females to construct a growth trajectory and then to project the asymptotic body size. H. Rodd, J. Stamps, and D. Reznick (unpublished data) analyzed growth data from Reznick (1983) and found that the asymptotic size of laboratory populations on restricted rations is directly proportional to food availability. They also found that the second generation, laboratory-reared descendants of wild-caught fish from high- and low-predation localities that were reared in groups on ad lib rations, did not differ in asymptotic body size. The asymptotic size, therefore, represents a second means for comparing growth and food availability in natural populations. Growth increments decline with initial body size, which means that the larger individuals increase in length less rapidly than small individuals. We estimate asymptotic size from the x-intercept of a regression line through these size-specific growth increments (initial size on the x-axis, size-specific growth increment on the y-axis). The data were compared with a nonparametric statistic (Wilcoxon test) because they were not normally distributed. Data from the two 1989 Ceniza pools were combined for one estimate of asymptotic size because the sample sizes within each pool were too small for an accurate estimate of the y-intercept. The "initial
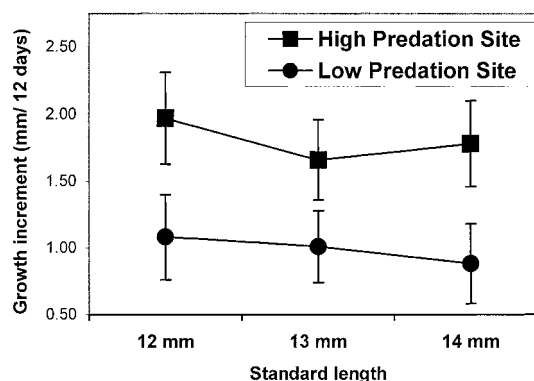

Figure 3: Growth increments (± 1 SE) of 12–14-mm guppies in the 14 mark-recapture pools. Guppies were classified by the millimeter size class that they were in at the beginning of the study. They were given a mark that was specific to that size class. The "growth increment" is the difference between their average size at the beginning of the time interval and the average size of those that were recaptured 12 d later. Standard errors are those associated with the least square means from the associated MANOVA.

length-growth increment" regression lines for the two Ceniza pools did not differ significantly in either slope or intercept, thus we could justify combining the two data sets.

Guppies from the high-predation localities had significantly larger asymptotic body sizes than guppies from low-predation localities (table 5). The reason that the high-predation guppies have larger asymptotic size classes is that the higher growth increments in the smaller size classes (fig. 3) tend to persist in the larger size classes.

Discussion

Guppies living in high- versus low-predation environments experience differences in more than just mortality rate. Specifically, sites associated with low predation had lower light levels and lower levels of primary productivity. Guppy populations at these sites were not more numerous per unit area, but they had more large, old fish and fewer small, young fish than populations in high-predation sites. These differences resulted in higher guppy biomass per unit area or volume at low-predation sites. Higher biomass

Table 4: The mean number of guppies (1 SE) per unit surface area or unit volume

	Number per unit area		Number per unit volume	
	>12 mm/m²	All size/m²	>12 mm/m³	All size/m³
High predation	4.3 (2.3)	8.3 (3.7)	20.5 (13.1)	45.5 (23.5)
Low predation	4.8 (2.1)	6.5 (3.7)	32.1 (12.1)	44.2 (23.5)

Note: Densities are evaluated either as the number >12 mm or as the total of all size classes, including individuals <12 mm.

Table 5: Comparison of the mean asymptotic body size (mm) for guppies from high- and low-predation localities

	N	Mean	Mean rank	Probability
High predation	6	30.9	9.8	.01
Low predation	7	21.9	4.6	…

Note: The two 1989 Ceniza (high predation) pools were lumped for this analysis because of the small sample sizes.

and lower primary productivity at low-predation sites was associated with lower growth rates, which suggests lower levels of food availability. Finally, there tended to be fewer smaller invertebrates in the low-predation sites, which is consistent with their lower productivity.

Indirect Effects of Predators

In the ecological literature, "indirect effect" refers to an effect of one species on another that is mediated through a third species (Wootton 1994). Our data were collected in part to evaluate the potential importance of such indirect effects in the interactions between guppies and their predators. One such effect is seen when a key predator includes a prey species as well as other predators of that prey species in its diet, as reported by Werner and McPeek (1994) in their evaluation of the bullfrog (*Rana catesbiana*), the greenfrog (*Rana clamitans*), the bluegill sunfish (*Lepomis macrochirus*), and invertebrate interaction. Sunfish prey on tadpoles, but they prey far more heavily on the invertebrates that eat tadpoles. Predatory invertebrates can be a thousand times more abundant when bluegills are absent. Similarly, Reimchen (1980) reports that salmonid fishes, which prey on sticklebacks, also prey heavily on odonate larvae, which, in turn, prey on sticklebacks. Lakes without salmonids have higher abundances of odonate larvae. In both studies, there is some indication that these indirect effects have had an evolutionary impact on the prey. Bullfrog tadpoles are far more active than greenfrog tadpoles and are more susceptible to predation by odonate larvae. They are also less palatable to fish. Sticklebacks from lakes without salmonids often have reduced spines and lateral plates relative to those from lakes with salmonids. Spines serve well as defense against predation by salmonids; however, spines might make sticklebacks more susceptible to predation by odonate larvae (Reimchen 1980).

Most of the piscivores that consume guppies also prey on other species of fish and macroinvertebrates. The killifish (*Rivulus hartii*), the dominant fish predator upstream at low-predation sites, consumes far more aquatic and terrestrial insects than guppies (Seghers 1973, 1978; Liley and Seghers 1975; Fraser and Gilliam 1992; Gilliam et al. 1993; Fraser et al. 1999). At high-predation sites, the pike cichlid (*Crenicichla alta*) and the various species of char-

acins that co-occur with it (Endler 1978) also include macroinvertebrates in their diet (D. Reznick, personal observation). Some of these macroinvertebrates, in turn, prey on guppies (D. Reznick, personal observation), so fish predators could potentially alter the interactions between guppies and macroinvertebrates in Trinidadian streams. However, we found no significant differences in the general composition of the invertebrate community between high- and low-predation sites; if anything, invertebrates tend to be more abundant in the high-predation sites, which is the opposite of the trend reported by both Werner and McPeek (1994) and Reimchen (1980). There is, therefore, no compelling reason to consider further an indirect effect mediated through an interaction among fish predators, macroinvertebrate predators, and guppies as an agent of selection. Instead, productivity and resource availability are more likely to be the causes of differences among high- and low-predation localities.

Another way in which predators can indirectly influence prey populations is through changes in resources (e.g., food), whose availability may increase or decrease depending on the circumstances. Per capita food resources can decline, for example, if prey are crowded into habitats that afford better protection, especially if those habitats are less productive. Power et al. (1985, 1989) found, in two different stream systems (Panama and Oklahoma), that predators cause prey to crowd into less productive habitat and, in the Oklahoma study, to feed less frequently. Skelly and Werner (1990) show that the presence of dragonfly larvae cause toad tadpoles to spend more time in refuges, to grow less rapidly, and to metamorphose at a smaller size relative to tadpoles that are not exposed to predators. Werner et al. (1983) found that, in the presence of bass, juvenile sunfish crowd in the weedy margins of ponds and sustain lower growth rates than when bass are absent. Fraser and Gilliam (1992) demonstrate that *Rivulus* move into stream margins or riffles in the presence of *Hoplias* and that their rates of growth and reproduction are reduced. Alternatively, predators may reduce the overall abundance of their prey and, hence, increase resource availability and the growth rate of the surviving prey. Such an effect has been demonstrated a number of times in experimental studies of aquatic communities (e.g., Werner et al. 1983; Wilbur 1987; Wilbur and Fauth 1990). Our data are consistent with this second scenario.

We found that guppies in high-predation localities are more abundant in stream margins, while those from low-predation localities are more abundant in the center of streams (table 3), which is consistent with a shift in habitat utilization in response to the threat of predation. However, we also found that guppies in high-predation sites tend to grow more rapidly and to attain higher asymptotic body sizes than their counterparts from low-predation localities

(fig. 3; table 5), so there is no evidence for a net reduction in resource availability when predators are present. In fact, just the opposite is true: guppies grow faster when constrained to stream margins by large predatory fish. There are two reasons for this: lower guppy biomass and greater periphyton productivity at high-predation sites.

A different form of indirect effect of predation might be an increase in resource availability to guppies that is mediated through the effects of larger predators on *Rivulus*, which are far less abundant in high-predation localities because they tend to be excluded by larger predators (Fraser et al. 1995). *Rivulus* and guppies potentially compete for resources (Gilliam et al. 1993), so this exclusion of *Rivulus* might further enhance the availability of resources to guppies in high-predation localities.

Guppies are also smaller in high-predation localities (fig. 2). This translates into an average of only one-fourth of the biomass/unit area at high- versus low-predation sites. The difference in size distribution repeats results reported by Rodd and Reznick (1997) that were based on collections made during different years and that only partially overlapped in the localities that were represented in this study. Rodd and Reznick (1997) argue that the differences in size distribution are a combined function of the higher mortality rates in high-predation sites and the evolved differences in life histories because guppies from high-predation sites mature at an earlier age and smaller size and also produce more offspring. The difference in biomass density should result in less competition for food.

The conclusion that guppies from high-predation communities grow faster is based on two indices of growth. First, juvenile guppies tended to grow faster during our 2-wk, mark-recapture experiments (fig. 3). Second, female guppies from high-predation localities had significantly higher asymptotic body sizes than guppies from low-predation localities. Because asymptotic body size of females is positively correlated with food availability and does not differ when fish from different localities are reared in a common environment (H. Rodd, J. Stamps, and D. Reznick, unpublished manuscript), these results are also consistent with higher food availability in high-predation environments.

Environmental Correlates of Predation

We also considered whether there were environmental correlates of stream type that were independent of predators but that could influence the evolution of guppy life histories. We found that high-predation localities tend to occur in larger streams with higher light levels and higher periphyton productivity, a general result found in other stream systems (Vannote et al. 1980; Hawkins et al. 1982; Power 1984; Lowe et al. 1986; Feminella et al. 1989; Steinman 1992). However,

our study sites were deliberately chosen to minimize such ecological differences among stream types. A random selection of high- and low-predation localities would likely reveal larger differences in these stream characteristics because high-predation localities are much larger, on average, than low-predation localities. Our one estimate of primary productivity in a larger high-predation stream (the Oropuche River) yielded an estimate of gross primary productivity (midstream = 534 mg C/m^2/d, stream edge = 382 mg C/m^2/d) that was greater than the mean of our high-predation localities and among the highest that we measured. More evidence for the effect of food availability on guppy growth independent of predation appears in a companion article (Grether et al., in press). In that study, three pairs of low-predation localities were compared in three different drainages that differed systematically in stream order and stream size. Grether et al. found that larger streams had higher light levels, higher productivity, and higher guppy growth rates—all in the absence of large fish predators.

We, thus, have consistent differences in resources between high- and low-predation environments that have two potential causes. First, there is a potential effect of predation mediated through the predator-induced shift in the size/age structure of guppies and, hence, reduced biomass of guppies per unit area. Second, there are environmental differences that are correlated with predators that result in a higher level of primary productivity. Both factors will contribute to higher levels of resource availability in high-predation localities. Such systematic differences in resource availability can select for evolutionary changes in the life history.

Resource Availability and Life-History Evolution

The potential impact of resource availability on life-history evolution has been considered in a variety of ways, but the predicted responses vary with the structure and assumptions of individual models. One way of considering the potential impact of resource limitation is to consider the difference between the predictions of models that either do or do not include density regulation since a decline in food availability with increasing density is one likely cause of density regulation. Charlesworth (1980) shows that an increase in mortality rate caused by some extrinsic factor, such as a predator, that is equal across all age classes results in no life-history evolution if the population size is growing exponentially. If density regulation is added in the form of a selective increase in juvenile mortality, then the same uniform increase in mortality rate selects for earlier maturity. More generally, the way life histories evolve in response to mortality selection changes when density regulation is included in the model. Furthermore, the way the life history evolves can be more a function of

how density regulation is manifested (e.g., reduced fecundity, increased mortality, delayed maturity) than of mortality selection (Kozlowski and Wiegert 1994; Mylius and Diekmann 1995; Benton and Grant 1999). Abrams and Rowe (1996) explicitly include an increase in resource availability as a possible indirect effect of predation in a theoretical consideration of the effects of a similar change in mortality rate. Their most general prediction was that such an indirect effect would cause the evolution of an increase in the size at maturity, although this prediction varies with the conditions of the model. A common feature of all of these models is that resource availability or surrogates like density dependence can be important agents of selection and potentially alter how a life history will evolve in response to demographic selection.

Two empirical studies that demonstrate the potential evolutionary consequences of food availability and population density are the *Drosophila* selection experiments of Mueller and his colleagues (e.g., Mueller and Ayala 1981; Mueller 1986, 1988*a*, 1988*b*; Mueller et al. 1991) and the comparative studies of natural populations of pitcher plant mosquitoes by Bradshaw and Holzapfel (1989). Both empirical programs demonstrate that high densities and low levels of resource availability associated with high density can select for significant differences among populations. Neither set of authors considered the same sort of life-history attributes that we do for guppies (e.g., age at maturity, fecundity, egg size). Instead, both consider population growth rate, which is a composite of these attributes. Mueller and Ayala (1981) and Mueller et al. (1991) compared populations selected under either high- or low-population densities. They found that the low-density selection lines had higher population growth rates at low densities, whereas the high-selection lines had higher population growth rates under high densities. In contrast, when Bradshaw and Holzapfel (1989) compared pitcher plant mosquitoes from populations that regularly experience differences in density and resource availability, they found no relationship between density, population growth rate, and population of origin. Both sets of authors found that individuals from high-density populations have higher competitive abilities than those from low-density populations (Mueller 1988*b*; Bradshaw 1989). Bradshaw and Holzapfel (1989) raise the interesting possibility that adaptation to such conditions may involve attributes other than life-history traits and, hence, may not be detectable with standard evaluations of the life history.

The implication of these theoretical and empirical studies is that systematic differences among populations in resource availability can contribute to the evolution of differences in life histories; however, how the life history will evolve is not so easily predicted. One reason for this uncertainty is that there are different ways in which resource availability can influence the life history. For example, when it acts as a

component of density regulation, then it is necessary to characterize how such regulation is manifested since the mechanism of regulation influences the nature of the response to selection. A second reason is that organisms appear to have diverse ways of adapting to differences in resources or population density, and these adaptations may not be manifested in terms of life-history traits.

Another Problem with Too Many Solutions?

Our general goal is to use comparative ecology as a way of defining the selective environment. This comparative ecological approach suggests two refinements to the conclusion that predators select for the evolution of life-history patterns through demographic selection. First, it suggests an indirect effect of predators because high-predation causes lower densities, which can, in turn, result in higher per capita food availability. Second, there are environmental factors correlated with predation that enhance this difference in food availability. Both factors suggest that the effects of demographic selection might be modified by resource availability. As in *Cepea* snails, resource availability and indirect effects of predation represent new solutions to the same problem. The structure of guppy life histories by themselves do not enable us to distinguish between mortality and food availability as alternative causes. Furthermore, it would be a mistake to treat these as independent alternatives. First, the same life history can evolve for different reasons. Second, distinguishing among alternative explanations is unrealistic if those alternatives are not independent. In our system, differences in resource availability may, in part, be caused by predation. Evolved differences among populations in life histories may be a combined response to differences in predation and resource availability.

Since there are clear differences among localities in resource availability, we feel that it must be considered as a potential agent of selection for life-history evolution. We will evaluate the plausibility of each potential agent of selection on its own as well as the interactions among these mechanisms in molding the evolution of guppy life histories. Our study system affords the opportunity to evaluate the independent contribution of resource availability to life-history evolution since there are streams of various dimensions that either do or do not contain predators. The environmental component of variation can, thus, be separated from predation, as it was done by Grether et al. (in press). We will build on their comparisons with field demography and laboratory genetics studies to define how such environmental factors can select for life-history evolution independently of predation.

Acknowledgments

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